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FRONTIER DIAGRAMS: PARTITION OF PHASE SPACE ACCORDING TO THE SIGNS OF EIGENVALUES OR SIGN PATTERNS OF THE CIRCUITS

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Nonlinear dynamic systems can be considered in terms of feedback circuits (for short, circuits), which are circular interactions between variables. Each circuit can be identified without ambiguity from the Jacobian matrix of the system. Of special relevance are those circuits (or unions of disjoint circuits) that involve all the variables of the system. We call them **"nuclei"** because, in the same way as, in Biology, the cell nucleus contains essential genetic information, in nonlinear dynamics, nuclei are crucial elements in the genesis of steady states. Indeed, each nucleus taken alone can generate one or more steady states, whose nature is determined by the sign patterns of the nucleus. There can be up to two nuclei in 2D systems, six in 3D systems,... n! in nD systems. However, many interesting systems of high dimensionality have only two, sometimes even one, nucleus.

This paper is based on an extensive exploitation of the Jacobian matrix of systems, in order to figure the global structure of phase space. In nonlinear systems, the value, and often the sign, of terms of the Jacobian matrix depend on the location in phase space. In contrast with a current usage, we consider this matrix, as well as its eigenvalues and eigenvectors, not only in close vicinity of steady states of the system, but also everywhere in phase space. Two distinct, but complementary approaches are used here.

In Sec. 2, we define frontiers that partition phase space according to the signs of the eigenvalues (or of their real part if they are complex), and where required, to the slopes of the eigenvectors. From then on, the exact nature of any steady state that might be present in a domain can be identified on the sole basis of its location in that domain and, in addition, one has at least an idea of the possible number of steady states.

In Sec. 3, we use a more qualitative approach based on the theory of circuits. Here, phase space is partitioned according to the sign patterns of elements of the Jacobian matrix, more specifically, of the nuclei. We feel that this approach is more generic than that described in Sec. 2. Indeed, it provides a global view of the structure of phase space, and thus permits to infer much of the dynamics of the system by a simple analysis of sign patterns within the Jacobian matrix. This approach also turned out to be extremely useful for synthesizing systems with preconceived properties.

For a wide variety of systems, once the partition process has been achieved, each domain comprises at most one steady state. We found, however, a family of systems in which two steady states (typically, two stable or two unstable nodes) differ by neither of the criteria we use, and are thus not separated by our partition processes. This counter-example implies non-polynomial functions.

It is essential to realize that the frontier diagrams permit a reduction of the dimensionality of the analysis, because only those variables that are involved in nonlinearities are relevant for the partition process. Whatever the number of variables of a system, its frontier diagram can be drawn in two dimensions whenever no more than two variables are involved in nonlinearities.

Pre-existing conjectures concerning the necessary conditions for multistationarity are discussed in terms of the partition processes.

Keywords: Phase space partition; feedback circuits; nuclei; Jacobian matrix.

1. Introduction

This work can be characterized by an extensive use of the Jacobian matrix of dynamical systems. Admittedly, in nonlinear systems it is only in close vicinity of steady states that the eigenvalues and eigenvectors of the Jacobian matrix have a simple physical meaning. Yet, the Jacobian matrix is after all the matrix of the partial derivatives of the system, which describes how the elements of the system interact. Provided one deals with regular and differentiable functions, the matrix itself, as well as its eigenvalues and eigenvectors, are defined everywhere in phase space, and not only at the level of steady states.[1]

This granted, we first define, as described in Sec. 2, a basic frontier F1 that partitions phase space according to the **parity** of the number of positive eigenvalues. In two-variable systems, this classifies steady states into saddle points on one side of the frontier, nodes and foci on the other side.

A second step, realized by frontier F2, permits to separate regions according to the sign of the real part of complex eigenvalues. Consider, for example, in a three-variable system, a region that has a real positive eigenvalue and a pair of complex eigenvalues whose real part is negative (in our formulation, $+/--$), and another region in which the real part of the complex eigenvalues is positive ($+/++$). These two regions will be separated by an F2 frontier.

In particular cases, one can have two adjacent regions that differ by the signs of two **real** eigenvalues. In such cases, they are separated by a double F1 frontier. After the second step of the partition process, phase space is partitioned into regions that are homogeneous as regards the **signs** of the eigenvalues or their real part, and not only the **parity** of these signs. In order to characterize completely the nature of the steady states, one has to use an additional boundary, "F4", which separates regions according to the presence or absence of complex eigenvalues. We draw this boundary when present. However, as one never finds two neighboring steady states that differ only by the real versus complex character of a pair of eigenvalues we do not consider the F4 boundary as a frontier.

At that stage, one still frequently finds two or more steady states in a given region. Their eigenvalues have not only the same signs (as expected from the mode of partition), but, in symmetrical systems, possibly the same values. In most cases, one deals with saddle points whose separatrices are oriented in contrasting ways, or with foci that turn in opposite directions. These differences can be ascribed to the signs of the slopes of the eigenvectors. This lead us to consider a third type of frontier (F3), and a

[1]Some feel that it is illegitimate to evaluate the eigenvalues and eigenvectors anywhere in phase space. In fact, each Jacobian matrix represents not only the very system of ODE's from which it has been derived, but also an infinite set of related systems that differ from each other and from the initial system by the values $\{k, l, \ldots\}$ of terms of degree zero. The Jacobian matrix built from a system

$$\dot{x} = f_x(x, y, \ldots)$$
$$\dot{y} = f_y(x, y, \ldots),$$

etc. thus describes not only this particular system but also the more general system

$$\dot{x} = f_x(x, y, \ldots) - k$$
$$\dot{y} = f_y(x, y, \ldots) - l,$$

etc. ($k, l, \ldots$ real).

Provided one deals with functions that are regular and differentiable everywhere, for any value of $\{x, y, \ldots\}$, and thus for every point of phase space, one can find a value of vector $\{k, l, \ldots\}$, such that point $\{x, y, \ldots\}$ is a steady state of the system. Thus, each point of phase space is a potential steady state of the general system described by the Jacobian matrix, and the eigenvalues and eigenvectors of the matrix can be legitimately evaluated at this point.

third step of partition, based on the slopes of the eigenvectors.

In Sec. 3, we reformulate the above in terms of the theory of circuits, and partition phase space according to the sign patterns of the nuclei. The partition of phase space described in Sec. 2 is quantitative but largely descriptive. In contrast, the approach developed in Sec. 3 permits to infer essential features of systems by a simple examination of their Jacobian matrix, and also to operate "in reverse" by synthesizing *ad hoc* systems. We feel that the qualitative analysis of Sec. 3 is more generic than that developed in Sec. 2, even though the two approaches are in fact complementary.

Once either of the partition processes has been achieved, it was found (see Sec. 2.4) for a wide variety of systems that a domain contains at most one steady state. However, a family of systems characterized by sigmoid (non-polynomial) interactions displays a pair of steady states (two stable or two unstable nodes) that are not separated by any of our frontiers (see Sec. 2.4).

This paper also deals with the conditions of multistationarity and with the number of steady states in nonlinear dynamic systems. The total number of solutions of the steady state equations, complex solutions included, depends on the degrees in the ODE's. However, steady states are the **real** solutions of the steady state equations. Whether there is more than one real solution, thus more than one steady state (**multistationarity**), is subject to necessary conditions concerning the signs of the elements of the Jacobian matrix. The basic principle is that the presence of a positive circuit in the Jacobian matrix (or more generally in the graph of interactions) of a system is a necessary condition for multistationarity (conjecture: [Thomas, 1981], formal proofs: [Plahte *et al.*, 1995; Snoussi, 1998; Gouzé, 1998; Cinquin & Demongeot, 2002; Soulé, 2003]).

In principle, the frontiers that define the domains are lines in two-variable systems, surfaces in three variables, etc. However, the representation of the partition need not involve all the variables of the system: only those variables that take part in nonlinear terms in the differential equations have to be represented in the diagrams. Thus, the partition of phase space in an n-variable system can be represented in two dimensions whenever not more than two of the variables are involved in nonlinear terms in the ODE's.

2. Partitions of Phase Space According to the Signs of Eigenvalues or Slopes of Eigenvectors

2.1. *A primary frontier (F1 = "green" frontier) partitions phase space according to the parity of the number of positive eigenvalues*

Phase space can be first split according to the **parity** of the number of positive[2] eigenvalues. In two variables, this amounts to ask where the two eigenvalues have the same sign and where they have opposite signs. In the first case, any steady state that might be present in the domain would be a node or a focus, in the second case, a saddle point. In three variables, one asks where the eigenvalues are ($+++$ or $+--$) and where they are ($++-$ or $---$), etc.... When one passes the frontier between two such regions of phase space, **one** eigenvalue changes its sign, and on the frontier itself **this** eigenvalue is nil.

The characteristic equation can be written:

$$\lambda^n + a_{n-1}\lambda^{n-1} + \cdots + a_2\,\lambda^2 + a_1\lambda + a_0 = 0,$$

or, as well:

$$\lambda^n - S\lambda^{n-1} + \cdots + (-1)^n P = 0,$$

in which S is the sum and P the product of the roots of the characteristic equation, and thus of the eigenvalues of the Jacobian matrix. It is well known that a_0, the term of degree zero of the characteristic equation, equals plus or minus the determinant of the Jacobian matrix depending on the parity of the number of variables. More formally, $a_0 = (-1)^n$ det, in which n is the number of variables and det, the determinant of the Jacobian matrix. As on the other hand $a_0 = (-1)^n P$, the equation of frontier F1 is simply

$$\mathbf{a_0 = 0}$$

To be more concrete, let us consider system (I):

$$\dot{x} = x - x^3 + a_{12}y$$
$$\dot{y} = a_{21}x + y - y^3$$

[2]Note that the parities of the number of positive and number of negative eigenvalues are the same if the number of variables is even, but opposite for an odd number of variables.

the Jacobian matrix of which is $\begin{pmatrix} 1-3x^2 & a_{12} \\ a_{21} & 1-3y^2 \end{pmatrix}$. This system was chosen because it displays many steady states in spite of its simple structure. The steady state equations are both of degree 3, and the total number of solutions (complex solutions included) is $3^2 = 9$.

The characteristic equation is:

$$\lambda^2 + (3x^2 + 3y^2 - 2)\lambda + (1-3x^2)(1-3y^2) - a_{12}a_{21} = 0$$

and thus the equation of the primary frontier is:

$$(1-3x^2)(1-3y^2) - a_{12}a_{21} = 0$$

Figure 1 provides diagrams of this primary partition of phase space, as well as the location of the steady states and the signs of the eigenvalues (or their real part if they are complex: Sec. 2.5) in the various regions, in three cases:

(a) the two-circuit (nondiagonal terms) is negative ($a_{12} = -0.3$, $a_{21} = +0.3$),
(b) the two-circuit is absent (a_{12} **or** (inclusive) $a_{21} = 0$),
(c) the two-circuit is positive ($a_{12} = +0.3$, $a_{21} = +0.3$). Similar results, would be obtained with $a_{12} = -0.3$ and $a_{21} = -0.3$.

In all three cases, for the parameter values used, there are nine steady states, in other words, all the solutions of the steady state equations are real.

By construction, this first frontier partitions phase space according to the parity of the number of positive eigenvalues, namely, for a two-variable system, according to whether these eigenvalues have different signs (+−, saddle point) or whether they (or their real part) have the same sign (++ or −−). Here, there are four saddle points and five nodes or foci.

For increasing values of a_{12} or a_{21} (i.e. a stronger two-nucleus to compete with the variable (1 + 1)-nucleus) the frontiers progressively depart from the situation of Fig. 1(b) (no two-nucleus) according to the signs of the competing parameters. More precisely, if the competing nucleus generates by itself a saddle point, the domain of phase space imparted to potential saddle points will be enlarged as in Fig. 1(c), and vice versa. In any case, the general pattern of the frontier is remarkably robust. As for the steady states, for increasing values of parameters a_{12} or a_{21}, they converge two by two, collide as they reach the F1 frontier and disappear, replaced (not surprisingly) by a pair of complex solutions of the steady state equations. The remaining steady state shows features as expected for the system in which the competing nucleus is alone. In case (a), it remains an unstable focus, surrounded by a limit cycle for sufficient values of the nondiagonal parameters.

The location and number of steady states may also vary by changing the value of a term of degree zero in one of the ODE's. This situation is interesting, because the value of a term of degree zero of course modifies the location and possibly the number of steady states, but it has no effect on the Jacobian matrix, and hence no effect on the frontiers.

The logic behind all these patterns will appear in a simpler way when we will revisit this system in terms of the sign patterns in the Jacobian matrix (Sec. 3).

The aim of Fig. 2 is to show frontier F1 together with the nullclines of the system [Fig. 2(a)], and with the separatrices that limit the basins of attraction of the stable steady states [Fig. 2(b)]. It can

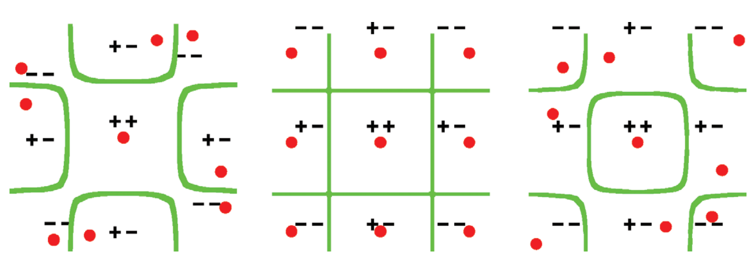


Fig. 1. These diagrams show how the "green" frontier F1 (whose equation is $a_0 = 0$) partitions phase space into domains homogeneous as regards the parity of the signs of the eigenvalues (or their real part). On one side of the frontier, the number of positive eigenvalues is odd, on the other side, even. The systems considered in (a)–(c), are three variants (the two-circuit negative, absent and positive, respectively) of system (I). The steady states are seen as red points and the F1 frontier as a green line. The symbols ++, +− or −− indicate the signs of the eigenvalues or their real part in the region considered. The real versus complex character of the eigenvalues depends on another boundary: see Fig. 3(b).

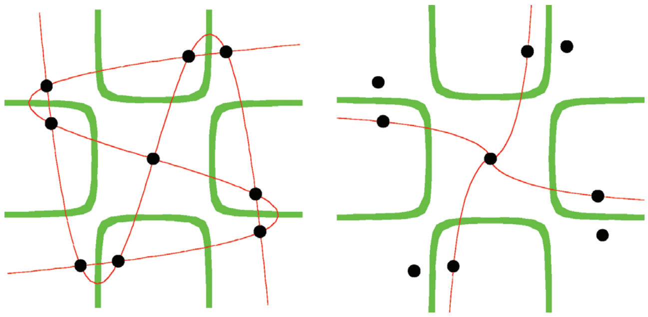


Fig. 2. System (I): $\begin{aligned}\dot{x} &= x - x^3 + a_{12}y \\ \dot{y} &= a_{21}x + y - y^3\end{aligned}$ with $a_{12} = -0.3$ and $a_{21} = +0.3$. (a) Frontier F1 (green) together with the nullclines ($\dot{x} = 0$, $\dot{y} = 0$), whose intersections are the steady states. (b) The same frontier F1 (green), together with the lines (separatrices) that separate the basins of attraction of the four stable nodes. This is to draw the attention on the fact that our frontier F1 has nothing in common with either the nullclines or the separatrices.

be seen that the frontier F1 has nothing in common with either the nullclines or the separatrices. In particular, the steady states of the saddle point type are located **on** the separatrices, but usually **far away** from our frontier.

In some systems, function a_0 is everywhere positive or everywhere negative. In such cases, there is no F1 frontier and the parity of the number of positive eigenvalues is the same everywhere in phase space.

2.2. *A secondary, "blue" frontier (F2) may achieve the partition of phase space according to the signs of eigenvalues*

Frontier F1 has operated a first, major partition that has split phase space into domains according to the **parity** of the number of positive eigenvalues. As expected and illustrated by Fig. 1(a), after this primary partition a region may remain composite as regards the **signs** of the eigenvalues. In the present case, there are four domains in which the eigenvalues have opposite signs (any steady state in these domains would thus be a saddle point), and a composite region in which the eigenvalues (or their real part) are either both positive or both negative. In order to pursue the partition down to the level of the signs of the eigenvalues, one needs a second type of frontier along which two eigenvalues, rather than only one, change sign.

This is realized by the "blue" frontier F2. The equation of this frontier can be obtained by a generalization of the "astuce de Gaspard–Nicolis" [1987]. The idea is that a simultaneous switch of the signs of two eigenvalues takes place where the real part of a pair of conjugated complex eigenvalues crosses the value zero. In order to find the equation of this frontier, one inserts thus the value $i\,\omega$ into the characteristic equation, writes that the sum of real terms and the sum of imaginary terms are both zero and proceeds to appropriate substitutions (for more detail, see Appendix). Note the connection between both the F1 frontier and the Gaspard–Nicolis approach, as we use them, and the Routh–Hurwitz criterion. The main difference is that we are interested in all possible sign patterns of the eigenvalues everywhere in phase space, rather than only in whether a particular steady state can be stable.

If $\mathbf{a_i}$ is the coefficient of the term of degree $\mathbf{i}$ in the characteristic equation, the equation of F2 is simply, in two variables:

$$\mathbf{a_1 = 0}, \quad \text{with the constraint } \mathbf{a_0 > 0},$$

in three variables:

$$\mathbf{a_1 a_2 - a_0 = 0}, \quad \text{with the constraint } \mathbf{a_1 > 0},$$

in four variables:

$$\left(\frac{\mathbf{a_1}}{\mathbf{a_3}}\right)^{\mathbf{2}} - \mathbf{a_2}\left(\frac{\mathbf{a_1}}{\mathbf{a_3}}\right) + \mathbf{a_0} = \mathbf{0},$$

$$\text{with the constraint } \frac{\mathbf{a_1}}{\mathbf{a_3}} > \mathbf{0}$$

In system (I, a), the equation of the secondary frontier is $3x^2 + 3y^2 - 2 = 0$, a circle whose relevant part is that for which $a_0 > 0$. Figure 3 shows the partition of phase space by the primary and secondary frontiers, as well as the steady states. It is

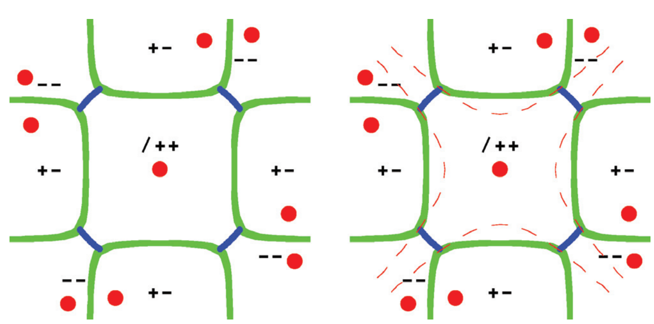


Fig. 3. System (I), with $a_{12} = -0.3$ and $a_{21} = +0.3$. (a) Not only the "green" frontier F1 but also the "blue" frontier F2 is shown. Phase space is now partitioned according to the signs of the eigenvalues (and not only according to their parity as was the case in Fig. 1). (b) The boundary F4 has been drawn in addition: inside, the eigenvalues are complex, outside, they are real.

seen that phase space is now partitioned into nine domains, homogeneous for the signs of the eigenvalues (and not only for their parity). For the parameter values used here, each of the nine domains contains a steady state.

It should be mentioned that, by construction, an F2 frontier is necessarily embedded into a region of phase space that comprises complex eigenvalues.

2.3. *F3 ("black") frontiers: A partition taking into account the signs of the slopes of the eigenvectors*

We express the eigenvectors as their **slope**, i.e. in 2D systems, by the ratio of their y to x components. The eigenvalues $\lambda_1, \lambda_2, \ldots$ generate, respectively, eigenvectors $v1, v2, \ldots$ whose slopes $K1, K2, \ldots$ are given, in 2D, by

$$K = \frac{\lambda - a_{11}}{a_{12}}, \tag{1}$$

or equivalently by

$$K = \frac{a_{21}}{\lambda - a_{22}}. \tag{2}$$

Eliminating the eigenvalues provides a relation (known as the distribution relation) between the slopes of the eigenvectors and the terms of the Jacobian matrix:

$$a_{12}K^2 + (a_{11} - a_{22})K - a_{21} = 0 \tag{3}$$

2.3.1. *Frontier F3**

From relation (3), it is immediately seen that for

$$a_{11} - a_{22} = 0, \quad K_{\pm} = \pm\sqrt{\frac{a_{21}}{a_{12}}}.$$

"$a_{11} - a_{22} = 0$" may simply come from the fact that the two diagonal terms are equal everywhere. But more generally, a_{11} and a_{22} are functions of x and y, and in this case $a_{11} - a_{22} = 0$ (if it exists) is usually a line. This line defines a frontier **F3*** along which the slopes of the two eigenvectors are opposite. Besides, in this case the slopes of the eigenvectors are either real or purely imaginary.

2.3.2. *Frontier F3***

From (2), it is seen that upon crossing a line $a_{21} = 0$ one of the slopes is nil, and from (1), upon crossing a line $a_{12} = 0$ the slope of the other eigenvector undergoes a vertical asymptote. This defines a pair of frontiers F3** at the level of which the slope of one of the eigenvectors changes sign through a vertical asymptote, and the other vanishes, usually with a change of sign. It is essential to realize that along the lines $a_{12} = 0$ or $a_{21} = 0$, the two-nucleus vanishes and the eigenvalues are thus equal to the diagonal terms. This point will be considered in more detail in Sec. 3.3 in order to emphasize the relation between frontiers and nuclei.

2.3.3. *Examples of F3* and F3** frontiers*

Coming back to our model system, Fig. 1(c) (system I with the two-circuit positive) shows five domains containing each a steady state (four stable and one unstable nodes), and a sixth region that contains four steady states. These four steady states are extremely similar. Not only are they all four saddles, but also in the present case they have identical eigenvalues. However, two adjacent saddle points differ from each other qualitatively as regards the orientations of their separatrices. As will be discussed below (Sec. 3.3), the different orientations of the separatrices of the different saddle points can be anticipated from the simple fact that they can originate from different sign patterns:

$$\begin{pmatrix} + & \\ & - \end{pmatrix}, \begin{pmatrix} - & \\ & + \end{pmatrix}, \begin{pmatrix} & + \\ + & \end{pmatrix} \text{ or } \begin{pmatrix} & - \\ - & \end{pmatrix}.$$

For example, a saddle point is repulsive in x and attractive in y, or attractive in x and repulsive in y depending on whether it has been generated by a nucleus of the first or second type. This is evidenced by contrasting slopes of the eigenvectors and leads us to consider an F3* frontier $a_{11} - a_{22} = 0$, along which the slopes of the eigenvectors are opposite. In Fig. 4, this "black" frontier has been drawn only in the composite domain, which it partitions in such a way that the four saddle points are now in distinct domains. Note that in this system, there is no F3** frontier, since a_{12} and a_{21} are constant.

In contrast, in system (II):

$$\dot{x} = a_{11}x + y - y^3$$
$$\dot{y} = x - x^3 + a_{22}y$$

as the diagonal terms of the Jacobian matrix are constant, it is frontier F3* that is absent, but frontiers F3** ($a_{12} = 0$ and $a_{21} = 0$) are present. They correspond to $1 - 3y^2 = 0$ and $1 - 3x^2 = 0$, respectively, and in this case frontier F3** thus

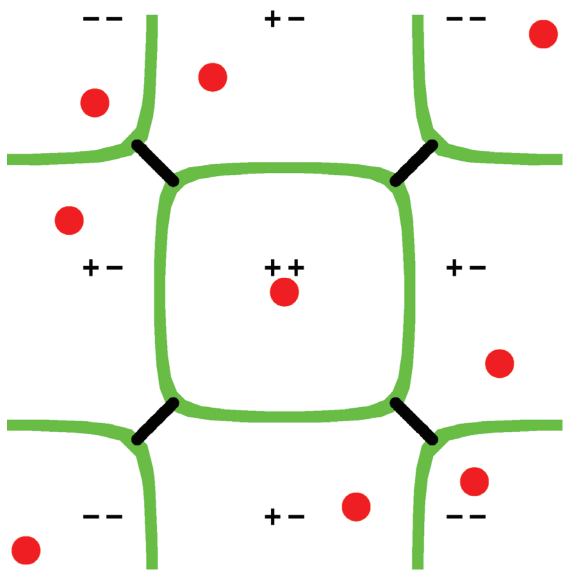


Fig. 4. System (I), with a_{12} and $a_{21} = +0.3$ (the two-circuit positive). Here there is no "blue" (F2) frontier. The partition of phase space is completed by the "black" (F3) frontier. In the domains separated by this frontier, the signs of the eigenvalues are the same, but the slopes of the eigenvectors are different.

As the two-circuit is positive, the discriminant is positive everywhere and the eigenvalues are real everywhere; there is no F4 boundary.

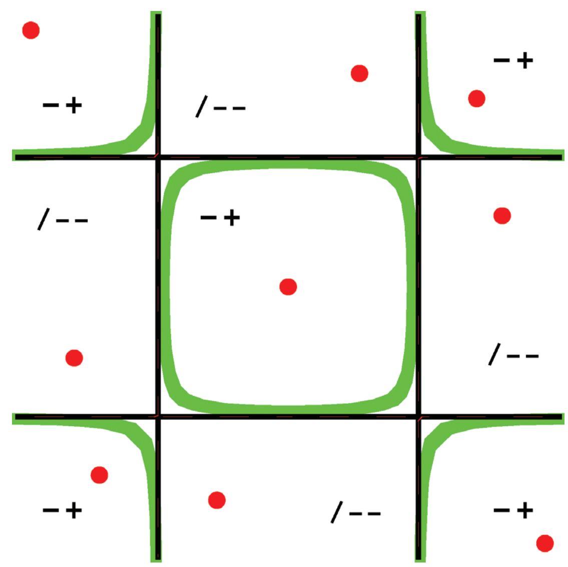


Fig. 5. System (II), with a_{11} and $a_{22} = -0.3$. Here, there is again no F2 frontier. The black (F3) frontier is given by $a_{12} = 0$ and $a_{21} = 0$. In the present case, it consists of straight lines $x = \pm 1/\sqrt{3}$ and $y = \pm 1/\sqrt{3}$. Frontier F4 (real versus complex eigenvalues) coincides with F3. Within the crescents at the angles of the square, the eigenvalues are real negative $(--)$. This is not shown in the figure for reasons of steric hindrance.

consists of four straight lines parallel two by two (Fig. 5).

In this system, when the diagonal terms have the same sign,[3] the F1 frontier partitions phase space into five domains each comprising a saddle point, and a composite region comprising four foci. These foci are qualitatively different since the trajectories run clockwise around two of them, counter clockwise around the two others. This is reflected at the level of the eigenvectors even though the eigenvalues may be the same. In a simple case, a center runs counter clockwise if the eigenvectors associated with the eigenvalues $\lambda_1 = i$ and $\lambda_2 = -i$ are $\begin{bmatrix} 1 \\ +i \end{bmatrix}$ and $\begin{bmatrix} 1 \\ -i \end{bmatrix}$, (and the slopes of the imaginary part of the eigenvectors, i and $-i$) respectively; it runs clockwise if they are $\begin{bmatrix} 1 \\ -i \end{bmatrix}$ and $\begin{bmatrix} 1 \\ +i \end{bmatrix}$, (and the slopes, $-i$ and i), respectively. Note that whether a focus turns clockwise or counter clockwise can be anticipated from whether it is generated by a sign pattern $\begin{pmatrix} & + \\ - & \end{pmatrix}$ or $\begin{pmatrix} & - \\ + & \end{pmatrix}$.

In practice, F3 frontiers have been worked out only where they were required to separate similar steady states. So far, they have been mostly applied to 2D systems.

2.4. *At most one steady state per domain?*

To summarize Secs. 2.1–2.3, frontiers F1, F2 and F3 (if any) partition phase space into domains homogeneous as regards the signs of the eigenvalues and of the slopes of the eigenvectors. For a wide class of systems, it was found that the domains delimited in this way contain at most one steady state, as if two neighboring steady states had to differ by the signs of the eigenvalues or else by the signs of the slopes of the eigenvectors.

However, we found a class of systems in which two similar steady states (two stable, or two unstable nodes) bracket a steady state of another nature (a saddle point), but are not separated from each

[3] If the diagonal terms have opposite signs, the overall distribution of saddle points and foci remains the same, except that now one deals with four domains containing each a focus and a composite domain containing five saddle points.

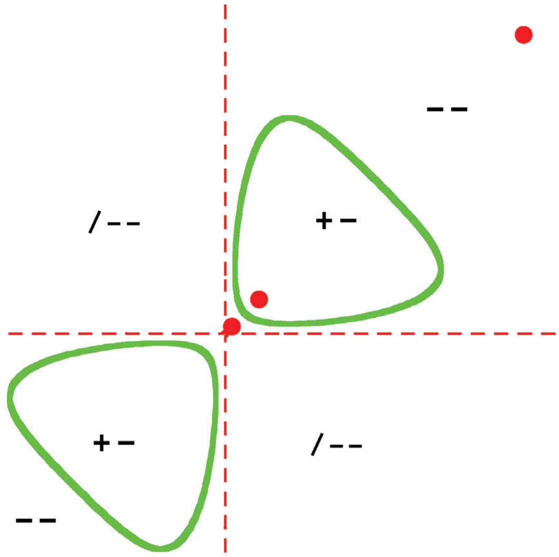


Fig. 6. The system: $\begin{cases} \dot{x} = 0.05 + \frac{3y^2}{(1+y^2)} - x \\ \dot{y} = 0.05 + \frac{3x^2}{(1+x^2)} - y \end{cases}$, whose nonlinearities are Hill functions (widely used in biological models), has three steady states, namely a saddle point flanked by two stable nodes. It is seen that the two nodes are not separated by the F1 frontier. There is no F2 and no F3* frontiers and the F3** frontiers coincide with the axes and also fail to partition the nodes. An F4 boundary separates the regions of complex and real eigenvalues.

other by any of our types of frontiers. The simplest example is a two-element positive circuit with sigmoid nonlinearities and linear negative diagonal terms. The sigmoids used are Hill functions (but hyperbolic tangents behave similarly). System:

$$\dot{x} = -x + \frac{3y^2}{(1+y^2)}$$

$$\dot{y} = \frac{3x^2}{(1+x^2)} - y$$

has three steady states, namely two stable nodes and a saddle point. An F1 frontier surrounds the saddle point but does not extend in such a way as to separate the two nodes. There is neither an F2 nor an F3* frontier since the diagonal terms of the Jacobian matrix are constant. There is a pair of F3** frontiers, but they fail to separate the nodes. Of course, the two nodes are dealt by the attractive separatrix, which crosses the saddle point and partitions phase space into its two basins of attraction. However, we hesitate to treat this line as an additional frontier, if only because, in contrast with our frontiers, it has generally no analytical expression. Figure 6 shows the steady states, frontier F1 and the F4 boundary.

This counter-example should not be overlooked, as many regulatory interactions in biology have a sigmoid shape, and sigmoid functions are thus extensively used in biological modeling. On the other hand, as pointed out by Soulé, it does not imply polynomial functions. All the polynomial systems tested so far obey the "rule".

2.5. *Partition according to the real versus complex character of steady states*

A fourth boundary partitions phase space according to the occurrence or not of complex eigenvalues. As is well known, in two or three variables the equation of this boundary writes $d = 0$, in which d is the discriminant of the characteristic equation. Within a domain defined by frontiers F1, F2 or F3, one never finds two steady states that differ only by the real versus complex character of a pair of eigenvalues; in fact, boundary F4 does not play any role in the determination of the **number** of steady states. This is why we call it "boundary" rather than "frontier".

We nevertheless included it (as red dotted curves) where relevant in our graphics [e.g. Fig. 3(b)], because as long as one does not take this aspect into account, the nature of steady states is not entirely determined.

2.6. *Systems without F1 but with F2 or F3 frontiers*

The "Jacobian real conjecture", states that (at least for polynomial systems) if the determinant of the Jacobian matrix has no zero value the system cannot have more than one steady state. In view of this conjecture, we initially believed that the presence of an F1 frontier (in two dimensions, a line of equation $a_0 = 0$) was a necessary condition for multistationarity. Here, follow two counter-examples. These two simple systems have no F1 frontier, yet they have two steady states, separated by an F2 or F3 frontier. In fact, in these systems, $a_0 = 0$ has a solution of 0 measure ($x = 0$, $y = 0$), but this is not a frontier, since a point cannot partition a two-dimensional system, and there is thus no F1 frontier. Anyway, we found subsequently a variant in which a_0 has no zero value at all but nevertheless there are two steady states.[4]

2.6.1. *A system without an F1 frontier but with two steady states separated by an F2 frontier*

In system

$$\dot{x} = xy - 1$$
$$\dot{y} = -1 - x^2 + y^2$$

with Jacobian matrix $\begin{pmatrix} y & x \\ -2x & 2y \end{pmatrix}$, there is no F1 frontier since $a_0 = 2(x^2 + y^2)$ is positive everywhere, except at a single point ($x = 0$, $y = 0$). Frontier F2 is defined by $a_1 = 0$, with the constraint that $a_0 > 0$ (but in the present case $a_0 > 0$ everywhere) except at $\{0, 0\}$. Thus, F2 corresponds to the line $y = 0$, which partitions phase space into two domains. There are two steady states, a stable focus ($/--$) and an unstable focus ($/++$), located on either side of F2. This F2 frontier suffices to isolate the two steady states. There is also an F4 boundary, which separates the regions with real versus complex eigenvalues.

2.6.2. *A system without an F1 frontier but with two steady states separated by F3 frontiers*

In system

$$\dot{x} = -xy + 1$$
$$\dot{y} = 1 - x^2 + y^2$$

with Jacobian matrix $\begin{pmatrix} -y & -x \\ -2x & 2y \end{pmatrix}$, there is no F1 frontier, since $a_0 = -2(x^2 + y^2)$ is negative everywhere except at a single point ($x = 0, y = 0$). There is no F2 frontier either, since $a_1 = 0$ is an F2 frontier only where $a_0 > 0$, here nowhere. Incidentally, there is no F4 frontier either (and no possible complex eigenvalues) as the discriminant of the characteristic equation is positive everywhere.

This system has two steady states. Both are saddle points that differ by the contrasting orientations of their separatrices, as expected from the fact that they are separated by F3 frontiers.

These two examples clearly show that F2 and F3 frontiers can exist in the absence of an F1 frontier, and that multistationarity can be associated with either of these three types of frontiers, taken alone or together. The two systems just described belong to a special class of systems that we call "mirror systems" for obvious reasons (see the Jacobian matrices). Mirror systems will be revisited in Sec. 3.3 and in more detail in Sec. 3.4 in terms of the sign patterns of the nuclei.

2.7. *Some three-element systems yielding deterministic chaos*

(a) A simplified Rössler system [Thomas, 1996, 1999]

$$\begin{aligned} \dot{x} &= -y - z \\ \dot{y} &= x + ay \qquad \text{with } a = 0.365 \text{ and } c = 2\,. \\ \dot{z} &= x^2 - cz \end{aligned}$$

The Jacobian matrix is $\begin{pmatrix} 0 & -1 & -1 \\ 1 & a & 0 \\ 2x & 0 & -c \end{pmatrix}$. This system has two steady states, a saddle-focus of type $-/++$ and a saddle-focus of type $+/--$. As these steady states differ by the signs of all three eigenvalues, it is not surprising to find two frontiers: an F1 frontier at which level the real eigenvalue changes sign, and an F2 frontier at which level the real part of the

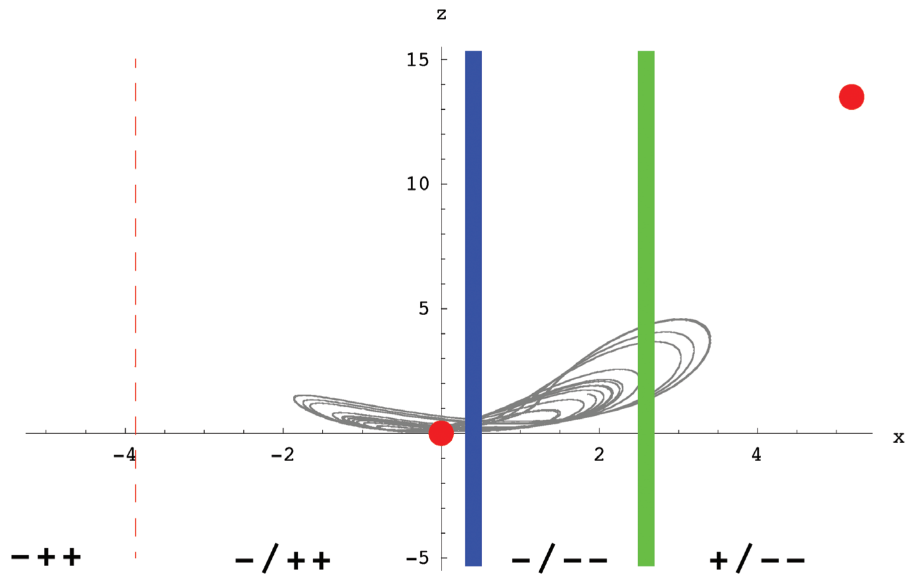
[4]For system

$$\dot{x} = xy + 1$$
$$\dot{y} = -x^2 - \log|x| + y^2$$

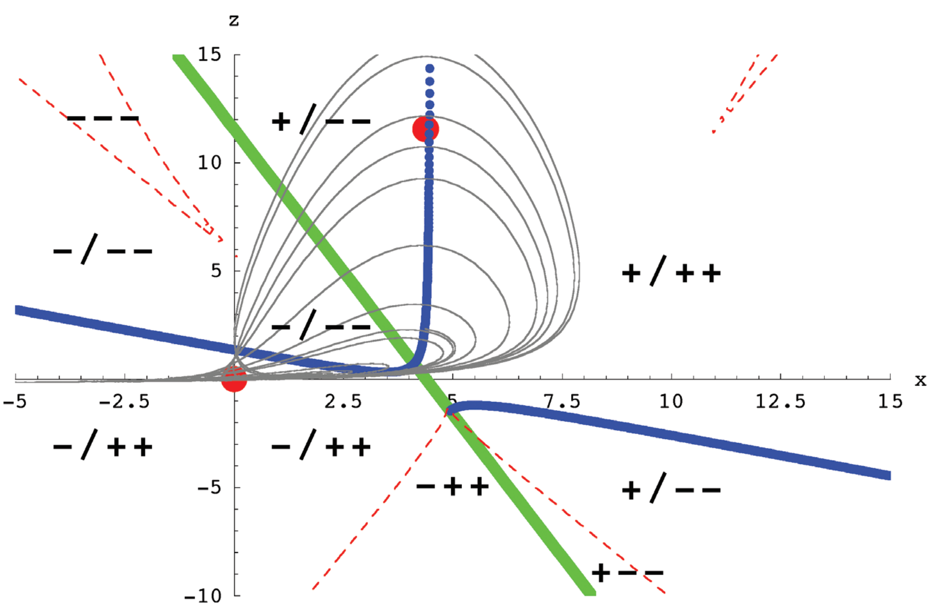
whose Jacobian matrix is

$$\begin{pmatrix} y & x \\ -\left(2x + \dfrac{1}{x}\right) & 2y \end{pmatrix}, \quad a_0 = 2(x^2 + y^2) + 1$$

has no zero point, yet the system has two steady states. Note that this system is not defined along the line $x = 0$. It cannot be taken as a counter-example to the real Jacobian conjecture, which deals only with polynomial systems. There exists, however, a counter-example to the real Jacobian conjecture [Pinchuk, 1994]. This very complex system has of course no F1 frontier, but there are quite involved F2, F3 and F4 frontiers. The two steady states are separated by an odd number of F3** frontiers.



(a)



(b)

Fig. 7. (a) A simplified Rössler system; (b) A classical variant of Rössler's most popular system; (c) A continuous variant of Chua's chaotic attractor.

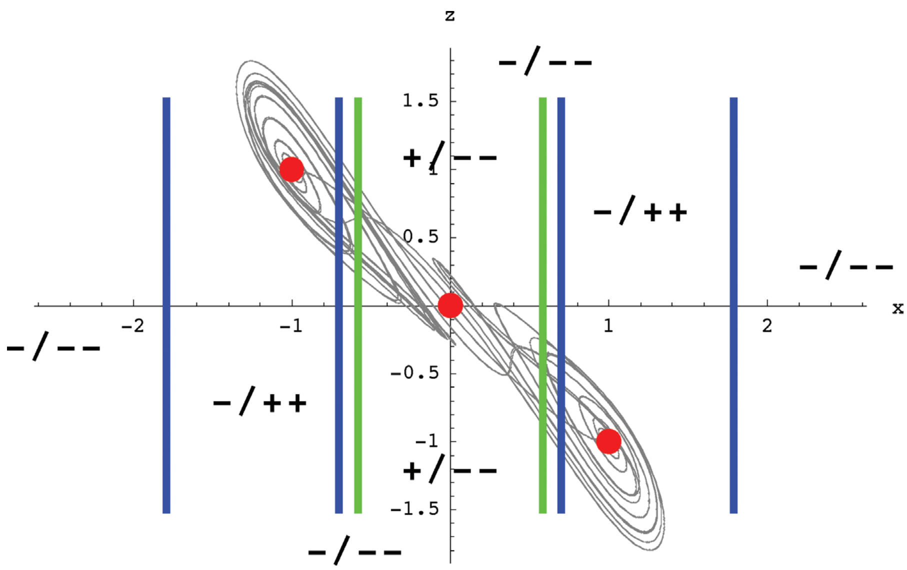
complex conjugate eigenvalues changes sign. As a result, the two essential domains that contain each one of the steady states are separated by an empty "no-man's land" within which the eigenvalues are of type $-/--$ [Fig. 7(a)].

Remark that in this system the nonlinearity affects only one variable (x). Consequently, the frontiers are planes in phase space ($x\ y\ z$). In subspace $x\,z$ they are vertical straight lines x = constant. This system will be revisited in Sec. 3.

(b) A classical variant of Rössler's most popular system

$$\begin{aligned}\dot{x} &= -y - z\\ \dot{y} &= x + ay, \qquad \text{with } a = 0.32,\ b = 0.3 \text{ and } c = 4.\\ \dot{z} &= bx + xz - cz\end{aligned}$$

The Jacobian matrix is $\begin{pmatrix} 0 & -1 & -1 \\ 1 & a & 0 \\ b+z & 0 & x-c \end{pmatrix}$. This variant was described by Rössler [1979] himself



(c)

Fig. 7. (*Continued*)

and thoroughly analyzed by Gaspard and Nicolis [1983].

There are again two steady states of the same types as in the preceding case. Again, the two domains ($-/++$ and $+/--$) containing the steady states differ by the signs of all three eigenvalues, and they are separated by an F1 and an F2 frontier, between which there is a "no-man's land" of type $-/--$. As the nonlinearity affects two variables (x and z), the frontiers are now cylinders in space x, y, z and they are no more vertical straight lines in space x, z [Fig. 7(b)].

(c) A continuous variant of Chua's system.

$$\dot{x} = x - x^3 + 10y$$
$$\dot{y} = x - y + z$$
$$\dot{z} = -14y$$

The Jacobian matrix is $\begin{pmatrix} 1-3x^2 & 10 & 0 \\ 1 & -1 & 1 \\ 0 & -14 & 0 \end{pmatrix}$. The Chua attractor [1997] is a remarkably simple three-element system that displays a chaotic dynamics. It involves a single nonlinearity, which was piecewise linear in its original form. Continuous variants with a cubic nonlinearity can be found in [Khibnik *et al.*, 1993; Huang *et al.*, 1996; Tsuneda, 2004]. Here, we used a continuous variant in which the nonlinearity is $x - x^3$. As only one variable (x) is involved in the nonlinearity, the frontiers are planes and, in 2D sections, vertical straight lines. As seen in Fig. 7(c), frontier F1 consists of two straight lines that suffice to separate the three steady states (a saddle-focus $+/--$ and two saddle-foci $-/++$), but there are in addition two frontiers F2, so that for increasing values of x one passes from $-/++$ to $-/--$ via a blue (F2) frontier, to $+/--$ via a green (F1) frontier, to $-/--$ again via a green (F1) frontier and from this to $-/++$ via a blue (F2) frontier. We would like to stress the contrast between the simplicity of the logical structure of the system (and of the partition diagrams) and the complexity of the trajectories.

3. From the Viewpoint of the Circuits

3.1. *A brief description of circuits*

Since in the Jacobian matrix of a system $a_{ij} = \partial f_i/\partial x_j$, a nonzero value of a_{ij} means that variable x_j influences the evolution of variable x_i, and one can draw an arrow $x_j \to x_i$ in the influence graph of the system; the interaction is labeled "positive" or "negative" according to the sign of a_{ij}.

As a result, a **circuit** can be defined from a set of nonzero elements a_{ij} of the Jacobian matrix, such that the i (row) and j (column) indices form a cyclic permutation. For example, if elements a_{12}, a_{23} and a_{31} of the matrix are nonzero, there exists a circuit $x_1 \to x_3 \to x_2 \to x_1$, whose oriented edges (arrows) are the a_{ij} elements considered.

A circuit is positive if it comprises an **even** number of **negative links**, negative if odd. For example, a_{12} and a_{21} both negative define a positive two-circuit between variables x and y. Positive and negative circuits have sharply contrasting effects. In short, the occurrence of a positive circuit somewhere in phase space is a necessary condition for multistationarity. (Conjecture I: [Thomas, 1981, 1994]; formal demonstrations: [Plahte *et al.*, 1995; Snoussi, 1998; Gouzé, 1998; Cinquin & Demongeot, 2002; Soulé, 2003]). The occurrence of a negative circuit somewhere in phase space is a necessary condition for sustained oscillations and more generally for the mere existence of an attractor (punctual, periodic or chaotic) (Conjecture II: [Thomas, 1981], partial demonstrations [Plahte *et al.*, 1995; Snoussi, 1998; Gouzé, 1998; Toni *et al.*, 1999]).

In fact, one has to consider not only circuits proper, but also unions of two or more disjoint circuits, these are unions of two or more circuits that do not share any variable (for sake of simplicity, we will call them simply **unions**). Each circuit or union can be represented by the product of the corresponding elements of the Jacobian matrix. For example, $a_{12}a_{21} \cdot a_{33}$ is the union of a two-circuit in x y and of a one-circuit in z, and we describe it as a $(2+1)$-union.

We call **nucleus**, a circuit or a union that implies all the variables of the system. The crucial role played by nuclei can be understood from the following. As recalled above, the characteristic equation can be written: $\lambda^n + a_{n-1}\lambda^{n-1} + \cdots + a_2\lambda^2 + a_1\lambda + a_0 = 0$. The coefficients a_i are sums of products, each of which represents a circuit or a union (each with a "signature" + or −). As remarked earlier (see [Eisenfeld & De Lisi, 1985; Thomas, 1994] or [Plahte *et al.*, 1995]), the term a_0 comprises the products that describe the circuits or unions dealing with all the n variables (in other words, the nuclei), the term a_1, the circuits or unions that deal with $n-1$ of the variables, etc. For example, in three variables,

$$\begin{aligned} a_0 &= -a_{12}a_{23}a_{31} - a_{13}a_{21}a_{32} + a_{11}a_{23}a_{32} \\ &\quad + a_{22}a_{13}a_{31} + a_{33}a_{12}a_{21} - a_{11}a_{22}a_{33}, \\ a_1 &= -a_{12}a_{21} - a_{23}a_{32} - a_{31}a_{13} + a_{11}a_{22} \\ &\quad + a_{22}a_{33} + a_{33}a_{11} \quad \text{and} \\ a_2 &= -a_{11} - a_{22} - a_{33}. \end{aligned}$$

In particular, a_0, the term of degree 0, provides us with the list of the nuclei of the system (represented each by the product of the corresponding elements of the Jacobian matrix, endowed with its signature). For example, if in a particular system $a_0 = a_{12}a_{21}a_{33} - a_{11}a_{22}a_{33}$, it means that the system has two (out of the six possible) nuclei, namely the $(2+1)$-nucleus $a_{12}a_{21}a_{33}$ and the $(1+1+1)$-nucleus $a_{11}a_{22}a_{33}$.

Note that frontier F1 depends exclusively on the term a_0 of the characteristic equation, and thus only on the nuclei of the system. Other circuits, off-circuit terms of the Jacobian matrix or constant terms of the ODE's, affect the location of steady states (and may change their number), but not the primary partition based on the parity of the number of positive eigenvalues. The other frontiers depend not only on the nuclei, but also on circuits that do not belong to a nucleus.

The sign of circuits or unions was defined by Eisenfeld and De Lisi [1985] (who call them "generalized loops") as $(-1)^{p+1}$, in which p is the number of positive circuits involved. In practice, this amounts to say that a circuit or union (and in particular a nucleus) is positive if it comprises an **odd** number of **positive circuits**, negative otherwise. This definition can be justified in particular by the fact that the sign (signature included) of any product is known if one knows the Eisenfeld sign of the corresponding circuit or union. As a matter of fact, this sign is opposite to the Eisenfeld sign.

In nonlinear systems, the value, and even the sign, of one or more elements of the Jacobian matrix depends on one or more variables. As a result, the sign of a circuit or union may depend on the location in phase space. In this (very frequent) situation, we call the circuit or union **ambiguous.** Whether a circuit or union is ambiguous or not depends on the nature of the nonlinearities. For example, a nonlinearity in x^3 results in a term x^2 (whose sign is constant) in the Jacobian matrix, and it will thus not generate an ambiguous circuit. More generally, a nonlinear term in an ODE can render a circuit ambiguous only if it is nonmonotonous.

A conjecture more demanding than Thomas's conjecture I is due to M. Kaufman (see [Thomas & Kaufman, 2001]). It states that in order to display multistationarity, a system must be ambiguous, or else comprise two nuclei of opposite Eisenfeld signs. This conjecture will be further analyzed and slightly updated in the discussion.

3.2. *Circuits and steady states*

The tight relation between circuits and steady states results from the fact that only those elements of the Jacobian matrix that belong to a circuit are present in the characteristic equation. Thus, the eigenvalues at a given location of phase space depend **only** on the circuits present in the Jacobian matrix. As mentioned above, off-circuit elements of the matrix, as well as constant terms in the differential equations, influence the **location and number** of steady states, but not the eigenvalues at a **given** location.

The relation between circuits and steady states is particularly simple in the case of an "isolated nucleus". By that we are referring to systems that comprise only one nucleus, and no other circuit, but the ODE's may comprise one or more off-circuit elements and terms of degree zero. As our systems are usually nonlinear, the value and even the sign of elements of the Jacobian matrix may depend on the location in phase space. Thus even an isolated nucleus may display various sign patterns depending on the location, and generate steady states of various natures. **However, for an isolated nucleus, the signs of the eigenvalues computed at a given point of phase space (and thus, the exact nature of any steady state that might be present at that point) are entirely determined by the sign pattern of the nucleus at that location.** Tables 1 and 2 provide the nature of the steady states generated by isolated nuclei of a defined sign pattern in two- and three-dimensional systems, respectively.

For example, in three dimensions, the eigenvalues of an isolated three-circuit, say $a_{12}a_{23}a_{31}$, are the three components of the cubic root of the product $a_{12}a_{23}a_{31}$. This invariably generates a saddle-focus, whose eigenvalues are $+/--$ (a positive real root and a pair of conjugated complex roots whose real part is negative) or $-/++$ depending simply on whether the circuit is positive or negative. In the presence of an appropriate nonlinearity, the three-circuit can be positive or negative according to the location. In this case, phase space will comprise domains that differ by the character ($+/--$ or $-/++$) of the eigenvalues. The steady states will be saddle-foci of either type depending on whether the circuit is positive or negative in the domain considered, and their number will be determined by the nature of the nonlinearity (see Sec. 3.3). In the three-element system

$$\begin{aligned} \dot{x} &= y^2 - 1 \\ \dot{y} &= z^2 - 1\,, \\ \dot{z} &= x^2 - 1 \end{aligned}$$

there are eight steady states, all unstable. All of them are saddle foci of either type as expected.

More generally, each nucleus **taken alone** can generate steady states that are characteristic of it in this sense that the signs of their eigenvalues are entirely predictable from the sign patterns of the nucleus. In particular, in the case of an isolated nucleus, there is a simple correspondence between its Eisenfeld sign in a domain and the parity of the number of positive eigenvalues in that domain (where a nucleus has a positive Eisenfeld sign there is an odd number of positive eigenvalues).

For systems that comprise more than one nucleus, or even simply a nucleus plus additional elements that do not add up to an additional nucleus, one may have to use quantitative methods as described, for example, in Sec. 2. However, as we will see in Sec. 3.3, much of the structure of phase space can still be understood from a proper analysis of sign patterns. Note that in two-variable systems there cannot be more than two nuclei. In three-variables already, there can be up to six nuclei, but many interesting systems, including systems that generate deterministic chaos, have only two, sometimes even only one.

Table 1. Steady states generated by isolated nuclei in two-dimensional systems.

This table gives the signs of eigenvalues and the nature of steady states for all possible sign patterns of a single nucleus. For the last line, the steady state is a center (/00), a stable focus ($/--$) or an unstable focus ($/++$) depending on whether the trace is nil, negative or positive.

Nucleus	Signs of the Eigenvalues	Nature of the Steady State
$\begin{bmatrix} - & \cdot \\ \cdot & - \end{bmatrix}$	$--$	Stable node
$\begin{bmatrix} + & \cdot \\ \cdot & + \end{bmatrix}$	$++$	Unstable node
$\begin{bmatrix} + & \cdot \\ \cdot & - \end{bmatrix}, \begin{bmatrix} - & \cdot \\ \cdot & + \end{bmatrix}$	$+-$	Saddle points of contrasting orientations
$\begin{bmatrix} \cdot & - \\ - & \cdot \end{bmatrix}, \begin{bmatrix} \cdot & + \\ + & \cdot \end{bmatrix}$	$+-$	Saddle points of contrasting orientations
$\begin{bmatrix} \cdot & - \\ + & \cdot \end{bmatrix}, \begin{bmatrix} \cdot & + \\ - & \cdot \end{bmatrix}$	/..	Centres (foci) running in opposite directions

3.3. *Partition of phase space according to the sign patterns of nuclei*

In nonlinear systems, a nucleus may display more than one sign pattern. In this case, we say that it is

Table 2. Steady states generated by isolated nuclei in three-dimensional systems.

This table gives the signs of the eigenvalues and the nature of the steady states for various sign patterns of single nuclei. Not all possibilities are explicitly shown, but all can be derived from those shown in the table, by cyclic permutations of the variables or of the elements of the two-circuits. For items 6 and 7, the focus may be a center (and the eigenvalues are then $-/00$ or $+/00$, respectively), for example if one deals with a pure nucleus (the other terms of the Jacobian matrix are nil).

Nucleus	Signs of the Eigenvalues	Nature of the Steady State
$\begin{bmatrix} - & \cdot & \cdot \\ \cdot & - & \cdot \\ \cdot & \cdot & - \end{bmatrix}$	$---$	Stable node
$\begin{bmatrix} + & \cdot & \cdot \\ \cdot & - & \cdot \\ \cdot & \cdot & - \end{bmatrix}$	$+--$	Saddle with one unstable manifold
$\begin{bmatrix} + & \cdot & \cdot \\ \cdot & + & \cdot \\ \cdot & \cdot & - \end{bmatrix}$	$++-$	Saddle with two unstable manifolds
$\begin{bmatrix} \cdot & - & \cdot \\ - & \cdot & \cdot \\ \cdot & \cdot & - \end{bmatrix}, \begin{bmatrix} \cdot & + & \cdot \\ + & \cdot & \cdot \\ \cdot & \cdot & - \end{bmatrix}$	$+--$	Saddle with one unstable manifold
$\begin{bmatrix} \cdot & - & \cdot \\ - & \cdot & \cdot \\ \cdot & \cdot & + \end{bmatrix}, \begin{bmatrix} \cdot & + & \cdot \\ + & \cdot & \cdot \\ \cdot & \cdot & + \end{bmatrix}$	$++-$	Saddle with two unstable manifolds
$\begin{bmatrix} \cdot & - & \cdot \\ + & \cdot & \cdot \\ \cdot & \cdot & - \end{bmatrix}$	$-/++$ or $-/--$	Saddle — focus or stable node — focus
$\begin{bmatrix} \cdot & - & \cdot \\ + & \cdot & \cdot \\ \cdot & \cdot & + \end{bmatrix}$	$-/++$ or $-/--$	Saddle — focus or stable node — focus
$\begin{bmatrix} \cdot & - & \cdot \\ \cdot & \cdot & - \\ - & \cdot & \cdot \end{bmatrix}, \begin{bmatrix} \cdot & - & \cdot \\ \cdot & \cdot & + \\ + & \cdot & \cdot \end{bmatrix}$	$-/++$	Saddle — focus with two unstable manifolds
$\begin{bmatrix} \cdot & + & \cdot \\ \cdot & \cdot & + \\ + & \cdot & \cdot \end{bmatrix}, \begin{bmatrix} \cdot & - & \cdot \\ \cdot & \cdot & - \\ + & \cdot & \cdot \end{bmatrix}$	$+/--$	Saddle — focus with one unstable manifold

variable. For example, $\begin{pmatrix} & 1-3y^2 \\ 1-3x^2 & \end{pmatrix}$ has four distinct sign patterns, as each of the two elements can be positive or negative. Phase space can be partitioned according to the sign patterns of this variable nucleus. As we will see below, in the present case phase space is cut into nine domains according to the four sign patterns: we say that the **variability** of this nucleus is four and its **multiplicity** is nine (variability describes the number of distinct sign patterns, multiplicity refers to the number of domains into which phase space can be cut in terms of these sign patterns).

In most cases, a nucleus that is variable is also **ambiguous** (i.e. not only its sign pattern, but also its Eisenfeld sign depends on the location in phase space). However, a nucleus can be variable without being ambiguous. In the system

$$\begin{aligned} \dot{x} &= xy - 1 \\ \dot{y} &= x^2 - 1 \end{aligned},$$

whose Jacobian matrix is $\begin{pmatrix} y & x \\ 2x & 0 \end{pmatrix}$, the unique nucleus is always positive (and it is thus not ambiguous), yet it has two distinct sign patterns, $\begin{pmatrix} & - \\ - & \end{pmatrix}$ and $\begin{pmatrix} & + \\ + & \end{pmatrix}$. It is thus variable. Incidentally, it has two steady states (see Sec. 3.4). Variability, as well as ambiguity, is of course dependent on the nonlinearities present in the ODE's.

In Sec. 2, we have seen how to partition phase space according to the signs of the eigenvalues and, where required, to the slopes of the eigenvectors. Here, we consider the **sign patterns of variable nuclei** and their relation with the number and nature of steady states. Let us revisit the two first systems analyzed on a quantitative basis in Sec. 2.

3.3.1. *Saddle points with contrasting orientations*

System I has two nuclei, a variable $(1+1)$-nucleus with four sign patterns and a constant two-nucleus. The sign of element $1-3x^2$ in the Jacobian matrix is "plus" for low absolute values of x $(< 1/\sqrt{3})$, "minus" for higher values, and similarly, the sign of element $1-3y^2$ is "plus" for low absolute values of y, "minus" for higher values. Phase space is thus partitioned into nine domains according to the four sign patterns of the variable $(1+1)$-nucleus:

$$\begin{matrix} \begin{pmatrix} - & \\ & - \end{pmatrix} & \begin{pmatrix} + & \\ & - \end{pmatrix} & \begin{pmatrix} - & \\ & - \end{pmatrix} \\ \begin{pmatrix} - & \\ & + \end{pmatrix} & \begin{pmatrix} + & \\ & + \end{pmatrix} & \begin{pmatrix} - & \\ & + \end{pmatrix}, \\ \begin{pmatrix} - & \\ & - \end{pmatrix} & \begin{pmatrix} + & \\ & - \end{pmatrix} & \begin{pmatrix} - & \\ & - \end{pmatrix} \end{matrix}$$

with the following expectations (see Table 1) as regards the possible nature of steady states:

stable node	*saddle point*	*stable node*
saddle point	*unstable node*	*saddle point*
stable node	*saddle point*	*stable node*

We already know from Sec. 2 that there are nine steady states of the expected nature, and this occurs not only when the nucleus considered is alone, but also in the presence of additional elements, provided the weight of these elements remains sufficiently low. This correspondence between the multiplicity of the variable nucleus and the total number of solutions of the steady state equations will be discussed below (Sec. 4). In the system considered, the four saddle points correspond to either of two distinct sign patterns: $\begin{pmatrix} + & \\ & - \end{pmatrix}$ or $\begin{pmatrix} - & \\ & + \end{pmatrix}$ (see Sec. 2.3). In the first case, the steady state is attractive in y and repulsive in x, whereas in the second case it is attractive in x and repulsive in y. Accordingly, although the eigenvalues of these four steady states have the same signs (and in the present case, even the same values) the slopes of the eigenvectors, and hence the orientation of the separatrices near the saddle point, are contrasting. In the type of analysis used in Sec. 2, this leads to a "black" frontier (F3), based on the orientations of the eigenvectors.

3.3.2. *Foci turning in opposite directions*

If one turns to system II, the following partition of phase space is obtained according to the sign patterns of the variable nucleus (in this case, the two-nucleus):

$$\begin{matrix} \begin{pmatrix} & - \\ - & \end{pmatrix} & \begin{pmatrix} & - \\ + & \end{pmatrix} & \begin{pmatrix} & - \\ - & \end{pmatrix} \\ \begin{pmatrix} & + \\ - & \end{pmatrix} & \begin{pmatrix} & + \\ + & \end{pmatrix} & \begin{pmatrix} & + \\ - & \end{pmatrix} \\ \begin{pmatrix} & - \\ - & \end{pmatrix} & \begin{pmatrix} & - \\ + & \end{pmatrix} & \begin{pmatrix} & - \\ - & \end{pmatrix} \end{matrix}$$

and the expectations as regards the possible nature of steady states are:

saddle point	*focus*(*centre*)	*saddle point*
focus(*centre*)	*saddle point*	*focus*(*centre*).
saddle point	*focus*(*centre*)	*saddle point*

Again, we know from Sec. 2 that there are nine steady states of the expected nature, not only when the nucleus considered is alone, but also in the presence of diagonal elements, provided the weight of these elements is not too high. The four foci (centres if the trace is zero) display either of two sign patterns: $\begin{pmatrix} & + \\ - & \end{pmatrix}$ or $\begin{pmatrix} & - \\ + & \end{pmatrix}$. The difference is that the trajectories run clockwise in one case, counter clockwise in the other. Here again, two steady states may have the same eigenvalues, but differ by the slopes of the eigenvectors. The F3 frontier described in Sec. 2 separates domains within which foci or centres turn in opposite directions. This can thus be understood in terms of the sign patterns of the Jacobian matrix as well as in terms of the slopes of the eigenvectors.

3.3.3. *Three-dimensional systems*

In the examples just described, the variable nucleus has four distinct sign patterns, the multiplicity of the nuclei considered is nine and the systems have up to nine steady states. In similar three-dimensional systems (some of which display beautiful chaotic dynamics), there are 8 (2^3) distinct sign patterns (each of the three elements of the nucleus can be + or −), the multiplicity of the variable nucleus is 27 (3^3) and there are 27 steady states for a wide range of parameter values. Again, the multiplicity of the variable nuclei fits with the total number of solutions of the steady state equations. In related three-dimensional system in which the nonlinearity is $\sin x$ instead of $(x - x^3)$, variability is again 8, but the multiplicity of the nucleus is infinite. The number of steady states indeed tends to infinity as the diagonal terms tend to zero [Thomas, 1999; Thomas *et al.*, 2004].

In any case, the position and the actual number of steady states are progressively affected by increasing weights of another nucleus, but as well by circuits that do not add up to a nucleus, and even by off-circuit elements of the matrix or by constant terms of the ODE's. In contrast, the F1 frontier depends only on the nuclei present.

Let us now reconsider one of the 3-D systems of Sec. 2.7 in terms of the sign patterns of individual nuclei. The Jacobian matrix of our simplified Rössler system is: $\begin{pmatrix} & -1 & -1 \\ 1 & a & \\ 2x & & -c \end{pmatrix}$.

Here follow the sign patterns of the two individual nuclei, to which we have added (between brackets) the sign of an additional diagonal term where required in order to know the sign of the real part of complex eigenvalues:

$$\underset{\text{Nucleus I}}{\begin{pmatrix} & - & \\ + & (+) & \\ & & - \end{pmatrix}} \quad \text{and} \quad \underset{\text{Nucleus II}}{\begin{pmatrix} & & - \\ & + & \\ 2x & & (-) \end{pmatrix}}.$$

Nucleus I, if alone, would generate a saddle-focus of type $(-/++)$. Nucleus II is a variable, ambiguous nucleus with two sign patterns:

$$\underset{\text{Nucleus II a}}{\begin{pmatrix} & & - \\ & + & \\ - & & \end{pmatrix}} \quad \text{and} \quad \underset{\text{Nucleus II b}}{\begin{pmatrix} & & - \\ & + & \\ + & & (-) \end{pmatrix}}.$$

according simply to the sign of variable x.

If Nucleus II were alone, these sign patterns would generate, respectively, a saddle point of type $(-++)$ and a saddle-focus of type $(+/--)$. Obviously, the fixed Nucleus I will be dominant for small absolute values of x, the variable Nucleus II for higher absolute values. One expects thus, for increasing values of x, domains characterized by the following signs of their eigenvalues:

$$\underset{\text{(Nucleus II a)}}{-++} \qquad \underset{\text{(Nucleus I)}}{-/++} \qquad \underset{\text{(Nucleus II b)}}{+/--}$$

Nuclei II a and I differ only by the real versus complex character of the eigenvalues. They are thus not expected to generate distinct steady states. In contrast, Nuclei I and II b differ by the signs of all three eigenvalues; this implies that their regions be separated by two frontiers, an F2 frontier at which level the real part of a pair of complex eigenvalues changes sign and an F1 frontier at which level one real eigenvalue changes sign.

Thus, on the one hand there are two contrasting domains directly generated by the sign patterns of nuclei of the system; these domains are characterized by eigenvalues of signs $-/++$ and $+/--$, respectively, and contain indeed each a steady state of the expected type. On the other hand, there is an intermediate domain, in the present case, of type $(-/--)$, whose occurrence results only indirectly, for logical reasons, from the sign patterns of the nuclei. While the domains $-/++$ and $+/--$ are generated, respectively, by the sign patterns of "Nucleus I" and "Nucleus II b", this is, $\begin{pmatrix} & - & \\ + & (+) & \\ & & - \end{pmatrix}$ and $\begin{pmatrix} & & - \\ & + & \\ + & & (-) \end{pmatrix}$ (and contain indeed each a steady state of the expected type), the "no-man's land" between these two domains corresponds to regions of unsettled competition between the two nuclei.

The other three-element systems of Sec. 2.5 can be treated in similar terms.

3.4. *Mirror systems*

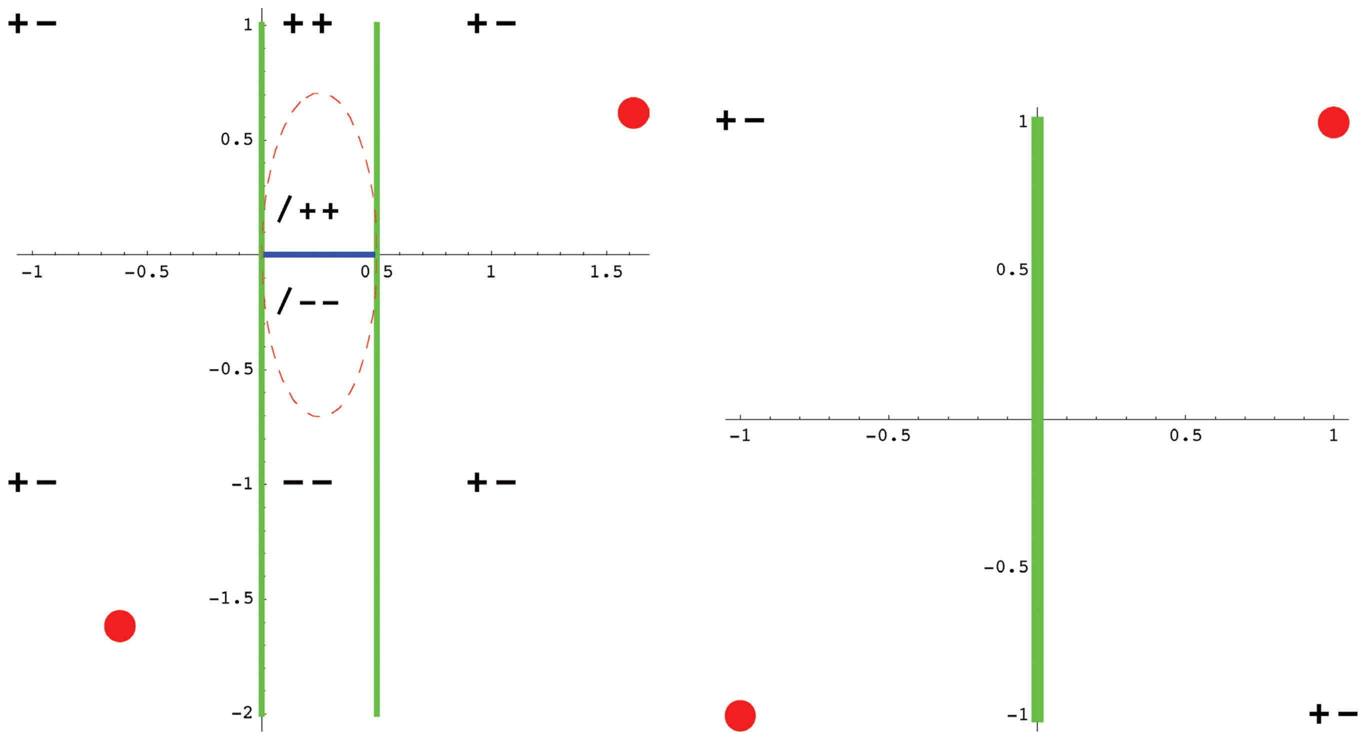
3.4.1. *A double F1 frontier*

Consider the system:

$$\dot{x} = xy - 1$$
$$\dot{y} = x^2 - 1$$

already briefly mentioned in Sec. 3.3.

A simple look at the Jacobian matrix $\begin{pmatrix} y & x \\ 2x & 0 \end{pmatrix}$ will justify its qualification as a "mirror" system. The only nucleus is not ambiguous, as in the present system it is always positive. However, it is variable, as it has two distinct sign patterns, namely: $\begin{pmatrix} & - \\ - & \end{pmatrix}$



(a) (b)

Fig. 8. System $\begin{matrix} \dot{x} = xy - 1 \\ \dot{y} = x^2 - bx - 1 \end{matrix}$. As $a_0 = x(2x - b)$, for b nonzero (a), frontier F1 (green) comprises two lines, $x = 0$ and $x = b/2$. Outside these lines, a_0 is negative, and any steady state has to be a saddle point. Between these lines a_0 is positive and there is space for an F2 frontier (blue) and an F4 boundary (dashed, red).

For $b = 0$ (b), the two F1 frontiers have fused; as a result, a_0 is negative, the eigenvalues are $\begin{pmatrix} & - \\ + & \end{pmatrix}$ on both sides of this double F1 frontier (and there is neither an F2 frontier nor an F4 boundary). Both steady states are saddle points, but their orientations are contrasting; the slopes of both eigenvectors change sign (one by crossing the value 0, the other via a vertical asymptote) at the level of frontier F3**, not represented because it coincides with the double F1 frontier. The contrasting character of the two saddle points can also be predicted from the sign patterns of the two-nucleus, which is $\begin{pmatrix} & - \\ - & \end{pmatrix}$ for negative values of x, $\begin{pmatrix} & + \\ + & \end{pmatrix}$ for positive values.

and $\begin{pmatrix} & + \\ + & \end{pmatrix}$, depending on the sign of x. There are two steady states. Both are saddle points, but the orientations of the separatrices at these points are different. This explains why one finds an F3 frontier (based on the slopes of the eigenvectors) when this system is analyzed as in Sec. 2. There is also an F1 frontier. This frontier is peculiar, however, in the sense that as one passes this frontier one of the eigenvalues takes the value zero but does not change sign. This is why it separates two domains that do not differ by the signs of the eigenvalues. In fact, one deals with a double frontier F1, as shown by system:

$$\begin{aligned} \dot{x} &= xy - 1 \\ \dot{y} &= x^2 - bx - 1 \end{aligned},$$

of which our mirror system is a particular case. One can see that there are two F1 frontiers. One eigenvalue changes its sign at the level of both F1 frontiers. When b vanishes, the two F1 frontiers fuse and the representative curve of this eigenvalue is tangent to the x-axis at the level of this unique frontier [Figs. 8(a) and 8(b)].

By exchanging the right members of the ODE's, or by changing the sign of either of these right members, one gets variants of the mirror system, in which the nullclines and frontiers remain unchanged, but the nature of the steady states is modified. Note that the Lorenz system comprises a mirror circuit.

3.4.2. *A "double mirror" system*

Consider now the system

$$\begin{aligned} \dot{x} &= xy - 1 \\ \dot{y} &= x^2 + y^2 - 4 \end{aligned},$$

the Jacobian matrix of which is: $\begin{pmatrix} y & x \\ 2x & 2y \end{pmatrix}$, hence the label of "double mirror" system. In the present case, the two nuclei have opposite Eisenfeld signs: the two-nucleus is everywhere positive and the $(1+1)$ nucleus is everywhere negative (either two negative or two positive one-circuits, thus, an even number of positive circuits).

The two sign patterns of the two-nucleus are $\begin{pmatrix} & - \\ - & \end{pmatrix}$ and $\begin{pmatrix} & + \\ + & \end{pmatrix}$, suggesting two saddle points of contrasting orientations, and the two sign patterns of the $(1+1)$-nucleus are $\begin{pmatrix} - & \\ & - \end{pmatrix}$ and $\begin{pmatrix} + & \\ & + \end{pmatrix}$, suggesting a stable and an unstable node. The system has indeed four steady states of the expected natures. Coming back to the description in terms of frontiers, $a_0 = 2(y^2 - x^2)$ and there is thus a frontier F1 of equation $y = \pm x$, which suffices to isolate the four steady states. There is no F2 frontier, since the line $y = 0$, is located in the region within which $a_0 < 0$, and there is no F4 frontier either (and no complex eigenvalues) as the discriminant of the characteristic equation is positive everywhere. On the other hand, there are F3 frontiers ($x = 0$ and $y = 0$). They account nicely for the fact that the two saddle points (which in the present case have the same eigenvalues) have contrasting orientations.

3.4.3. *Multistationarity without an F1 frontier*

Consider now the closely related system:

$$\begin{aligned} \dot{x} &= xy - 1 \\ \dot{y} &= -x^2 + y^2 - 1 \end{aligned},$$

whose Jacobian matrix is $\begin{pmatrix} y & x \\ -2x & 2y \end{pmatrix}$. This system was already described above (Sec. 2.6.1) as an example of the possibility of having multistationarity in the absence of an F1 frontier. Now, we will re-examine it in terms of its sign patterns. The two sign patterns of the two-nucleus are $\begin{pmatrix} & + \\ - & \end{pmatrix}$ and $\begin{pmatrix} & - \\ + & \end{pmatrix}$, suggesting two foci running in opposite directions according to the sign of x, and the two sign patterns of the $(1+1)$-nucleus are $\begin{pmatrix} - & \\ & - \end{pmatrix}$ and $\begin{pmatrix} + & \\ & + \end{pmatrix}$, suggesting respectively a stable node in the region $(y < 0)$ and an unstable node in the region $(y > 0)$.

What one finds in fact is a pair of foci, a stable one and an unstable one, running in opposite directions (as already mentioned in Sec. 2.6.1). Thus, the result is that predicted from the sign patterns of the two-nucleus. However, it suffices to increase the weight of the $(1+1)$-nucleus to reverse the situation: if in the second equation one puts $3y^2$ instead of y^2, the two steady states are those expected from the sign patterns of the $(1 + 1)$-nucleus.

But why is it that in the preceding example we had the four steady states expected from the sign patterns, while here we find only two of them? In the preceding example, the presence of two nuclei of opposite Eisenfeld signs permitted the existence of an F1 frontier that by itself generated domains adequate to harbour four steady states. In the present system, we deal with two nuclei with the same Eisenfeld sign (but both variable), which results usually (and in particular in the present situation) in the absence of an F1 frontier. In this situation, the two nuclei compete for the generation of steady states.

We will come back to the relation between these results and conjectures concerning the conditions of multistationarity in the discussion.

3.4.4. *Multistationarity generated by nonvariable nuclei*

So far, we have described systems comprising at least one variable (and usually ambiguous) nucleus. What about systems that have only **nonvariable** nuclei? Consider the system:

$$\begin{aligned} \dot{x} &= x + y \\ \dot{y} &= x^3 + y \end{aligned}$$

whose Jacobian matrix is: $\begin{pmatrix} 1 & 1 \\ 3x^2 & 1 \end{pmatrix}$.

In such a case all terms of the Jacobian matrix have a constant sign. However, one can still reason in terms of the sign patterns of the two nuclei, namely $\begin{pmatrix} & + \\ + & \end{pmatrix}$ and $\begin{pmatrix} + & \\ & + \end{pmatrix}$ for the two-nucleus and the $(1+1)$-nucleus, respectively. Obviously, for small values of $3x^2$ (thus, for small absolute values of x) the $(1+1)$-nucleus will be dominant and in this region any steady state will be an unstable node. For higher values of $3x^2$ (thus for higher absolute values of x) there will be two regions in which the two-nucleus will be dominant, and any steady state will be a saddle point. More quantitatively, depending on whether $x < -1/\sqrt{3}$, $-1/\sqrt{3} < x < 1/\sqrt{3}$

or $1/\sqrt{3} < x$, we will have three domains that may contain a saddle point, an unstable node and a saddle point again, respectively. Note that the lines that differentiate the relative weights of the two nuclei are nothing else than the F1 frontiers. This system has indeed three steady states, $(-1, 1)$, $(0, 0)$ and $(1, -1)$, two saddle points bracketing an unstable node, as expected.

If one changes the sign of any single term in these equations, multistationarity disappears (there is a single steady state left: $(0, 0)$, but it reappears if one changes two signs). This fully agrees with Kaufman's conjecture (see Sec. 3.1), since in the original system, the two nuclei have opposite Eisenfeld signs (a positive two-nucleus and a negative $(1+1)$-nucleus), thus allowing for steady states of opposite parities; changing the sign of a single term results in two nuclei of the same Eisenfeld sign.

Incidentally, one can check with this system: (i) that in the absence of any positive circuit: $\begin{pmatrix} - & + \\ - & - \end{pmatrix}$ or $\begin{pmatrix} - & - \\ + & - \end{pmatrix}$ there is a single steady state and (ii) that in the absence of any negative circuit: $\begin{pmatrix} + & + \\ + & + \end{pmatrix}$ (here, one of the two **nuclei** is negative, but there is no negative **circuit**) the system can have multiple steady states, but all of them are unstable (one unstable node and two saddle points) and there is no attractor.

3.5. *Competition between two nuclei*

The last example aims to show how informative can be an essentially qualitative analysis of the sign patterns of circuits in the Jacobian matrix. The system differs from system I only by the signs in the second ODE:

$$\dot{x} = x - x^3 + by$$
$$\dot{y} = -bx - (y - y^3)$$

with the Jacobian matrix: $\begin{pmatrix} 1-3x^2 & +b \\ -b & -(1-3y^2) \end{pmatrix}$. It comprises a variable $(1+1)$-nucleus and a constant, negative, two-nucleus. If the variable nucleus were alone, phase space would be partitioned as follows as regards the sign patterns:

$$\begin{pmatrix} - & \\ & + \end{pmatrix}\begin{pmatrix} + & \\ & + \end{pmatrix}\begin{pmatrix} - & \\ & + \end{pmatrix}$$
$$\begin{pmatrix} - & \\ & - \end{pmatrix}\begin{pmatrix} + & \\ & - \end{pmatrix}\begin{pmatrix} - & \\ & - \end{pmatrix}$$
$$\begin{pmatrix} - & \\ & + \end{pmatrix}\begin{pmatrix} + & \\ & + \end{pmatrix}\begin{pmatrix} - & \\ & + \end{pmatrix}$$

with potential steady states:

saddle	*unstable node*	*saddle*
stable node	*saddle*	*stable node*
saddle	*unstable node*	*saddle*

Note that this includes saddle points of two contrasting orientations.

The sign pattern of the two-nucleus, $\begin{pmatrix} & + \\ - & \end{pmatrix}$, opens the possibility to have a region with complex eigenvalues. But where in phase space does one expect this situation to take place? In two-dimensional systems, the discriminant of the characteristic equation can be written: $d = (a_{11} - a_{22})^2 + 4a_{12}a_{21}$. When d is written in this form, it is immediately obvious that in order to have complex eigenvalues terms a_{12} and a_{21} must have opposite signs (which is the case here) and that a_{11} and a_{22} should not be too unequal. This amounts to write $3x^2 + 3y^2 - 2 \approx 0$, the equation of a circular strip of average radius $\approx \sqrt{2/3}$. Any steady state present in this region would have to be a focus (running in the clockwise direction in view of the sign pattern of the $(1+1)$-nucleus). From the analytic expression of d, one can see that the stronger the two-circuit, the wider the complex region.

Let us now apply the quantitative method of Sec. 2 in order to check these qualitative predictions. Figure 9(a) shows that for low values (here 0.2) of parameter b there are nine steady states of the nature expected from the sign patterns of the variable nucleus. For sufficiently high values of parameter b [here 0.6, Fig. 9(b)], two triplets of steady states have fused to yield two steady states, now located in the complex region. In the present case, they are located on frontier F2, so that they must be centers. Figures 9(c) and 9(d) show trajectories for $b = 0.2$ and 0.6, respectively. This illustrates the nature of the steady states already characterized by the signs of their eigenvalues. In Fig. 9(d), one sees that there are indeed two centers running in the same (clockwise) direction. Note also the presence of closed trajectories surrounding the two centers and the saddle point located between them.

4. Discussion

As remarked by Christophe Soulé, one question is whether or not a system can have more than one steady state; another question is how many steady

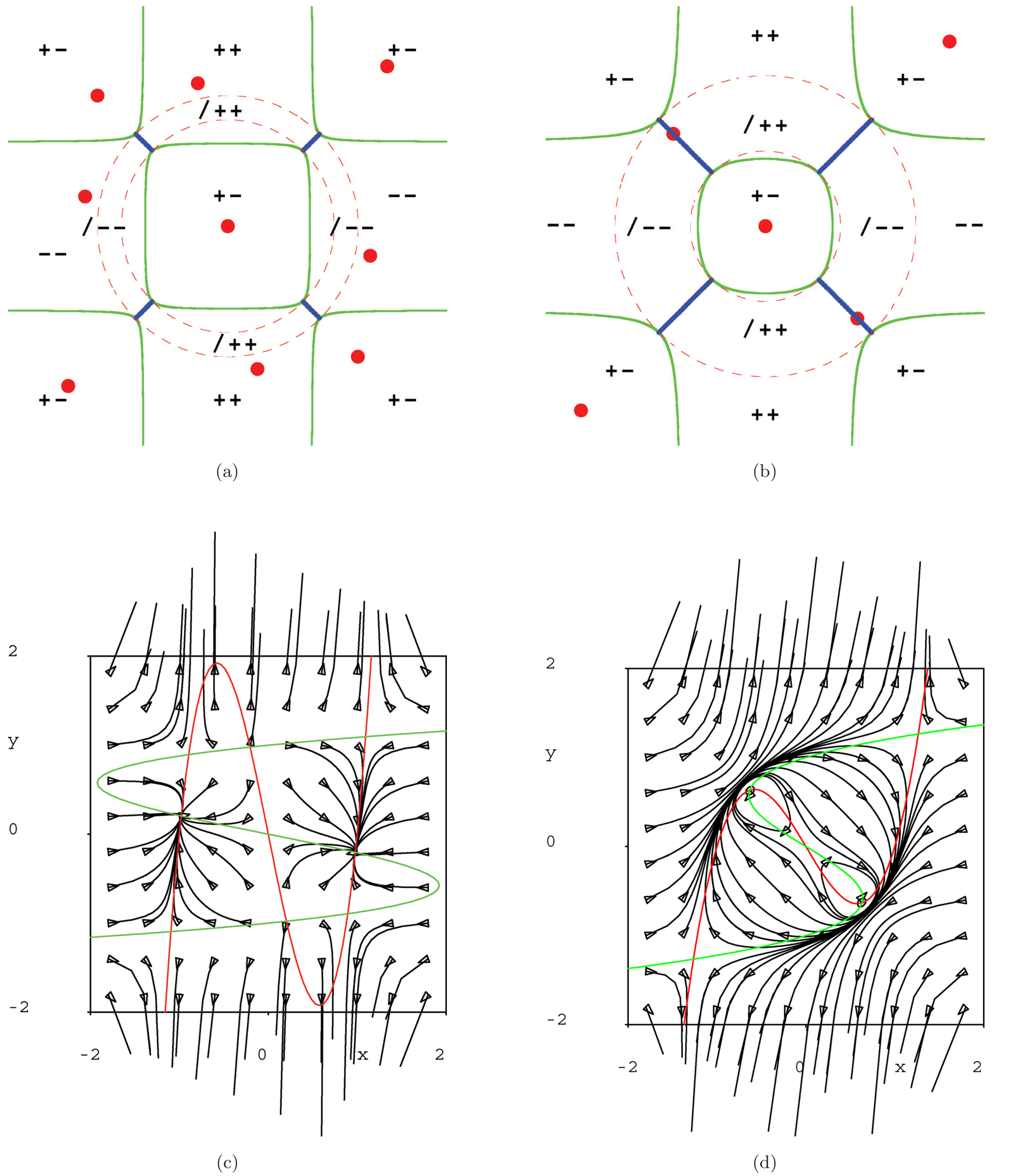


Fig. 9. System $\begin{array}{l}\dot{x} = x - x^3 + by \\ \dot{y} = -bx - y + y^3\end{array}$ (a and b) Frontiers F1 (green) and F2 (blue), boundary F4 (red, dotted), steady states (red points) and signs of the eigenvalues; (c and d) trajectories from evenly spaced initial states (black). The nullclines $\dot{x} = 0$ and $\dot{y} = 0$ are drawn in red and green, respectively. (a and c) Parameter $b = 0.2$; (b and d) Parameter b $= 0.6$. In (b), two steady states are located on frontier F2. This is why the real part of their (complex) eigenvalues is nil; one deals thus with centers, as illustrated by the trajectories in (d). Note also that the inner parts of boundary F4 (a circle) and frontier F1 (not a circle) are distinct. Within the narrow crescents between them, the eigenvalues are real.

states can be generated by a given logical structure. In previous publications, we have shown that the mere occurrence of multistationarity (as well as other features such as the possibility to display a chaotic behavior) is tightly dependent on the sign pattern of the circuits but extremely robust versus the detailed nature of the nonlinearities. In sharp contrast, for trivial algebraic reasons, the number of steady states is strongly dependent on the degrees of the nonlinearities. The maximal number of solutions (real or not) of the steady state equations is a simple function of the degree of these equations, at least in polynomial systems. The problem is of course: how many of them are real, and thus, how many of them are indeed steady states?

4.1. *Multistationarity or not?*

As regards the question of whether or not a system can have multiple steady states, a basic rule remains that at least one circuit be positive at least somewhere in phase space.[5] As mentioned above, this old conjecture has now been formally demonstrated in full generality [Soulé, 2003]. A more demanding constraint is due to M. Kaufman [Thomas & Kaufman, 2001]. Her conjecture states that in order to have multiple steady states, a system must comprise an ambiguous nucleus, or else two nuclei of opposite Eisenfeld signs.[6] Kaufman's conjecture is verified in practice, except for the somewhat unusual but quite interesting systems that we call "mirror systems" (Sec. 3.4). These systems display multistationarity. Yet, they may comprise a single nucleus that is variable but not ambiguous. For example, a two-nucleus whose sign patterns are "+−" and "−+" is negative everywhere and a two-nucleus whose sign patterns are "++" and "−−" is positive everywhere.

In view of the existence of such systems in which a single nucleus generates multistationarity in the absence of ambiguity, Kaufman's conjecture should be updated by simply substituting "variable" for "ambiguous".[7]

4.1.1. *The relation between the Kaufman conjecture and the occurrence of a frontier F1*

There is a simple relation between the Eisenfeld sign of a nucleus and its "signed product" in the characteristic equation; these signs are opposite whatever the number of variables. Thus, whenever a system comprises two or more nuclei **all of which display the same Eisenfeld sign everywhere in phase space**, all the terms of the determinant of the Jacobian matrix have the same sign (opposite to the Eisenfeld sign). Consequently, in such systems a_0, the term of degree 0 of the characteristic equation, is either positive everywhere or negative everywhere. In this situation there is no "green" frontier F1 and no partition according to the parity of the number of positive eigenvalues. In contrast, when the system comprises an ambiguous nucleus or two nuclei of opposite Eisenfeld signs, a_0 comprises a term of variable sign or two terms of opposite signs, and it is no more complied to have a constant sign everywhere in phase space. This allows for the presence of an F1 frontier, and thus for domains of opposite polarities.

Thus, if the presence of an F1 frontier were a necessary condition for multistationarity,

[5]Note that a positive circuit involving a single variable may be responsible for multiple steady state values of all the variables of the system, and also that the required nonlinearity does not necessarily have to be located on the positive circuit itself. This is the case, for example, in a variant of Rössler's system in which the nonlinearity is x^3. In this system the only positive circuit is a linear one-circuit, responsible for multistationarity (and also required for the chaotic dynamics).

[6]Note that whenever one of these constraints is satisfied, the basic requirement for the presence of a positive circuit is automatically fulfilled, since an ambiguous nucleus is necessarily positive somewhere in phase space, and two nuclei of opposite Eisenfeld signs comprise necessarily a positive circuit.

[7]Note that while the condition "either two nuclei of opposite Eisenfeld signs, or an ambiguous nucleus" does guarantee by itself the presence of a positive circuit, required anyway for multistationarity, the condition "either two nuclei of opposite Eisenfeld signs, or a **variable** nucleus" does not guarantee by itself the presence of a positive circuit $\Big($a variable nucleus such as $\begin{pmatrix} & -x \\ x & \end{pmatrix}$ has no positive circuit$\Big)$. However, in dimension two, in order to have such a mirror system one needs a nonlinearity in each of two differential equations, and one of them must be a product involving two variables, as in the system already described:

$$\begin{aligned} \dot{x} &= 1 - xy \\ \dot{y} &= x^2 - 1 \end{aligned}$$

whose Jacobian matrix is $\begin{pmatrix} -y & -x \\ 2x & 0 \end{pmatrix}$. This provides automatically an ambiguous one-circuit (here, $-y$ at the position a_{11}, and the positive circuit required for multistationarity is present for negative values of y).

Kaufman's conjecture would be a direct consequence of the relation between the Eisenfeld sign of a nucleus and its "signed product". However, as described in Secs. 3.5, multistationarity can take place in the absence of an F1 frontier, and besides, the example of mirror systems shows that multistationarity can be generated by a single nucleus that is variable, but not ambiguous.

4.2. *How many steady states?*

The number of solutions (real or not) of the steady state equations depends on the degree of the ODE's. The question "is more than one of these solutions real (in other words, is there multistationarity)" has been discussed at length in the preceding section, and found to depend critically on the logical structure (nuclei) of the systems. Now, we ask **how many** of these solutions are real, in other words, how many steady states are there?

Phase space can be partitioned into domains that are homogeneous as regards the signs of the eigenvalues (and thus, the nature of potential steady states) and of the slopes of the eigenvectors. As mentioned in Sec. 2.4, for a wide variety of systems, each domain contains at most one steady state, as if a domain was a niche for one, and no more than one, potential steady state. The impact of our counter-example is discussed in the same section.

As discussed in Sec. 3, phase space can also be partitioned more simply according to the sign patterns of the terms of the Jacobian matrix. More specifically, one splits the Jacobian matrix into its individual nuclei and analyzes their sign patterns and the number of domains (multiplicity) into which phase space can be partitioned according to these sign patterns. As far as we can tell, the multiplicity puts an upper limit to the number of steady states of the system. This tentative conclusion applies also to systems that have no variable nucleus. In this case, provided the system has two nuclei of opposite Eisenfeld signs, they have distinct sign patterns and can partition phase space according to the respective weights of the nuclei (see Sec. 3.4.4: "*Multistationarity generated by nonvariable nuclei*").

4.3. *A global view of phase space*

In the two preceding sections, we dealt mostly with the number of steady states. However, we feel that the main interest of the partition processes is elsewhere.

The quantitative process described in Sec. 2 can be limited to the use of frontiers F1, F2 (and F4 where appropriate). At this stage of the analysis, phase space is partitioned into domains that are perfectly homogeneous as regards the signs of the eigenvalues, and of their real part if they are complex. This provides us with the frame within which trajectories are wound, and the exact nature of any steady state that might be present in a domain is determined by the very fact of being located within this domain. If one proceeds to the next step of the partition process, steady states are now further classified according to the sense of rotation (for foci) or the orientation of their separatrices (for saddle points), thus giving a global, yet passably detailed idea of the organization of the trajectories.

The first approach has the merit of being rigorous, but it does not tell in an obvious way **why** phase space is partitioned as it is. This gap is filled by the second approach. The general strategy consists of first identifying the nuclei present in the Jacobian matrix, then analyzing how each of them would behave if it were alone, and finally compute how they can interact with each other. When none of the nuclei is variable (as in the example of Sec. 3.4.4), the nuclei compete or not depending on whether their Eisenfeld signs are opposite or not (cf. Kaufman's conjecture); and their competition, if any, results in a partition according to the respective weights of the nuclei. If, however, one or more nucleus is variable, it is convenient to start from a variable nucleus, identify its sign patterns and see how phase space can be partitioned according to these sign patterns. One can then consider the alternative situations in which either of the other nuclei would be alone, and see how its presence would modify the partition. Even where one has finally to return the first approach to gain a fully correct view, the fact of having begun in terms of the sign patterns usually permits to understand why phase space is partitioned as it is.

Finally, we would like to emphasize again the fact that the "frontier diagrams" can usually be represented in a restricted dimensionality, since only those variables that are involved in nonlinearities appear in the Jacobian matrix, and thus in the equations of the frontiers. An n-variable system in which only two variables are involved in nonlinearities gives frontier diagrams in two dimensions.

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Appendix
The "Astuce de Gaspard-Nicolis"

In their analysis of the deterministic chaos generated by the Rössler equations, Gaspard and Nicolis [1983] derived state diagrams in parameter space at the level of steady states. In particular, they established which relation between parameters would result in eigenvalues of the structure $(i\omega, -i\omega, \lambda)$ at steady states of this particular system. For that, instead of going back to the quite involved analytic expressions of the eigenvalues, they took an elegant shortcut; starting from the characteristic equation of the Rössler system at steady states, they replaced λ_1 and λ_2 by $i\omega$, wrote that the sums of real terms and complex terms are both 0, and proceeded to appropriate substitutions.

Here, the situation is different, as instead of working in parameter space with defined (steady) values of the variables, we work in phase space with predetermined values of the parameters. Also, even though much of our work deals with three-variable systems, we wish to generalize the approach as regards the number of variables.

Coming back to the characteristic equation of a two-variable system:

$$\lambda^2 + a_1\lambda + a_0 = 0,$$

we assume that its roots are purely imaginary and write:

$$(i\omega)^2 + a_1(i\omega) + a_0 = 0$$
$$-\omega^2 + a_1 i\omega + a_0 = 0$$
$$-\omega^2 + a_0 = 0 \to \omega^2 = a_0$$
$$a_1 i\omega = 0 \to a_1 = 0$$

Thus, in two variables, the equation of frontier F2 is $\mathbf{a_1 = 0}$, with the constraint that $\mathbf{a_0 > 0}$. In three variables, we have:

$$(i\omega)^3 + a_2(i\omega)^2 + a_1(i\omega) + a_0 = 0$$
$$-i\omega^3 - a_2\omega^2 + a_1 i\omega + a_0 = 0$$
$$-i\omega^3 + a_1 i\omega = 0 \to -\omega^2 + a_1 = 0 \tag{A.1}$$
$$-a_2\omega^2 + a_0 = 0 \tag{A.2}$$

Replacing in (A.2) ω by its value in (A.1), we get

$$a_0 - a_1 a_2 = 0, \quad \text{with the constraint } a_1 > 0$$

In four variables:

$$(i\omega)^4 + a_3(i\omega)^3 + a_2(i\omega)^2 + a_1(i\omega) + a_0 = 0$$
$$\omega^4 - a_3 i\omega^3 - a_2\omega^2 + a_1 i\omega + a_0 = 0$$
$$\omega^4 - a_2\omega^2 + a_0 = 0 \tag{A.3}$$

$$-a_3 i\omega^3 + a_1 i\omega = 0 \to \omega^2 = \frac{a_1}{a_3} \tag{A.4}$$

Replacing in (A.3) ω^2 by its value in (A.4), we get

$$\mathrm{F2} \equiv \left(\frac{a_1}{a_3}\right)^2 - a_2\left(\frac{a_1}{a_3}\right) + a_0 = 0,$$

with the constraint: $a_1/a_3 > 0$ ($a_3 \neq 0$)

The same procedure applies when one or more a_i coefficient is zero or for characteristic equations of higher order.

Glossary

Circuit: a set of nonzero terms a_{ij} of the Jacobian matrix whose i (row) and j (column) indices are in cyclic permutation defines a circuit, whose oriented edges (arrows) are the a_{ij} elements considered. A circuit is usually symbolized by the product of its elements, for example: $a_{12}a_{23}a_{31}$. A circuit is positive or negative depending on the sign of this product, this is, depending on whether it comprises an even or an odd number of negative elements.

Disjoint circuits: circuits that do not share any variable.

Union: the union of two or more disjoint circuits.

Nucleus: a circuit or a union that involves all the variables of the system.

Eisenfeld sign of a nucleus (or a circuit or a union): the sign of a nucleus is $(-1)^{(p+1)}$ in which p is the number of positive circuits in the nucleus (or union or circuit). In practice, the Eisenfeld sign is + iff the nucleus (or the union or the circuit) comprises an odd number of positive circuits.

Variable nucleus: a nucleus that can display more than one sign pattern according to the location in phase space.

Ambiguous nucleus: a nucleus whose (Eisenfeld) sign depends on the location in phase space.

Isolated nucleus: A system whose Jacobian matrix comprises only one nucleus and no other circuit. However, the matrix may contain off-circuit terms, and the ODE's may contain constant terms, which do not appear in the Jacobian matrix. These additional elements influence neither the eigenvalues nor our frontiers, but they affect the location, and possibly the number of the steady states.

Note added in proof: A Mathematica program for 2D frontiers, refined by P. Nardone, can be supplied (rthomas@dbm.ulb.ac.be)