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Global qualitative description of a class of nonlinear dynamical systems

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Abstract

In this paper we propose a methodology to derive a qualitative description of the behavior of a system from an incompletely known nonlinear dynamical model. The model is written as an algebraic structure with unknown parameters and/or functions. Under some hypotheses, we obtain a graph describing the possible transitions between regions, defined by the trends of the state variables and their relative positions. A qualitative simulation of the model can be compared with on-line data for fault detection purpose. We give the example of a nonlinear biological model (in dimension three) for the growth of cells in a bioreactor. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

The prediction and the analysis of the behavior of a dynamical system is a difficult task, which suffers from a lack of efficient tools. Indeed, it is well known that a nonlinear dynamical model can exhibit very complicated behavior [23], even in low dimensions. When the model is not completely known (some parameters or functions are not known), as it happens frequently for example in the biological field [1], the problem is even more complicated. Therefore the difficulty consists in describing the behavior, at least qualitatively, of this model with incomplete knowledge.

The dynamical description of such a qualitative model is one of the goals of the qualitative reasoning (QR) approach [20]. If the model is sufficiently known (i.e., with known parameter uncertainties), then the semi-quantitative methods can be used [2,20].

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In some cases, it is possible to mathematically analyze the algorithms of qualitative simulation [11]. For low dimensional systems, phase plane analysis can give some interesting hints on the transient behavior [24], and if the system is linear or piecewise linear the qualitative behavior can be approached [25]. A view of the structure of some class of systems can also give results on asymptotic properties of the system [17,18]. Some specific models or structures can be investigated more thoroughly [15,27,28].

In the sequel, we propose an approach that derives the qualitative transient behavior and the asymptotic behavior from a dynamical model defined only by sign properties. This method is suitable for a class of systems (loop structured systems with monotonous interactions) that find numerous applications in the biological field including gene regulation models [16], compartmental systems [21], cellular growth [8], and development of stage structured populations [9]. We emphasize nevertheless that the analysis can also be applied to other models, provided that there are enough zeros in the Jacobian matrix. Indeed, the proposed approach has been applied to a broad spectrum of models whose structure is not the ideal loop structure. In particular, competition between two species [3], trophic nets [5], structured populations [7] have been considered.

The analysis presented here is the continuation of a methodology proposed in [4]: from the study of the extradiagonal terms of the Jacobian matrix of the system, one can derive two graphs called transition graphs. The first determines the qualitative behavior of the velocity $\dot{x}$ and summarizes for almost any trajectory the possible successions in time of monotonous (increasing or decreasing) phases. The second one determines the qualitative behavior of $(x - x^\star)$ (where $x^\star$ is an equilibrium point), and predicts the possible transitions in time between qualitative regions of the space defined by the position of a point with respect to an equilibrium value.

In this paper we extend the qualitative description of the dynamics of loop structured systems, by relating the qualitative events corresponding to extrema to those corresponding to crossing of equilibrium values. We use the signs of the diagonal elements of the Jacobian matrix to show that qualitative features (tendencies of the state variables and positions toward the considered equilibrium) of any trajectory are restricted to a certain set. We propose a procedure to derive this set of possible qualitative features. This allows us to consider the domain Ω as partitioned by various regions delimited by the nullclines and the hyperplanes associated to an equilibrium $x^\star$. The transient behavior of the system can then be determined by a theorem giving the possible global behaviors, and represented into a graph describing the transients in terms of extrema and equilibrium crossings. We show also that the graph obtained can give results on the asymptotic properties of the system (stability of the equilibria, possibility of limit cycles, ...).

For the sake of simplicity, we suppose the system to be autonomous and without inputs. We could also consider the following controlled system:

$$\dot{x} = f\big(x, u(t)\big)$$

with the input $u(t)$ being constant on time intervals $]t_i, t_{i+1}[$. Of course, the whole analysis applies on each time interval. In [6], we have applied a similar methodology to a system forced by periodic inputs.

What are the main differences between our approach and the existing ones?

– we do not write a qualitative model or a qualitative differential equation, as in [2]: we consider a class of quantitative models, i.e., we write classical ordinary differential equations, where some parameters or some functions are not precisely defined, but belong to some class (for example, the parameter p_1 is positive, the function $\rho(x)$ is increasing); therefore we keep a global algebraic structure for the class of models;
– consequently, we keep the power of the mathematical tools for differential equations, because we can use the algebraic properties of the class of models;
– it is clear that the possible behaviors of a dynamical system in dimension greater than two are tremendously numerous; we are more interested by the validation of a sequence of experimental behaviors; a typical result would be that the sequence is compatible, or not, with the possible sequences generated by the model; this can be applied to the on-line fault detection, in order to detect a process failure;
– the method counters the problem of intractability in QR by exploiting mathematical constraints tailored to the class of equations;
– we examine also the transitions between regions, as in [11] and [24], but the regions we consider are more complicated: they are the intersection of sets in the space of state variables (corresponding to signs of deviations from a reference point) and (not rectilinear) sets in the space of velocities (corresponding to signs of velocities); we are able to eliminate some of these regions, because they are not compatible with the algebraic structure of the class of models;
– we do not use any approximations (such as linearization, or piecewise linear approximations ...) in our techniques. Of course, we have to do strong hypotheses on the class of models. These hypotheses can be smoothen (cf. the final remark).

Before entering technical details, we summarize our results. We have taken as a real life application the class of models classically used to represent growth of phytoplankton. The class of models is written:

$$(\Sigma) \quad \begin{cases} \dot{x}_1 = u(1 - x_1) - \rho(x_1)x_2, \\ \dot{x}_2 = (\mu(x_3) - u)x_2, \\ \dot{x}_3 = \rho(x_1) - \mu(x_3)x_3. \end{cases} \tag{1}$$

The functions ρ and μ represent the absorption rate and the growth rate (cf. Section 6 for details), and we keep them undefined, constraining them to be monotonic (increasing).

For this class of system the signs of the Jacobian matrix are ($\star$ represents either $+1$, -1 or 0):

$$\begin{pmatrix} -1 & -1 & 0 \\ 0 & \star & +1 \\ +1 & 0 & -1 \end{pmatrix}.$$

We remark that the interactions between variables are monotonous and the system has a loop structure: these are the two main hypotheses that we make.

The qualitative behavior is described by one of the two graphs in Figs. 8 and 9, depending on the initial conditions. The nodes represent a set of feasible qualitative states (determined by algebraic properties) defined by the sign of the position of the variables with respect to a reference point, and the sign of their velocities. If the initial qualitative state is known, we obtain a qualitative simulation by following the edges between the nodes. It is shown that, at most, one maximum, one minimum, one equilibrium crossing bottom-up and one top-down for each state variable are possible.

The paper is organized as follows: after some definitions (Section 2), we define the qualitative regions and compute the possible ones (Section 3); then we eliminate some "nongeneric" trajectories (Section 4), and give our main theorem describing the allowed transitions between regions (Section 5). The biological application is given in Section 6.

2. Definitions

Notations. The notations $x > 0$ for $x = {}^{t}(x_1, \dots, x_n) \in \mathbb{R}^n$ means that for all i, $x_i > 0$. For $y \in \mathbb{R}$ we consider the function "sign":

$$\operatorname{sign}(y) = \begin{cases} -1 & \text{if } y < 0, \\ 0 & \text{if } y = 0, \\ 1 & \text{if } y > 0. \end{cases}$$

For $x \in \mathbb{R}^n$, $\operatorname{sign}(x)$ is the vector with components $\operatorname{sign}(x_i)$. The matrix $\operatorname{diag}(x)$ is the diagonal matrix having $x \in \mathbb{R}^n$ on its main diagonal.

Let Ω be an open convex domain of $\mathbb{R}^n$ and f a C^1 mapping from Ω onto $\mathbb{R}^n$. We consider on Ω the autonomous differential system:

$$(\Sigma) \quad \dot{x} = f(x).$$

Definition 1. A system (Σ) has a loop structure if $f_i(x) = f_i(x_i, x_{i+1})$ $\forall i \in \{1, \dots, n\}$.

The velocity of each variable only depends on the variable itself and on the next one (the indexes are counted modulo n).

The Jacobian matrix of a loop structured system has therefore the following structure:

$$\begin{pmatrix} m_{1\,1}(x) & m_{1\,2}(x) & 0 & \dots & 0 \\ 0 & m_{2\,2}(x) & m_{2\,3}(x) & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & 0 \\ 0 & \dots & 0 & m_{n-1\,n-1}(x) & m_{n-1\,n}(x) \\ m_{n\,1}(x) & 0 & \dots & 0 & m_{n\,n}(x) \end{pmatrix}$$

where $m_{i\,j}(x) \stackrel{\text{def}}{=} \frac{\partial f_i}{\partial x_j}(x)$.

Definition 2. The system (Σ) has monotonous interactions on Ω if each partial derivative $\partial f_i / \partial x_j(x)$ for $i \neq j$ never cancels on Ω.

Thereby the off-diagonal terms of the Jacobian matrix are of fixed sign on Ω. The signs of the elements define what we call the structure of the system.

Example. In the following we will illustrate the definition and concepts that we introduce on the simple and intuitive example of the Lotka–Volterra [29] system describing the interaction between a population of preys (x_1) and a population of predators (x_2):

$$\begin{cases} \dot{x}_1 = ax_1 - bx_1x_2, \\ \dot{x}_2 = -cx_2 + dx_1x_2. \end{cases} \tag{2}$$

The parameters a, b, c and d are positive. As all the systems in dimension 2, system (2) has a loop structure. Its Jacobian matrix is the following:

$$\begin{pmatrix} a - bx_2 & -bx_1 \\ dx_2 & dx_1 - c \end{pmatrix}. \tag{3}$$

It is easy to verify that the variables of system (2) remain positive. We will then consider the domain $\Omega = \mathbb{R}_+^{\star 2}$. Therefore the off-diagonal terms of the Jacobian matrix (3) on $\mathbb{R}_+^{\star 2}$ are $m_{12}(x) = -bx_1$ and $m_{21}(x) = dx_2$, their signs are $t_{12}(x) = -1$ and $t_{21}(x) = +1$. △

We will consider the set $\mathcal{S}_n$ containing 2^n elements:

$$\mathcal{S}_n \stackrel{\text{def}}{=} \big\{\sigma = {}^{\text{t}}(\sigma_1, \dots, \sigma_n);\ \sigma_j \in \{-1, 1\}\big\}.$$

Thus $\mathcal{S}_n$ represents all the vectors of $\mathbb{R}^n$ whose components are either $+1$ or -1. We can impose an ordering on $\mathcal{S}_n$, such that σ^q is the qth element in the ordering. Conventionally, we will choose $\sigma^1 = {}^{\text{t}}(1, \dots, 1)$.

Example. For the above example, we will consider the four sign vectors σ^q of $\mathcal{S}_2$:

$$\sigma^1 = \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \quad \sigma^2 = \begin{pmatrix} -1 \\ 1 \end{pmatrix}, \quad \sigma^3 = \begin{pmatrix} -1 \\ -1 \end{pmatrix}, \quad \sigma^4 = \begin{pmatrix} 1 \\ -1 \end{pmatrix}. \qquad \triangle$$

Definition 3. For $x^\star \in \Omega$ the system with monotonous interactions (Σ) is diagonally $x^\star$-monotonous if for all j in $\{1, \dots, n\}$, for all q in $\{1, \dots, 2^n\}$, the sign of the partial derivative $\partial f_j / \partial x_j(x)$ is fixed on each domain:

$$W_{\sigma^q}(x^\star) \stackrel{\text{def}}{=} \big\{x \in \Omega;\ \operatorname{diag}\big(\sigma^q\big)(x - x^\star) > 0\big\}.$$

The domains $W_{\sigma^q}(x^\star)$ are called the orthants of the $x^\star$-deviation space or $x^\star$-orthants. These domains are delimited by the hyperplanes associated with $x^\star$. We denote $V_i(x^\star)$ the ith hyperplane associated with $x^\star$:

$$V_i(x^\star) \stackrel{\text{def}}{=} \big\{x \in \Omega;\ x_i = x_i^\star\big\}.$$

Example. Let us consider the equilibrium point of system (2):

$$x^\star = \begin{pmatrix} c/d \\ a/b \end{pmatrix}.$$

Fig. 1 presents the corresponding four regions of $W_{\sigma^q}(x^\star)$. These regions are separated by the two hyperplanes:

$$\begin{aligned} V_1(x^\star) &= \big\{x \in \mathbb{R}_+^{\star 2};\ x_1 = c/d\big\}, \\ V_2(x^\star) &= \big\{x \in \mathbb{R}_+^{\star 2};\ x_2 = a/b\big\}. \end{aligned}$$

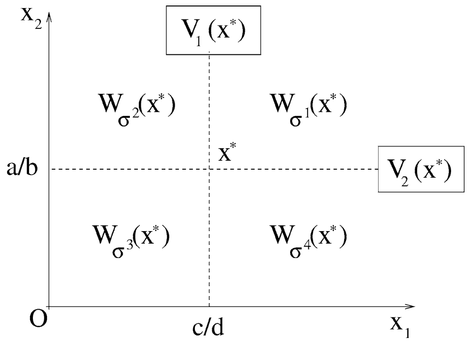

Fig. 1. The sets $V_i(x^\star)$ and $W_{\sigma^q}(x^\star)$ for the Lotka–Volterra example.

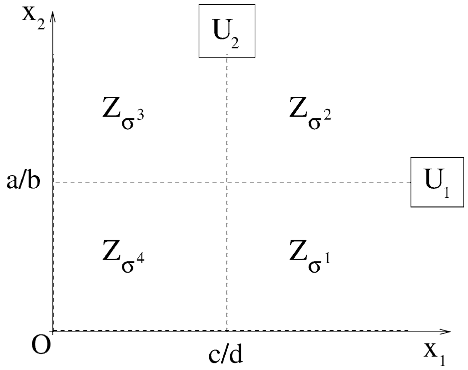

Fig. 2. The sets U_i and Z_{σ^q} for the Lotka–Volterra example.

The Lotka–Volterra system is diagonally $x^\star$-monotonous since the diagonal terms of its Jacobian matrix ($a - bx_2$ and $dx_1 - c$) are of fixed signs on each $W_{\sigma^q}(x^\star)$. △

In the same way, we define the orthants of the velocity space or z-orthants:

$$Z_{\sigma^p} \stackrel{\text{def}}{=} \{x \in \Omega;\ \operatorname{diag}(\sigma^p) f(x) > 0\}.$$

The z-orthants are delimited by the nullclines U_i:

$$U_i \stackrel{\text{def}}{=} \{x \in \Omega;\ f_i(x) = 0\}.$$

Example. Fig. 2 represents the nullclines U_i which are the borders between the 4 regions Z_{σ^p}. The two nullclines are:

$$U_1 = \{x \in \mathbb{R}_+^{\star 2};\ a - bx_2 = 0\},$$
$$U_2 = \{x \in \mathbb{R}_+^{\star 2};\ c - dx_1 = 0\}.$$

It is worth noting that in this particular case the nullclines U_i correspond to the $V_{i+1}(x^\star)$. Remark that the two nullclines corresponding respectively to $x_1 = 0$ and $x_2 = 0$ are not contained in the open set $\mathbb{R}_+^{\star 2}$. △

We consider also the following sets that are unions of sets previously defined:

- The union set of hyperplanes associated with $x^\star$: $V(x^\star) \stackrel{\text{def}}{=} \bigcup_{i=1}^{n} V_i(x^\star)$.
- The union set of nullclines: $U \stackrel{\text{def}}{=} \bigcup_{i=1}^{n} U_i$.

3. The set of possible qualitative events

In this section we will consider a monotonous (i.e., with monotonous interactions) loop structured system (Σ) and we will suppose that there exists an equilibrium point $x^\star \in \Omega$ for which (Σ) is diagonally $x^\star$-monotonous. We will then determine the set of orthants of the velocity space Z_{σ^p} compatible with a given orthant $W_{\sigma^q}(x^\star)$ of the $x^\star$-deviation space. In other words the question is to determine all the possible signs of $f(x)$ for x in a given $x^\star$-orthant, i.e., the following set of signs:

$$\mathcal{F}^q \stackrel{\text{def}}{=} \big\{\text{sign}\big(f(x)\big),\ x \in W_{\sigma^q}(x^\star) \setminus U\big\}. \tag{4}$$

In QSIM terminology [20], the goal of this section is to provide the constraints that determine the possible qualitative states of the system.

Example. This idea is illustrated in Fig. 3 where the sets $U_i(x^\star)$ and V_i are simultaneously represented. It is worth noting that, for each q, among the 4 *a priori* possible elements $\sigma^p \in \mathcal{S}_n$ only one is in $\mathcal{F}^q$: the sign of f is fixed in each set $W_{\sigma^q}(x^\star)$. From the analysis of Fig. 3, we have graphically:

$$\mathcal{F}^1 = \{\sigma^2\}, \quad \mathcal{F}^2 = \{\sigma^3\}, \quad \mathcal{F}^3 = \{\sigma^4\}, \quad \mathcal{F}^4 = \{\sigma^1\}. \qquad \triangle$$

First we will determine the elements of the set $\mathcal{F}^q$ which are obtained locally around equilibrium $x^\star$. Of course, the consideration of this linearized system can be not sufficient to give global information on the nonlinear system. In this case we will have to consider the original system.

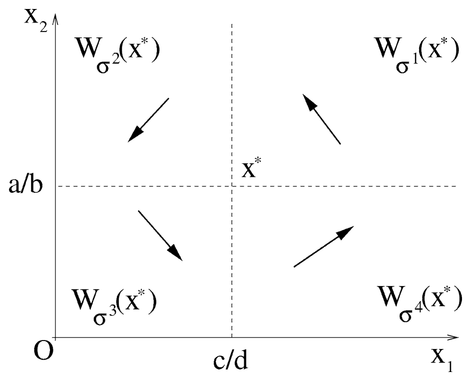

Fig. 3. The vector field in each domain $W_{\sigma^q}(x^\star)$.

3.1. Linear approach

As a first step, we will determine this set for the linearized of (Σ) around the point $x^\star$, which is:

$$\dot{\Delta x} = Df(x^\star)\,\Delta x, \tag{5}$$

where $Df(x)$ denotes the Jacobian matrix at point x, and $\Delta x \stackrel{\text{def}}{=} x - x^\star$. Note that $\operatorname{diag}(\sigma^q)\Delta x$ is a positive vector for $x \in W_{\sigma^q}(x^\star)$. Of course, as for the nonlinear case, we will exclude the nullclines of the linear system (linearized of a U_i).

We will consider the matrix $\mathcal{M}^q \stackrel{\text{def}}{=} Df(x^\star)\operatorname{diag}(\sigma^q)$, whose elements are denoted m_{kl}^q and whose signs are $s_{kl}^q = \operatorname{sign}(m_{kl}^q)$.

Example. At the point $x^\star$, the Jacobian matrix is:

$$Df(x^\star) = \begin{pmatrix} 0 & -bc/d \\ ad/b & 0 \end{pmatrix}.$$

We have then the signs of the four matrices $\mathcal{M}^q$:

$$\operatorname{sign}(\mathcal{M}^1) = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix}, \quad \operatorname{sign}(\mathcal{M}^2) = \begin{pmatrix} 0 & -1 \\ -1 & 0 \end{pmatrix},$$

$$\operatorname{sign}(\mathcal{M}^3) = \begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix}, \quad \operatorname{sign}(\mathcal{M}^4) = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}. \qquad \triangle$$

The problem of determining the possible signs for $Df(x^\star)\Delta x$ when $x \in W_{\sigma^q}(x^\star)$ is then equivalent to the determination of the set

$$\mathcal{L}^q \stackrel{\text{def}}{=} \{\operatorname{sign}(\mathcal{M}^q\,\xi),\ \xi > 0,\ (\xi + x^\star) \in \Omega\}. \tag{6}$$

Of course we have $\mathcal{L}^q \subset \mathcal{F}^q$: the sign patterns allowed close to $x^\star$ are included in the set of all possible sign patterns for the original nonlinear system.

We will determine the set $\mathcal{L}^q$, using two complementary lemma (remember that the s_{kl}^q take their values in $\{-1, 0, 1\}$).

Lemma 1. *Consider the linearized of a diagonally $x^\star$-monotonous loop structured system (Σ), at point $x^\star \in \Omega$. For a given σ^q, if there exists an index k such that one of the two conditions is satisfied*:

(1) $s_{k,k}^q = 0$,

(2) $s_{k,k}^q = s_{k,k+1}^q$,

then

$$\mathcal{L}^q = \{l^q = {}^{\mathrm{t}}(l_1^q, \ldots, l_n^q);\ l_j^q \in \{s_{j,j}^q \oplus s_{j,j+1}^q\}\}. \tag{7}$$

The table of the operator $\oplus$ ("generic qualitative sum") is given in Table 1.

Proof. Cf. Appendix A. □

Table 1
Table of rules for the (commutative) qualitative sum $\oplus$

$1 \oplus 1$	$\{1\}$
$-1 \oplus 1$	$\{-1, 1\}$
$-1 \oplus -1$	$\{-1\}$
$-1 \oplus 0$	$\{-1\}$
$1 \oplus 0$	$\{1\}$
$0 \oplus 0$	$\{0\}$

Lemma 1 states that, under the given conditions, all the signs *a priori* admissible are obtained. The following lemma covers the remaining cases, and it turns out that things are a bit more complicated:

Lemma 2. *Consider the linearized of a diagonally $x^\star$-monotonous loop structured system (Σ), with $x^\star \in \Omega$.*

If for every index k: $s^q_{k,k} = -s^q_{k,k+1}$, then

$$\mathcal{L}^q = \mathcal{S}_n - \mathcal{C}^q, \tag{8}$$

where the set $\mathcal{C}^q$ is obtained as follows from $D^q \stackrel{\text{def}}{=} {}^{\mathrm{t}}(s^q_{1,1}, s^q_{2,2}, \ldots, s^q_{n,n})$:

- *if* $\det[Df(x^\star)] < 0$,
$$\mathcal{C}^q = \left\{ \prod_{j=1}^{n} \sigma^q_j s^q_{j,j}\, D^q \right\},$$
- *if* $\det[Df(x^\star)] = 0$,
$$\mathcal{C}^q = \left\{ -\prod_{j=1}^{n} \sigma^q_j s^q_{j,j}\, D^q,\ \prod_{j=1}^{n} \sigma^q_j s^q_{j,j}\, D^q \right\},$$
- *if* $\det[Df(x^\star)] > 0$,
$$\mathcal{C}^q = \left\{ -\prod_{j=1}^{n} \sigma^q_j s^q_{j,j}\, D^q \right\}.$$

Proof. Cf. Appendix B. □

In this particular case one has to remove from the set of *a priori* admissible signs (which is $\mathcal{S}_n$ here) the particular element $\mathcal{C}^q$.

Example. Here we are in the case 1 of Lemma 1 where there exists an index k such that $s^q_{k,k} = 0$ ($k = 1$ or $k = 2$). Hence:

$$\mathcal{L}^1 = \{\sigma^2\}, \quad \mathcal{L}^2 = \{\sigma^3\}, \quad \mathcal{L}^3 = \{\sigma^4\}, \quad \mathcal{L}^4 = \{\sigma^1\}. \qquad \triangle$$

3.2. Global approach

In order to determine the set of possible signs for $f(x)$, we will rewrite the system (Σ) into another form. Using the fact that $\mathcal{L}^q \subset \mathcal{F}^q$, we will determine the various cases for which this inclusion is strict.

Lemma 3. *If $x^\star$ is an equilibrium point, the system (Σ) can be rewritten*

$$\dot{\Delta x} = A(x, x^\star).\Delta x.$$

If (Σ) has monotonous interactions, then matrix $A(x, x^\star)$ has the same off-diagonal signs as the Jacobian matrix $Df(x^\star)$ of (Σ). If moreover (Σ) is diagonally $x^\star$-monotonous, the diagonal terms of $A(x, x^\star)$ are of fixed signs in the various $W_{\sigma^q}(x^\star)$. The diagonal elements of $A(x, x^\star)$ have the same sign as those of $Df(x^\star)$ (except for the elements of $Df(x^\star)$ that are zero).

Proof. This is an application of the generalized first order Taylor formula [30]:

$$f(x) = f(x^\star) + \left[\int_0^1 Df\big(\alpha x + (1-\alpha)x^\star\big)\,\mathrm{d}\alpha\right](x - x^\star)$$

so that

$$A(x, x^\star) = \int_0^1 Df\big(\alpha x + (1-\alpha)x^\star\big)\,\mathrm{d}\alpha,$$

where the Jacobian matrix Df is of fixed sign on Ω. The results follow easily from the convexity of Ω [6]. □

Example. We have for the Lotka–Volterra system:

$$A(x, x^\star) = \begin{pmatrix} a - b/2(x_2 + x_2^\star) & -b/2(x_1 + x_1^\star) \\ d/2(x_2^\star + x_2) & d/2(x_1^\star + x_1) - c \end{pmatrix}. \tag{9}$$

△

We will use the same notations for $A(x, x^\star)$ as for $Df(x^\star)$, i.e., we will denote $\mathcal{M}^q(x) = A(x, x^\star)\mathrm{diag}(\sigma^q)$, and t^q_{kl} the (fixed) sign of its elements $m^q_{kl}(x)$.

We first consider the simple case where the diagonal elements of the Jacobian matrix are nonzero (and therefore matrix $A(x, x^\star)$ and $Df(x^\star)$ are of the same sign (cf. Lemma 3)). In this case the simple framework of Lemma 1 is satisfied:

Lemma 4. *Consider a diagonally $x^\star$-monotonous loop system (Σ) where $x^\star$ is an equilibrium point. If the following two conditions hold in $W_{\sigma^q}(x^\star)$:*

(1) $\forall k, t^q_{k,k} = s^q_{k,k} \neq 0$,

(2) $\exists k, t^q_{k,k} = t^q_{k,k+1}$,

then we have $\mathcal{F}^q = \mathcal{L}^q$.

Proof. It is straightforward that $\mathcal{F}^q \subset \{l^q; l_j^q \in \{t_{j,j}^q \oplus t_{j,j+1}^q\}\}$, for the same reasons as in the local case, when considering $z_k = m_{k,k}^q(x)\xi_k + m_{k,k+1}^q(x)\xi_{k+1}$ (see Appendix A for the notations).

But $\mathcal{L}^q = \{l^q; l_j^q \in \{s_{j,j}^q \oplus s_{j,j+1}^q\}t\} \subset \mathcal{F}^q$, and because the s^q equal the t^q we have $\mathcal{F}^q = \mathcal{L}^q$. $\square$

Remark 1. If $s_{k,k}^q = 0$ and $t_{k,k}^q \neq 0$, no conclusion can be drawn in the general case on the possible signs of the kth component z_k and one has to consider the analytical formulation of the model. Consider for example the following differential system defined on $\mathbb{R}^2$:

$$\begin{cases} \dot{x}_1 = x_2 - x_1^2, \\ \dot{x}_2 = x_1 - x_2^2. \end{cases} \tag{10}$$

For the equilibrium point $x^\star = {}^{\mathrm{t}}(0, 0)$, the Jacobian matrix has the following signs:

$$\begin{pmatrix} 0 & + \\ + & 0 \end{pmatrix} \tag{11}$$

so that for x in $\mathbb{R}_+^{\star 2}$, $\mathcal{L}^q = \{\sigma^1\}$. Nevertheless the matrix $A(x, x^\star)$ has the following signs:

$$\begin{pmatrix} - & + \\ + & - \end{pmatrix} \tag{12}$$

and it is clear from (10) that $\mathcal{F}^q = \mathcal{S}_2$.

Example. The above remark applies to the Lotka–Volterra system. Fig. 3 shows nevertheless that the nonlinear part does not provide more qualitative possibilities than the linear case: $\mathcal{F}^q = \mathcal{L}^q$. $\triangle$

We will now consider the other case corresponding to Lemma 2.

Lemma 5. *Consider a diagonally $x^\star$-monotonous loop system (Σ) where $x^\star$ is an equilibrium point. Suppose that for all k we have $t_{k,k}^q = -t_{k,k+1}^q$.*

If $\det(A(x, x^\star))$ *cancels and changes its sign on $W_{\sigma^q}(x^\star)$, then the set $\mathcal{F}^q$ covers all the possible orthants*:

$$\mathcal{F}^q = \mathcal{S}_n \tag{13}$$

if this is not the case, then

$$\mathcal{F}^q = \mathcal{S}_n - \mathcal{C}^q, \tag{14}$$

where the set $\mathcal{C}^q$ is obtained as follows from $D^q \stackrel{\text{def}}{=} {}^{\mathrm{t}}(t_{1,1}^q, t_{2,2}^q, \ldots, t_{n,n}^q)$:

- *if* $\det[A(x^\dagger, x^\star)] < 0$,
$$\mathcal{C}^q = \left\{ \prod_{j=1}^n \sigma_j^q s_{j,j}^q \, D^q \right\},$$
- *if* $\det[A(x^\dagger, x^\star)] > 0$,
$$\mathcal{C}^q = \left\{ -\prod_{j=1}^n \sigma_j^q s_{j,j}^q \, D^q \right\},$$

$x^\dagger \in W_{\sigma^q}(x^\star)$ being any point where the determinant of $A(x^\dagger, x^\star)$ does not cancel.

Proof. We have $\mathcal{L}^q \subset \mathcal{F}^q \subset \mathcal{S}_n$. From Lemma 8, we know that $\mathcal{L}^q$ corresponds to $\mathcal{S}_n$ except one or two elements. The question is to know if these elements can nevertheless be in $\mathcal{F}^q$. To answer this question, the same reasoning can be made as for the proof of Lemma 8, considering now $z_k = m^q_{k,k}(x)\xi_k + m^q_{k,k+1}(x)\xi_{k+1}$. This reasoning will give rise to a constraint on the sign of the determinant of $A(x, x^\star)$.

If the determinant can change its sign on $W_{\sigma^q}(x^\star)$, then D^q or $-D^q$ is possible on $W_{\sigma^q}(x^\star)$. $\square$

Remark. Let us remark that if there exists another equilibrium point $x^\dagger \in W_{\sigma^q}(x^\star)$, then $A(x^\dagger, x^\star)(x^\dagger - x^\star) = 0$ and therefore

$$\det\bigl(A(x^\dagger, x^\star)\bigr) = 0.$$

Then we are in the case of the above lemma.

3.3. Partition of the state space: possible regions

Definition 4. For $\sigma^p \in \mathcal{F}_q$ let us define the following open set:

$$\Omega_{\sigma^q\sigma^p}(x^\star) \stackrel{\text{def}}{=} W_{\sigma^q}(x^\star) \cap Z_{\sigma^p} = \bigl\{x \in W_{\sigma^q}(x^\star);\ \operatorname{diag}\bigl(\sigma^p\bigr) f(x) > 0\bigr\}. \tag{15}$$

Note that some $\Omega_{\sigma^q\sigma^p}(x^\star)$ are empty. The nonempty remaining $\Omega_{\sigma^q\sigma^p}(x^\star)$ represents therefore the qualitative situations allowed by the model (as described in the above section) and will be called the possible regions. Remark also that they do not intersect the nullclines U_i and the hyperplane $V_i(x^\star)$.

We can now consider the following partition of the state space Ω:

$$\Omega = \Biggl(\bigcup_{\sigma^q \in \mathcal{S}_n,\ \sigma^p \in \mathcal{F}^q} \Omega_{\sigma^q\sigma^p}(x^\star)\Biggr) \cup V(x^\star) \cup U. \tag{16}$$

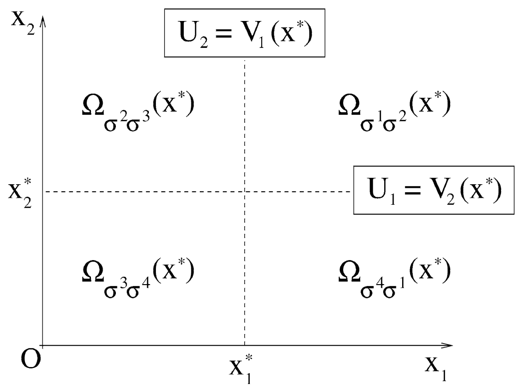

Fig. 4. Partition of the state space by the sets $\Omega_{\sigma^q\sigma^p}(x^\star)$.

Example. As a conclusion of the previous paragraph, we have seen that only the four sets $\Omega_{\sigma^1\sigma^2}(x^\star)$, $\Omega_{\sigma^2\sigma^3}(x^\star)$, $\Omega_{\sigma^3\sigma^4}(x^\star)$ and $\Omega_{\sigma^4\sigma^1}(x^\star)$ were not empty. The state space Ω is now partitioned according to Fig. 4. △

4. The restricted phase space

We remove here from Ω some manifolds for which trajectories may have undesirable behaviors (with respect to our goals): we show that this set of trajectories is of measure zero, under some technical assumptions. The final phase space will be named $\widetilde{\Omega}$. The technical details that guarantee that the removed trajectories are of zero measure (and therefore will not be observed) are presented in Appendix C.

Now we are able to define the open set $\widetilde{\Omega}$, which is Ω minus these sets of measure zero (in finite number) from the three properties presented in Appendix C (Properties C.2–C.4). In the particular case (let us call it case E) where the two surfaces U_i and $V_{i-1}(x^*)$ coincide on an open set, we do not remove the corresponding set. From now on, everything will take place in this restricted space $\widetilde{\Omega}$. For a possible region $\Omega_{\sigma^q\sigma^p}(x^\star)$ (see Section 3), we define the nonempty set:

$$\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star) \stackrel{\text{def}}{=} \Omega_{\sigma^q\sigma^p}(x^\star) \cap \widetilde{\Omega}$$

and the neighbors in $\widetilde{\Omega}$: two regions of the phase space are neighbors if they differ only by one sign (of a deviation or a velocity). It is to be remarked that we have suppressed (by restricting Ω) the possibility of going from one region $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ to another if they differ by more than one sign (except in the last case E which is a bit degenerate, but will occur in the example of Section 6).

Definition 5. Two domains $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star)$ and $\widetilde{\Omega}_{\sigma^{q_2}\sigma^{p_2}}(x^\star)$ are called:

- strict U-neighbors if $\sigma^{q_1} = \sigma^{q_2}$, and there exists a unique $k \in \{1, \dots, n\}$ such that $\sigma_k^{p_1} = -\sigma_k^{p_2}$;
- strict V-neighbors if $\sigma^{p_1} = \sigma^{p_2}$, and there exists a unique $k \in \{1, \dots, n\}$ such that $\sigma_k^{q_1} = -\sigma_k^{q_2}$.

Definition 6. In the case E, we say that $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star)$ and $\widetilde{\Omega}_{\sigma^{q_2}\sigma^{p_2}}(x^\star)$ are strict UV-neighbors if for all $i \neq k$, $\sigma_i^{p_1} = \sigma_i^{p_2}$, $\sigma_{i+1}^{q_1} = \sigma_{i+1}^{q_2}$ and $\sigma_k^{p_1} = -\sigma_k^{p_2}$, $\sigma_{k+1}^{q_1} = -\sigma_{k+1}^{q_2}$.

Example. In dimension 2 none of the trajectories must be removed, therefore $\widetilde{\Omega} = \Omega$. For the Lotka–Volterra system, the equilibrium hyperplanes $V_i(x^\star)$ are included in the nullclines U_{i+1} (we are in case E) and therefore the sets $\widetilde{\Omega}_{\sigma^i\sigma^{i+1}}(x^\star)$ and $\widetilde{\Omega}_{\sigma^{i+1}\sigma^{i+2}}(x^\star)$ are strict UV-neighbors. △

5. Transition between the domains $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$

We can now consider the restricted space $\widetilde{\Omega}$ partitioned in open domains $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$. We will then show that the transition between these domains obey some rules determined by the extradiagonal terms of the Jacobian matrix.

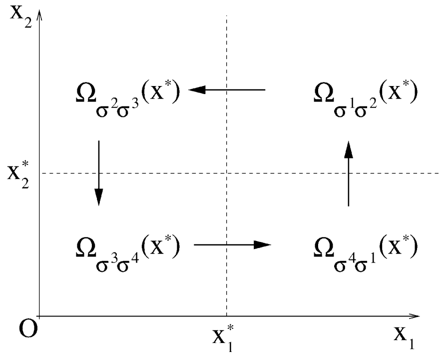

Fig. 5. Transitions between the sets $\Omega_{\sigma^q\sigma^p}(x^\star)$.

5.1. Transition theorem

Theorem 1 (Transitions between regions). *Consider a loop system* (Σ) *with monotonous interactions and an equilibrium point* $x^\star$. *Suppose that* $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star)$ *and* $\widetilde{\Omega}_{\sigma^{q_2}\sigma^{p_2}}(x^\star)$ *are two strict neighbors. We recall that* $t_{k,k+1}$ *is the sign of the element* $(k, k+1)$ *of the Jacobian matrix.*

- *Crossing of a* U_k:
  Assume they are strict U (*or* UV)*-neighbors. If* $t_{k,k+1}\sigma_{k+1}^{p_1} = \sigma_k^{p_1}$ (*respectively* $-\sigma_k^{p_1}$), *then the crossing of* U_k *is possible only from* $\widetilde{\Omega}_{\sigma^{q_2}\sigma^{p_2}}(x^\star)$ *to* $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star)$ (*respectively* $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star)$ *to* $\widetilde{\Omega}_{\sigma^{q_2}\sigma^{p_2}}(x^\star)$), *and it corresponds to a minimum* (*respectively a maximum*) *of variable* x_k.
- *Crossing of a* V_i:
  Assume they are strict V (*or* UV)*-neighbors. If* $t_{k,k+1}\sigma_{k+1}^{q_1} = \sigma_k^{q_1}$ (*respectively* $-\sigma_k^{q_1}$), *then the crossing of* $V_k(x^\star)$ *is possible only from* $\widetilde{\Omega}_{\sigma^{q_2}\sigma^{p_2}}(x^\star)$ *to* $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star)$ (*respectively* $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star)$ *to* $\widetilde{\Omega}_{\sigma^{q_2}\sigma^{p_2}}(x^\star)$), *and it corresponds for* x_k *to a crossing bottom-up* (*respectively top-down*) *of its equilibrium* $x_k^\star$.

We say that $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star)$ (*respectively* $\widetilde{\Omega}_{\sigma^{q_2}\sigma^{p_2}}(x^\star)$) *is accessible from* $\widetilde{\Omega}_{\sigma^{q_2}\sigma^{p_2}}(x^\star)$ (*respectively* $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star)$).

The proofs of these theorems are very similar and can be founded in [3,4].

Example. Fig. 5 illustrates this theorem by showing the flow on the boundaries between two neighbors. In dimension 2 these transitions could have been obtained from a more traditional phase plane analysis. △

5.2. Barriers in the state space

Lemma 6. *Suppose there exists two* C^1 *mappings*

$$\Phi : x \in \Omega \to \Phi(x) \in \mathbb{R}, \qquad \psi : u \in \mathbb{R} \to \psi(u) \in \mathbb{R},$$

verifying:

$$D\Phi(x).f(x) = \psi\big(\Phi(x)\big)$$

then $\mathcal{R} \stackrel{\text{def}}{=} \{x \in \Omega;\ \psi(\Phi(x)) = 0\}$ *separates* Ω *into positively invariant regions,*

$$\mathcal{R}^- \stackrel{\text{def}}{=} \big\{x \in \Omega;\ \psi\big(\Phi(x)\big) < 0\big\} \quad \textit{and} \quad \mathcal{R}^+ \stackrel{\text{def}}{=} \big\{x \in \Omega;\ \psi\big(\Phi(x)\big) > 0\big\}.$$

Proof. If we set $u = \Phi(x)$, u satisfies the first order scalar differential equation $\dot{u} = \psi(u)$. The zeros of ψ separate the space into invariant regions where ψ is always positive or negative. □

Corollary 1. *If there exists a region of the state space* $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ *such that*: $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star) \cap \mathcal{R}^- = \emptyset$ *(respectively* $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star) \cap \mathcal{R}^+ = \emptyset$*), then any trajectory initiated in* $\mathcal{R}^-$ *(respectively in* $\mathcal{R}^+$*) will never reach the region* $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$*.*

Corollary 2. *Any trajectory initiated in a region* $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star) \subset \mathcal{R}^+$ *(respectively* $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star) \subset \mathcal{R}^-$*), will never reach the regions* $\widetilde{\Omega}_{\sigma^{q_2}\sigma^{p_2}}(x^\star) \subset \mathcal{R}^-$ *(respectively* $\widetilde{\Omega}_{\sigma^{q_2}\sigma^{p_2}}(x^\star) \subset \mathcal{R}^+$*).*

Remarks.
- Such a property is quite frequent, for example in biotechnological models, where u is linked to mass conservation, and ψ is linear [1].
- Because u verifies a scalar differential equation, the nonempty limit sets are the equilibria; property P thus holds (cf. Appendix C).

5.3. Main theorem of behavior

The following theorem describes the behavior of the trajectories of a differential system (Σ) with monotonous interactions, loop structured and diagonally-monotonous: the domain Ω, restricted to $\widetilde{\Omega}$ (cf. Section 4) is partitioned into the possible regions $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star)$ (Section 3); the possible transition rules between these regions (cf. Section 5) are given by Theorem 1.

Theorem 2 (Global qualitative behavior). *Every trajectory of* (Σ) *in a domain* $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ *either*:
- *stays in* $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ *and goes to infinity*;
- *stays in* $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$*, and goes towards an equilibrium* $x^\dagger$ *in the closure of* $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$;
- *goes to one of the strict neighbors* $\widetilde{\Omega}_{\sigma^{q'}\sigma^{p'}}(x^\star)$ *that are accessible.*

Proof. Indeed, if a trajectory remains in a possible $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ (Section 3), then the $\dot{x}_k$ are of fixed sign, therefore the x_k are monotonous. If they are bounded, they have to converge towards an equilibrium in the closure of $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ or to go towards an accessible neighbor (Section 5). Moreover, this neighbor must be a strict neighbor, because we have removed the trajectories going to nonstrict neighbors (Section 4). □

Remark 2. Note that the trajectories cannot become unbounded in a domain $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ where for all i, $\sigma_i^q = -\sigma_i^p$, because that would mean that the state variables are decreasing above their equilibrium, or increasing under their equilibrium. If the state variables are positive (as often in biological modeling), a necessary condition for unboundedness in $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ is that there exists i for which $\sigma_i^q = \sigma_i^p = 1$.

Remark 3. The equilibrium $x^\star$ can be reached from a domain $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ if and only if $\sigma_k^p = -\sigma_k^q$ for all k. If this condition is not fulfilled for some k, then variable x_k is decreasing under its equilibrium $x_k^\star$, or increasing above its equilibrium and can therefore not converge.

Remark 4. A local linear study can also give interesting information on the possibility of convergence in a given region [4].

5.4. Graphical representation

We will represent each possible region $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ by a two column matrix of signs: the first column stands for σ^q, and the second for σ^p. For example, the region $\{x \in \Omega;\ x_1 > x_1^\star,\ x_2 < x_2^\star,\ x_3 > x_3^\star,\ \dot{x}_1 < 0,\ \dot{x}_2 < 0,\ \dot{x}_3 > 0\}$ is represented by the matrix:

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

A possible transition between two regions is represented by an oriented arrow between these regions, as determined by the conclusions of Theorem 1. A letter on the arrow will indicate if the variable x_k admits a minimum (m_k), a maximum (M_k), if it crosses its equilibrium $x_k^\star$ top-down (t_k) or bottom-up (T_k). The set of all $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ related by the arrows reflecting the transition rules of Theorem 1 is called the basic mixed transition graph. The nodes for which it is possible to converge to equilibrium (cf. Remark 3) will be called equilibrium nodes.

Our main theorem has now a "graphical version" (cf. the detailed example below and Figs. 8 and 9). For the sake of simplicity, we will restrict ourselves to the case where all the trajectories are bounded. We obtain then (cf. Figs. 8 and 9):

Theorem 3 (Graphical version of the global qualitative theorem). *On each nonequilibrium node, the trajectories follow an arrow of the graph and go towards an accessible node. On each equilibrium node, the trajectories either stay in the node and converge to equilibrium, or go towards an accessible node.*

Example. Now the qualitative behavior of the prey-predator system can be represented by a transition graph (Fig. 6). Fig. 5 illustrates this theorem by showing the flow on the boundaries between two neighbors. △

5.5. Asymptotic behavior

Some theorems (admitting a simple interpretation in terms of the graph) on the behavior of loop structured systems with monotonous interactions have already been given [4]. We

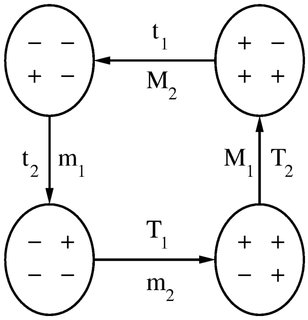

Fig. 6. Transition graph for the Lotka–Volterra system. Each node of the graph represents a qualitative feature: the first column deals with the sign of the deviation from the equilibrium point, and the second column represents the trend of the variable. m_i (respectively M_i) stands for a minimum (respectively a maximum) of x_i, and t_i (respectively T_k) represents a crossing of its equilibrium value top-down (respectively bottom-up).

will just give the following lemma, derived from considerations of both deviation from a reference point and trends of the variables.

Lemma 7. *If, in the transition graph of a system Σ, there is no cycle containing an extremum of variable x_k, then for almost every trajectories, x_k either goes towards an equilibrium in the closure of Ω or to infinity.*

Corollary 3. *If there is no cycle in the transition graph of a system Σ, almost all the trajectories go towards an equilibrium in the closure of Ω or diverge.*

In other words, it means that there is no periodic or recurrent behavior, nor chaos or other complex behavior.

6. Application: qualitative behavior of a general class of cell growth models

6.1. The class of models

To illustrate the qualitative analysis of loop structured systems we will consider a nontrivial application: the growth of phytoplankton in the oceans. We will consider a class of models used in oceanography to estimate the amount of carbon uptaken by the phytoplankton during the photosynthesis process. These models describe the behavior of phytoplanktonic biomass (x_2) growing on a substrate (x_1).

In the laboratory, the algal growth process in a continuous reactor (chemostat), for dimensionless variables (for a nonzero nutrient supply) can be described by the following system:

$$(\Sigma_{PGM}) \quad \begin{cases} \dot{x}_1 = 1 - x_1 - \rho(x_1)x_2, \\ \dot{x}_2 = (\mu(x_3) - 1)x_2, \\ \dot{x}_3 = \rho(x_1) - \mu(x_3)x_3. \end{cases} \tag{17}$$

The variable x_3 is the cell quota, i.e., the quantity of intracellular nutrient per biomass unit. The functions ρ and μ respectively represent the absorption rate of the substrate and the growth rate.

The validation of this class of models by comparison with experimental data is given in [6]. For more mathematical details on the models in the chemostat see [26].

Among the models (Σ_{PGM}), the Droop model [8,12] is largely used in the biological field. For this particular model we have:

$$\rho(x_1) = a_1 \frac{x_1}{a_2 + x_1}; \qquad \mu(x_3) = a_3\left(1 - \frac{a_4}{x_3}\right).$$

The functions used for ρ and μ are only conjectures and are not justified by a proper validation for transient conditions. In the following we keep a more general framework and we do only qualitative hypotheses, so that the analysis can be applied to any reasonable ρ and μ.

Hypotheses. Some hypotheses, corroborated by the experiments, are generally made by the biologists in order to represent growth of phytoplankton [22]: in the considered physical domain, $\Omega = \{x \in \mathbb{R}_+^{\star 3};\, x_1 > 0, x_2 > 0, x_3 > 0\}$:

(H1) The absorption rate ρ is a nonnegative bounded function of x_1. It is strictly increasing and verifies $\rho(0) = 0$.

(H2) The growth rate μ is a nonnegative strictly increasing function of x_3.

(H3) An equilibrium exists in the open domain Ω.

The class of models (Σ_{PGM}) verifying hypothesis (H1)–(H2)–(H3) is called the class of Phytoplanktonic Growth Models (PGMs). It can easily be verified that the Droop model is in this class.

6.2. The PGMs: a nontrivial loop structured class of systems with monotonous interactions

Property 1. *The PGMs are loop structured models with monotonous interactions in Ω.*

Proof. The Jacobian matrix has the following signs on Ω:

$$\begin{pmatrix} -1 & -1 & 0 \\ 0 & t_{22}(x) & +1 \\ +1 & 0 & -1 \end{pmatrix} \tag{18}$$

with

$$t_{22}(x) = \operatorname{sign}(\dot{x}_2) = \operatorname{sign}\bigl(\mu(x_3) - 1\bigr). \qquad \square \tag{19}$$

Property 2. *The PGMs have two equilibria*:

- $x^\star \in \Omega$:

$$x_3^\star = \mu^{-1}(1); \qquad x_1^\star = \rho^{-1}\bigl(\mu^{-1}(1)\bigr); \qquad x_2^\star = \frac{1 - \rho^{-1}(\mu^{-1}(1))}{\mu^{-1}(1)}.$$

- x^b, *an unstable equilibrium on the boundary of* Ω:

$$x_2^b = 0; \qquad x_1^b = 1; \qquad x_3^b \textit{ unique solution of: } \mu\big(x_3^b\big)x_3^b = \rho\big(x_1^b\big).$$

Proof. In accordance with hypothesis (H3), we have $x^\star \in \Omega$, i.e., $x_2^\star > 0$. Hypotheses (H1) and (H2) ensure the uniqueness of this equilibrium, because the applications μ^{-1} and $\rho^{-1} \circ \mu^{-1}$ are strictly increasing. Moreover, it is straightforward from a local study that x^b is unstable if $x_2^\star > 0$.

We will then consider the three hyperplanes $V_i(x^\star) = \{x \in \Omega;\ x = x_i^\star\}$ which separate the space Ω into eight regions $W_{\sigma^j}(x^\star)$. □

Property 3. *The PGMs are diagonally $x^\star$-monotonous in the domain Ω.*

Proof. It can be noticed that $t_{22}(x) = \mathrm{sign}(x_3 - x_3^\star)$, therefore in each domain $W_{\sigma^q}(x^\star)$, $t_{22}(x) = \sigma_3^q$ is fixed. We therefore have $\mathrm{sign}(\dot{x}_2) = \mathrm{sign}(x_3 - x_3^\star) = \sigma_3^q$.

We are therefore in the case E of Property C.4 (with $V_3(x^\star) \subset U_2$), it means that simultaneously when x_2 reaches an extremum, x_3 crosses its equilibrium $x_3^\star$. □

Property 4 (Mass conservation). *If $u = \Phi(x)$ denotes the total nutrient concentration in the chemostat*:

$$u \stackrel{\text{def}}{=} x_1 + x_2 x_3 \tag{20}$$

u satisfies the following differential equation:

$$\dot{u} = 1 - u. \tag{21}$$

Property 5. *The trajectories of the PGMs are bounded in the positively invariant domain Ω.*

Proof. The proof of Property 4 is straightforward from system (17). To show that Ω is positively invariant one has to consider the field on the boundaries:

- From (H1), for every x on the face $x_1 = 0$ we have: $\dot{x}_1 = 1 > 0$.
- For every x on the face $x_2 = 0$ it holds: $\dot{x}_2 = 0$.
- For every x on the face $x_3 = 0$: $\dot{x}_3 \geqslant 0$.

Moreover, to prove the boundedness of the trajectories, we first use Property 4 to show that u is bounded, i.e., x_1 and the product $x_2 x_3$ are bounded.

To show that x_3 is bounded, we consider a real a large enough to ensure that the strictly increasing function $\mu(a)a$ becomes larger than the upper bound of ρ (cf. (H1)). It follows that the field on every hyperplane $x_3 = b$, where $b \geqslant a$, verifies: $\dot{x}_3 < 0$.

The product $x_2 x_3$ is bounded, so that x_2 is also bounded (cf. [4] for details). □

In the sequel, we will remove the set of trajectories initiated from the manifolds presented in Table 2. Note that for a loop structured system with monotonous interaction in dimension 3, it is impossible to cross simultaneously two sets U_i (see [4]). The same proof shows that it is also impossible to cross simultaneously two sets $V_3(x^\star)$. As a consequence, the following results hold on the restricted set $\widetilde{\Omega}$:

$$\widetilde{\Omega} = \Omega \setminus \big\{U_1 \cap V_3(x^\star), U_3 \cap V_2(x^\star)\big\}.$$

Table 2
Table of the set of initial conditions for which the trajectories are removed

Manifold	Equations
$U_1 \cap V_3(x^\star)$	$1 - x_1 - \rho(x_1)x_2 = 0$ $x_3 = x_3^\star$
$U_3 \cap V_2(x^\star)$	$\rho(x_1) = \mu(x_3)x_3$ $x_2 = x_2^\star$

6.3. Study of the transition graphs

6.3.1. The possible qualitative situations

To obtain the set of possible domains allowed by the class of models (Σ_{PGM}), we can now apply results of Lemmas 4 and 5 for the 8 orthants $W_{\sigma^q}(x^\star)$. Note however that the Jacobian matrix (18) at the equilibrium point has a zero on its diagonal ($s_{22} = 0$), therefore (see Remark 1) the possible signs for $\dot{x}_2$ have to be determined directly from the system (Σ_{PGM}). The analysis follows here straightforward from Property 3: for $x \in W_{\sigma^q}(x^\star)$, $\operatorname{sign}(\dot{x}_2) = \sigma_3^q$.

The set of possible qualitative domains $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ now follows from the results of Section 3.2 after the computation of the sign of the 8 matrices $\mathcal{M}^q$ as shown in Table 3. We can remark that none of these matrices presents the case treated in Lemma 5.

Property 6. *There exist* 18 *possible qualitative regions* $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ *for the class of PGMs.*

These qualitative situations are listed in Table 3. Remark that *a priori* we have $2^6 = 64$ possible situations. The consideration of this set of possible domains therefore constitutes a first filter to test the structure of the model. If a qualitative event not belonging to this set can be experimentally observed, it means that the system cannot rely on the supposed structure.

6.3.2. The basic mixed transition graph

To go further into the description of the qualitative behavior of the model, we can now construct the mixed transition graph by applying Theorem 1 to all the strict neighbors $\widetilde{\Omega}_{\sigma^{q_1}\sigma^{p_1}}(x^\star)$ and $\widetilde{\Omega}_{\sigma^{q_2}\sigma^{p_2}}(x^\star)$ belonging to the set of feasible regions. It can be noticed that $V_3(x^\star) \subset U_2$, and then from Property C.4 (case E defined in Appendix C), there exists UV-neighbors.

Finally we obtain the mixed transition graph (Fig. 7) associated with the PGM (Σ_{PGM}). This graph summarizes the possible succession of extrema or equilibrium crossings from an initial qualitative situation.

It is noteworthy that the construction of this graph relies only on the sign of the Jacobian matrix (the peculiar case of Lemma 5 does not appear here), and not on the precise formulation of the model.

Table 3
For each σ^q, the matrices $\mathcal{M}^q$ and the sets $\mathcal{F}^q$ associated to the Droop model are represented (note that $\operatorname{sign}(\dot{x}_2) = \sigma_3^q$). The graphical representation of the feasible domains $\widetilde{\Omega}_{\sigma^q\sigma^p}(x^\star)$ is illustrated by a sign matrix: the first column contains the sign of the deviation from equilibrium $x^\star$, the second column the sign of the trend of the variables. The $\star$ means either $+1$ or -1

σ^q	$\begin{pmatrix}-1\\+1\\+1\end{pmatrix}$	$\begin{pmatrix}-1\\-1\\+1\end{pmatrix}$	$\begin{pmatrix}+1\\-1\\+1\end{pmatrix}$	$\begin{pmatrix}+1\\+1\\+1\end{pmatrix}$	$\begin{pmatrix}-1\\+1\\-1\end{pmatrix}$	$\begin{pmatrix}-1\\-1\\-1\end{pmatrix}$	$\begin{pmatrix}+1\\-1\\-1\end{pmatrix}$	$\begin{pmatrix}+1\\+1\\-1\end{pmatrix}$
M^q	$\begin{pmatrix}+1&-1&0\\0&0&+1\\-1&0&-1\end{pmatrix}$	$\begin{pmatrix}+1&+1&0\\0&0&+1\\-1&0&-1\end{pmatrix}$	$\begin{pmatrix}-1&+1&0\\0&0&+1\\+1&0&-1\end{pmatrix}$	$\begin{pmatrix}-1&-1&0\\0&0&+1\\+1&0&-1\end{pmatrix}$	$\begin{pmatrix}+1&-1&0\\0&0&-1\\-1&0&+1\end{pmatrix}$	$\begin{pmatrix}+1&+1&0\\0&0&-1\\-1&0&+1\end{pmatrix}$	$\begin{pmatrix}-1&+1&0\\0&0&-1\\+1&0&+1\end{pmatrix}$	$\begin{pmatrix}-1&-1&0\\0&0&-1\\+1&0&+1\end{pmatrix}$
F^q	$\begin{pmatrix}\star\\+1\\-1\end{pmatrix}$	$\begin{pmatrix}+1\\+1\\-1\end{pmatrix}$	$\begin{pmatrix}\star\\+1\\\star\end{pmatrix}$	$\begin{pmatrix}-1\\+1\\\star\end{pmatrix}$	$\begin{pmatrix}\star\\-1\\\star\end{pmatrix}$	$\begin{pmatrix}+1\\-1\\\star\end{pmatrix}$	$\begin{pmatrix}\star\\-1\\+1\end{pmatrix}$	$\begin{pmatrix}-1\\-1\\+1\end{pmatrix}$
Graphical representa–tion of the $\Omega_{\sigma^q\sigma^p}(x^*)$	$\begin{pmatrix}-&-\\+&+\\+&-\end{pmatrix}$ $\begin{pmatrix}-&+\\+&+\\+&-\end{pmatrix}$	$\begin{pmatrix}-&+\\-&+\\+&-\end{pmatrix}$	$\begin{pmatrix}+&+\\-&+\\+&-\end{pmatrix}$ $\begin{pmatrix}+&-\\-&+\\+&-\end{pmatrix}$ $\begin{pmatrix}+&+\\-&+\\+&+\end{pmatrix}$ $\begin{pmatrix}+&-\\-&+\\+&+\end{pmatrix}$	$\begin{pmatrix}+&-\\+&+\\+&+\end{pmatrix}$ $\begin{pmatrix}+&-\\+&+\\+&-\end{pmatrix}$	$\begin{pmatrix}-&-\\+&-\\-&+\end{pmatrix}$ $\begin{pmatrix}-&+\\+&-\\-&+\end{pmatrix}$ $\begin{pmatrix}-&-\\+&-\\-&-\end{pmatrix}$ $\begin{pmatrix}-&+\\+&-\\-&-\end{pmatrix}$	$\begin{pmatrix}-&+\\-&-\\-&+\end{pmatrix}$ $\begin{pmatrix}-&+\\-&-\\-&-\end{pmatrix}$	$\begin{pmatrix}+&+\\-&-\\-&+\end{pmatrix}$ $\begin{pmatrix}+&-\\-&-\\-&+\end{pmatrix}$	$\begin{pmatrix}+&-\\+&-\\-&+\end{pmatrix}$

6.3.3. Simplification of the basic mixed transition graph

The basic mixed transition graph can be simplified by considering the result of Lemma 6.

Property 7.

Depending on initial conditions some regions of Ω are unreachable:

- *if* $u(0) < 1$ *then the regions* $\begin{pmatrix}+&\star\\+&\star\\+&\star\end{pmatrix}$ *and the regions* $\begin{pmatrix}\star&-\\\star&-\\\star&-\end{pmatrix}$ *are unreachable*;
- *if* $u(0) > 1$ *then the regions* $\begin{pmatrix}-&\star\\-&\star\\-&\star\end{pmatrix}$ *and the regions* $\begin{pmatrix}\star&+\\\star&+\\\star&+\end{pmatrix}$ *are unreachable.*

The sign $\star$ means that it can be either $+$ or $-$.

Proof. Consider the application $\phi : x \to \phi(x) = u = x_1 + x_2x_3$. From Property 4 we have that $D\Phi(x).f(x) = 1 - \Phi(x)$.

Lemma 6 therefore says that the surface $x_1 + x_2x_3 = 1$ separates the space into 2 unconnected regions $\mathcal{R}^+ = \{x \in \Omega;\, x_1 + x_2x_3 > 1\}$ and $\mathcal{R}^- = \{x \in \Omega;\, x_1 + x_2x_3 < 1\}$.

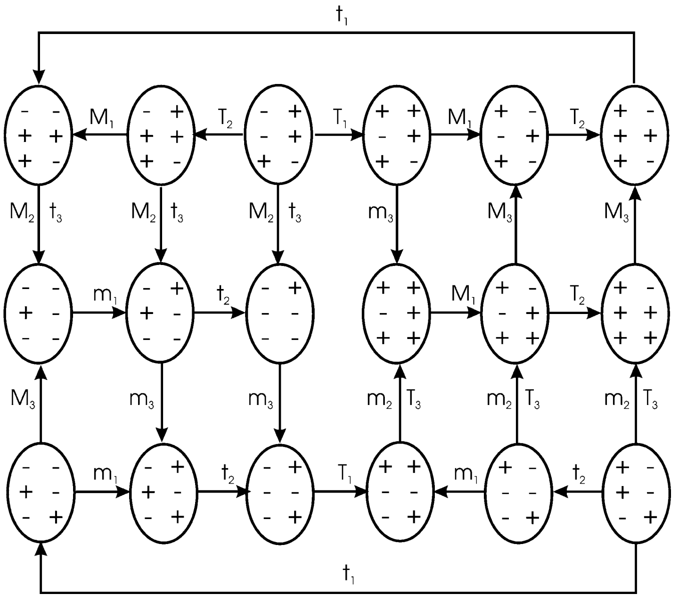

Fig. 7. Basic mixed transition graph. M_i (respectively m_i) denotes a maximum (respectively a minimum) for the variable x_i. T_i (respectively t_i) denotes a crossing of its equilibrium value bottom up (respectively top down) for the variable x_i.

Indeed, the regions $\left(\begin{smallmatrix} + & \star \\ + & \star \\ + & \star \end{smallmatrix}\right)$ are belonging to $\mathcal{R}^+$: if $\forall i,\ x_i > x_i^*$ then $x_1 + x_2x_3 - 1 > x_1^* + x_2^*x_3^* - 1 = 0$.

In the same way, the regions $\left(\begin{smallmatrix} \star & - \\ \star & - \\ \star & - \end{smallmatrix}\right)$ are belonging to $\mathcal{R}^+$: if $\forall i\, \dot{x}_i < 0$ then $\dot{u} = \dot{x}_1 + \dot{x}_2x_3 + x_2\dot{x}_3 < 0$, and from (21) $u - 1 = -\dot{u} > 0$. □

The proof is symmetrical for the regions contained in $\mathcal{R}^-$.

Lemma 8. *Almost every trajectory converges towards the equilibrium $x^\star$.*

Proof. If, depending on initial conditions, we remove the unreachable regions (see Lemma 7), then the cycle in graph of Fig. 7 disappears. Applying Lemma 7, we conclude that almost every trajectory either goes towards an equilibrium in the closure of Ω or to infinity. As these trajectories are bounded (Property 5), the only possibility is to go towards the unique stable equilibrium $x^* \in \Omega$ (the equilibrium on the boundary of Ω is unstable (Property 2)). In fact this equilibrium is globally stable (cf. [3]). □

Property 8. *In the considered domain, if $u(0) < 1$ (respectively $u(0) > 1$), the region $\left(\begin{smallmatrix} - & - \\ + & + \\ + & - \end{smallmatrix}\right)$ (respectively $\left(\begin{smallmatrix} + & + \\ - & - \\ - & + \end{smallmatrix}\right)$) is unreachable.*

Proof. From Lemma 8, in the domain Ω the PGMs have a unique, globally stable, equilibrium. In the case $u(0) < 1$, the qualitative situations mentioned in Property 7 disappear from the mixed transition graph. It can then be noticed that in this graph, two

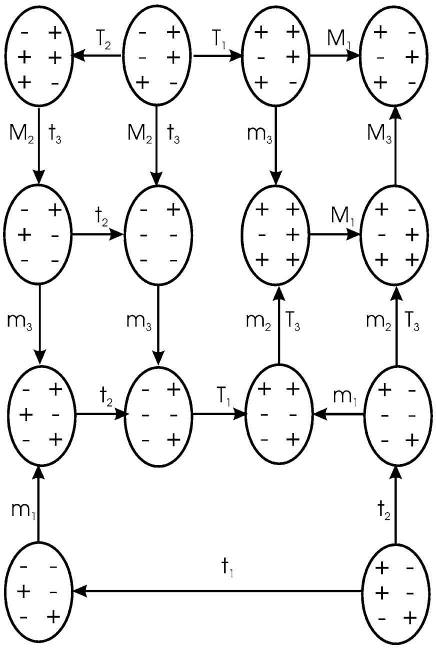

Fig. 8. Simplified mixed transition graph for $u(0) < 1$.

domains are positively invariant. Among these, the region $\left(\begin{smallmatrix} - & - \\ + & + \\ + & - \end{smallmatrix}\right)$ does not satisfy the conditions of Lemma 3; it can therefore not lead to the nontrivial equilibrium in the interior of Ω. $\square$

Properties 8 and 7 can now be used to simplify the mixed transition graph: depending on the initial condition for u, it can be reduced to two graphs (Figs. 9 and 8).

6.4. Summary of the qualitative behavior of the PGMs

Now we have the complete description of the transient behavior of the PGMs given by the two graphs (Figs. 8 and 9). From the analysis of these graphs, the following property holds:

Property 9. *The trajectories of the PGMs admit for each of the state variables at the most one minimum, one maximum, one bottom-up equilibrium crossing, and one top-down equilibrium crossing.*

More precisely, if we apply the necessary conditions to reach an equilibrium that have been given in Remark 3, then the equilibrium can be reached only from the following domains:

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

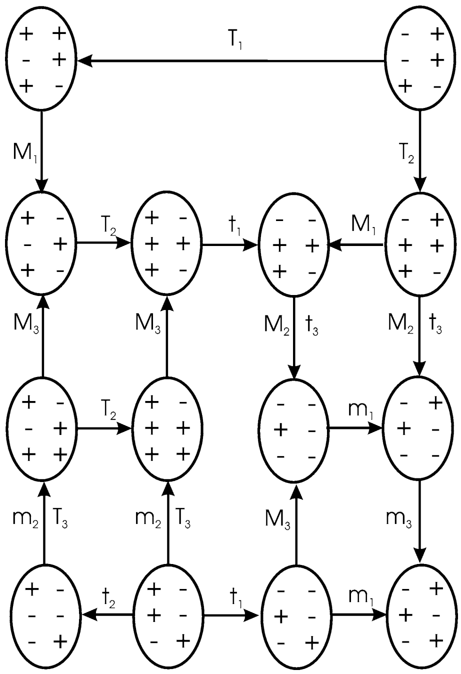

Fig. 9. Simplified mixed transition graph for $u(0) > 1$.

If we use more quantitative information about the model (if this information is assumed to be reliable enough), then the final domain from which equilibrium is reached can be precisely determined from a local study [4].

Note that the path to reach the final domain (i.e., the domain from which equilibrium is attained) is not unique. For some qualitative initial conditions, several paths can be followed. The actual path followed by a trajectory could be specified if we use more quantitative information on the model.

7. Application to fault detection or model validation

The proposed methodology can be used as the basis for a qualitative comparison between the actual behavior of a real system (obtained by the measurements) and the theoretical behavior contained in the transition graph. Note that the value of the equilibrium $x^\star$ is obtained from the experimental data.

The transition graph can thus serve to validate the structure of the model from the experimental observations of the temporal scenarios of qualitative transitions. Indeed, if the observed sequences of qualitative events do not correspond to a sequence contained in the graph, it points out a conflict between the model and the data.

Once the model has been validated, the comparison can be performed in real time to provide a fault detection tool. Here the measured qualitative transitions can be compared to the transition graph [13,14]. If the transitions does not correspond to any path of the graph, this means that the system behaves differently than the model which represents the standard working mode. A mismatch between the observations and the graph will then correspond to a qualitative change (failure) in the process.

For both objectives (validation or fault detection), the transition graph will give us a set of criteria to diagnosis the origin of the fault (in the model for validation or in the system for fault detection). The diagnosis will be deduced from the localization of the constraint contained in the graph that is violated. The reason for the conflict between the actual and the theoretical behavior can be of two main types (we assume here that only one fault happens at the same time):

- A transition for x_i does not respect the direction of an arrow. This means that the modeling of variable x_i is not consistent with the data. More precisely, it can result from a sign change in the extradiagonal term of the Jacobian matrix associated with this arrow (x_i): the interaction between x_i and x_{i+1} has changed. It can mean, e.g., that variable x_{i+1} is inhibiting x_i instead of enhancing it. It can also be the consequence of an interaction with another variable [7]. In this case, the loop structure is affected. A more detailed discussion of the use of the transition graphs to validate the structure of a model can be found in [4].
- An observed transition occurs towards a qualitative feature that does not exist in the graph. If the transition was compatible with the transition rules imposed by the extra-diagonal terms of the Jacobian matrix, this may indicate that the topology of the space as induced by the partition of the $\Omega_{\sigma^q\sigma^p}(x^\star)$ is wrong. This points out a change in the sign of a diagonal term of the Jacobian matrix. It remains to find out which variable is affected by such a change. This can be done by exploring the effect of a change in each of the signs of the diagonal elements on the possible regions $\Omega_{\sigma^q\sigma^p}$.

The noise in the data can make the comparison—even on a qualitative basis—difficult. We have proved in [6] that the constraints dealing with the trends of the variables still hold after removing noise with a simple moving average filter. This approach has been applied to analyze the response of a population of phytoplankton to a periodic input of nutrient [6]. Although is was based only on the simple diagnosis obtained with trends of the state, it revealed a qualitative change in the behavior of the population for high frequency of nutrient supply: it seems that the cell division synchronizes on the nitrogen source.

Finally, the presented methodology can also be used in the context of model identification with an inverse problem perspective. How to find the model structure from a set of data? If there is a large number of available experiments which contain a sufficient amount of qualitative information (qualitative transitions), one can report these observations in a graph and observe the transitions that are always performed in the same way, and the qualitative domains that are reached. This should lead to the identification of an experimental transition graph. The next step will then consist in finding a model structure that generates the observed graph. If the system has a loop structure (or a structure close to this ideal case), this will be straightforward from the proposed analysis. The important point is that this analysis is independent of the parameter values, as a consequence it only provides the model structure. Quantitative modeling steps are then necessary to get a complete modeling.

This can find important applications, e.g., in the field of genomics, where data on the temporal evolution of gene expression is available. This method could help to clarify the interactions between the genes in the framework of the so called reverse engineering approach [10].

Of course, a computer implementation of the method will be necessary when the system complexity will be too high. The complexity can both be due to an increase in the state variables, or to additional interactions between the variables which make the model differ from the loop structure. The implementation of the methods will then consist in automatically generating a graph from the model structure and supporting the comparison between the graph and the available experiments. Finally, for the reverse engineering purpose, it will allow to automatically identify a graph and generate possible model structures from the data analysis.

8. Conclusion

For the studied class of systems we have obtained a global qualitative description of the transient behavior as well as of the asymptotic behavior. We want to stress the fact that these results are global (i.e., they do not result from local linear considerations). It is noteworthy that the qualitative behavior of these systems results only from the signs of the Jacobian (if we exclude the particular case for which the sign of the determinant must be known). Therefore, this analysis is particularly well adapted to the biological context, where the only sure *a priori* knowledge of the process is the sign of the interactions between variables.

In the analysis we have removed the trajectories for which two qualitative events appear at the same time (except for the case E defined in Appendix C). These trajectories are of zero measure and thus they will never be observed in the real system. This simplifies the analysis and differs from most of the qualitative studies where these special cases are not removed.

Finally, let us stress that the hypothesis on the loop structure of the model is quite strong. In fact, our methodology can be applied (for a system with monotonous interactions) even if the system has not exactly a loop structure [3,5,7]. It is easy to see that some transitions between two regions will be permitted in the two directions, allowing a more complex behavior. However, for the transitions being allowed in only one way, we are still able to compare the model and the data. Moreover, it can happen that some regions are still invariant (for example, if the Jacobian matrix has positive signs outside the main diagonal, the region with positive signs is invariant). In this case it is possible to derive interesting results for such more general systems. Much work remains to be done in this direction.

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Appendix A. Proof of Lemma 1

If $\sigma \in \mathcal{L}^q$, then there exists $\xi \in \Omega^{+\star}$ such that: $\sigma = \operatorname{sign}(\mathcal{M}^q \xi)$. If we denote $z = \mathcal{M}^q \xi$, we have:

$$z_j = m^q_{j,j}\xi_j + m^q_{j,j+1}\xi_{j+1}.$$

While ξ_j and ξ_{j+1} are positive, the possible signs σ_j for z_j are in the set $\{s^q_{j,j}, s^q_{j,j+1}\}$ (remember that the sets $z_j = 0$ have been removed).

It follows that $\mathcal{L}^q \subset \mathcal{A}^q$, where $\mathcal{A}^q$ is the set of *a priori* possible signs:

$$\mathcal{A}^q \stackrel{\text{def}}{=} \left\{l^q; l^q_j \in \left\{s^q_{j,j} \oplus s^q_{j,j+1}\right\}\right\}.$$

We will show that all the elements of $\mathcal{A}^q$ have a preimage by $\operatorname{sign}(\mathcal{M}^q\xi)$.

If condition (1) or (2) is fulfilled for k, $\operatorname{sign}(z_k) = s^q_{k,k+1} = s^q_{k,k+1} \oplus s^q_{k,k}$. We will fix ξ_k to an arbitrary positive value.

If we consider $z_{k-1} = m^q_{k-1,k-1}\xi_{k-1} + m^q_{k-1,k}\xi_k$, there exists two possibilities:

(i) One of the two conditions is fulfilled: $s^q_{k-1,k-1} = 0$ or $s^q_{k-1,k-1} = s^q_{k-1,k}$. For any $\xi_{k-1} > 0$, we have:

$$\operatorname{sign}(z_{k-1}) = s^q_{k-1,k} = s^q_{k-1,k} \oplus s^q_{k-1,k-1}.$$

(ii) In the other case, $s^q_{k-1,k-1} = -s^q_{k-1,k}$, and we choose:

$$\xi_{k-1} = -\varepsilon \frac{m^q_{k-1,k}}{m^q_{k-1,k-1}}\xi_k \quad \text{with } \varepsilon \in \left\{\frac{1}{2}, \frac{3}{2}\right\}.$$

Then $z_{k-1} = (1-\varepsilon)m^q_{k-1,k}\xi_k$. If we take $\varepsilon = \frac{1}{2}$ we have $\operatorname{sign}(z_{k-1}) = s^q_{k-1,k}$, if we take $\varepsilon = \frac{3}{2}$ we obtain $\operatorname{sign}(z_{k-1}) = -s^q_{k-1,k} = s^q_{k-1,k-1}$.

The same reasoning can be applied to $z_{k-2}, z_{k-3}, \ldots, z_1, z_n, \ldots, z_{k+1}$, hence $\xi_{k-2}, \ldots, \xi_{k+1}$ can be chosen such that the result follows.

Appendix B. Proof of Lemma 2

We will show that among the set $\mathcal{A}^q = \mathcal{S}_n$ corresponding to the set of *a priori* possible signs for z (see argue given in the proof of Lemma 1), one single element is not in $\mathcal{I}m\{\operatorname{sign}(\mathcal{M}^q\xi)\}$.

(1) We will first assume that $D^q = {}^{\mathrm{t}}(s^q_{1,1}, s^q_{2,2}, \ldots, s^q_{n,n}) = \sigma^1$, i.e., for every k: $s^q_{k,k} = 1$. The other cases are symmetrical and they will be detailed at the end of the proof.

We first show that it is possible to find $\xi \in \Omega^{+\star}$ such that there exists k for which $z_k z_{k+1} < 0$ (z_k is defined in Appendix A). For the sake of clarity, we will first find such ξ ensuring $z_1 < 0$ and $z_n > 0$. For a fixed $\xi_2 > 0$, it is possible to find $\xi_3 > 0$ such that z_2 is of desired sign (cf. proof of preceding lemma). In the same way $\xi_4 > 0$ to $\xi_n > 0$ can be chosen to obtain an arbitrary (and fixed) sign for z_3 to z_{n-1}.

Now we have to choose a $\xi_1 > 0$ such that $z_1 < 0$ and $z_n > 0$. This is possible if we take:

$$\xi_1 < \min\left(-\frac{m^q_{1,2}}{m^q_{1,1}}\xi_2, -\frac{m^q_{n,n}}{m^q_{n,1}}\xi_n\right).$$

This result can clearly be extended to all the situations where there exists an index k such that $z_k z_{k+1} < 0$.

Let us prove that to find ξ such that z is positive, it is necessary to have $\det(\mathcal{M}^q) > 0$. Indeed, to have $z_p > 0$ for every p, there must exists a positive ξ such that the following conditions hold for every p:

$$\xi_{p+1} < \frac{m^q_{p,p}}{-m^q_{p,p+1}}\xi_p \tag{B.1}$$

it follows that:

$$\xi_n < \prod_{j=1}^{n-1} \frac{m^q_{j,j}}{-m^q_{j,j+1}}\xi_1 < \prod_{j=1}^{n} \frac{m^q_{j,j}}{-m^q_{j,j+1}}\xi_n. \tag{B.2}$$

Condition (B.2) imposes:

$$\lambda^q \stackrel{\text{def}}{=} \prod_{j=1}^{n} m^q_{j,j} + (-1)^{n+1} \prod_{j=1}^{n} m^q_{j,j+1} > 0. \tag{B.3}$$

It is noteworthy that, for the loop structured system (Σ), λ^q is nothing but the determinant of matrix $\mathcal{M}^q$:

$$\lambda^q = \det\bigl(\mathcal{M}^q\bigr) = \det\bigl(Df(x^\star)\bigr) \prod_{j=1}^{n} \sigma^q_j.$$

Reciprocally, let us show that if λ^q is positive, it is possible to find a positive ξ such that z is positive.

First, we choose an arbitrary ξ_1. We compute ξ_2 to ξ_n by the following induction formulae for $1 \leqslant p \leqslant n-1$:

$$\xi_{p+1} = \varepsilon \frac{m^q_{p,p}}{-m^q_{p,p+1}}\xi_p \tag{B.4}$$

with:

$$\varepsilon \stackrel{\text{def}}{=} \left(\prod_{j=1}^{n} \frac{-m^q_{j,j+1}}{m^q_{j,j}}\right)^{1/n},$$

while λ^q is positive, it implies $\varepsilon < 1$, and thus condition (B.1) holds for $1 \leqslant p \leqslant n-1$ implying $z_p > 0$. We now have to prove that this gives also $z_n > 0$. If we compute ξ_n we get:

$$\xi_n = \varepsilon^{n-1} \prod_{j=1}^{n-1} \frac{m^q_{j,j}}{-m^q_{j,j+1}}\xi_1$$

and then

$$\frac{m^q_{n,n}}{-m^q_{n,1}}\xi_n = \frac{\xi_1}{\varepsilon} > \xi_1$$

and therefore $z_n > 0$.

We have then found a positive ξ ensuring $z > 0$.

(2) The proof has now to be achieved by symmetry for a general D^q: the problematic cases correspond to $\mathrm{sign}(z) = D^q$. The problem is then equivalent to find $\xi > 0$ such that $\mathrm{sign}(\mathrm{diag}(D^q)z) = \sigma^1$, it consists therefore in considering matrix $\mathrm{diag}(D^q)\mathcal{M}^q$, whose determinant is $\det[Df(x^\star)]\prod_{j=1}^n \sigma^q_j s^q_{j,j}$.

Appendix C. The set of trajectories that can be removed from Ω

C.1. Motivations

We want to remove a set of trajectories initiated from some $(n-2)$-dimensional manifold M, typically the intersection between two isoclines. It is clear that, in finite time, such a set of trajectories is $(n-1)$-dimensional, but the limit set (in positive time) can be, in some (rather intricate) case, of nonempty interior. This case is undesirable, because if we remove this set, it can be that we remove the trajectories that are experimentally observed. We will therefore suppose that the differential system is such that the limit set of any manifold M of dimension $(n-2)$ is of measure zero (property P). There are many cases where such a property is verified, and many ways to check it. Let us list some sufficient conditions:

- if the system admits a Lyapunov function for the equilibrium x^*, then it is globally stable. The limit set of any manifold is x^* itself;
- if the system admits a function $V(x)$ decreasing along the trajectories, then the Lasalle's theorem [19] gives us that the limit sets of any bounded trajectories are contained into the set $\{x; \frac{\mathrm{d}}{\mathrm{d}t}V(x) = 0\}$. If this set is of measure zero (if it is contained in an $(n-1)$-manifold for example), then the property is verified;
- if there exists an application $h : \mathbb{R}^n \to \mathbb{R}^p$, with $p < n$ of class C^1, regular at every point, such that

  $$\frac{\mathrm{d}}{\mathrm{d}t}h(x) = g\big(h(x)\big)$$

  along the trajectories of the system Σ, and if the limit sets of the new differential system in $\mathbb{R}^p$

  $$\big(\Sigma^1\big) \quad \big\{\dot{h} = g(h)$$

  verify property P, then the system Σ verifies property P (indeed, because of the regularity of h, the preimage of a set of measure zero is of measure zero). For example, if we know that the limit sets of Σ^1 are a finite number of points (it is the case in dimension one), then the property stands for Σ^1, and therefore for Σ.

  For example, for biological, ecological or chemical models, it is often the case that some mass balance or mass conservation relation holds, giving easily a scalar differential equation; Property P is therefore verified.

Now we examine each set of initial conditions of the trajectories we want to remove. It is roughly the intersection between the $V_i(x^*)$ and U_j, because there are two signs that change simultaneously. In all the following, *we suppose that the above property P holds*.

C.2. Remaining in a nullcline or in an equilibrium hyperplane

We recall first that it is not possible to stay on a nullcline.

Property C.1. *A trajectory cannot remain in a $V_i(x^*)$ set or in a U_i set, unless it is the equilibrium point $x^\star$.*

The proof is in [4]. The idea is to write that the manifold is invariant, and to differentiate enough times to obtain the result.

C.3. Intersecting nullclines and equilibrium hyperplanes

Property C.2. *For loop structured systems with monotonous interactions, the set of trajectories intersecting simultaneously two (different) $V_i(x^*)$ is of measure zero.*

Indeed, the intersection of the two hyperplanes $x_i = x_i^*$ and $x_j = x_j^*$ is a $(n-2)$-dimensional plane. Because of property P, the trajectories are of measure zero.

Property C.3. *The set of trajectories intersecting simultaneously two (different) U_i is of measure zero.*

The intersection is defined by $f_i(x) = f_j(x) = 0$. The derivative of this application is of full rank two because the interactions are monotonous. Therefore the preimage of 0 is a manifold of dimension $(n-2)$, and property P applies.

Property C.4. *For loop structured systems with monotonous interactions, the set of trajectories intersecting simultaneously U_i and $V_j(x^*)$ $(j \neq i-1)$ is of measure zero. The set of trajectories intersecting simultaneously U_i and $V_{i-1}(x^*)$ is of measure zero except in the case (let us call it case E) where the system (Σ) is such that the two surfaces coincide on an open set.*

In the first case, the intersection is defined by $x_i = x_i^*$, $f_j(x_j, x_{j+1}) = 0$, and the same reasoning as above applies. If $j = i-1$, then the intersection $\{x \in \Omega,\ f_{i-1}(x_{i-1}, x_i^\star) = 0\}$ can be of dimension $(n-1)$: take for example the Lotka–Volterra system, the equilibrium hyperplane $V_i(x^\star)$ is included in the nullcline U_{i+1}.

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