

BASIC METHODS OF THE DEVELOPMENT AND ANALYSIS OF MATHEMATICAL MODELS

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Contents

1	Discrete time models	2
1.1	Making a model	2
1.2	The state space; basic vocabulary	3
1.3	Linear discrete equations	3
1.3.1	The homogeneous constant linear system	4
1.3.2	The homogeneous time-varying linear system	5
1.3.3	The non-homogeneous linear system	5
1.3.4	The controlled linear system	5
1.3.5	Conversion to matrix linear form	5
1.4	Basic study of the homogeneous constant linear system	6
1.5	Basic study of the non homogeneous constant linear system	7
1.6	Basic study of the homogeneous time-varying linear system	7
1.7	Positive linear systems	8
1.7.1	Basic properties of positive linear constant systems	8
1.7.2	Basic properties of non-homogeneous positive linear systems	10
1.7.3	Various properties of positive linear systems	11
1.8	Nonlinear discrete systems	11
1.8.1	Useful elements of the study	12
1.8.2	Stability	12
1.8.3	Local study around an equilibrium	12
1.8.4	Liapunov functionals	14
1.8.5	The one-dimensional example	15
1.8.6	Bifurcation with respect to a parameter	15
2	Continuous time models	15
2.1	The concept of differential system	15
2.1.1	Solutions of differential equations	15
2.1.2	Continuous dependence of solutions, stability	17
2.2	Linearisation	17
2.2.1	Linear systems	17
2.2.2	Stability in the linear approximation	18
2.2.3	The Chemostat with two competing species	19
2.3	Autonomous Systems	20
2.3.1	Lotka-Volterra Equations for Predator-Prey Systems	21
2.3.2	Limit sets	22
2.3.3	Poincaré-Bendixon theory	23
2.3.4	The Gause predator prey model with Holling-type interaction	23

Glossary

- continuous: the value taken by the time belongs to \mathbb{R} , the set of real numbers

Each domain has its own methodology for building models; in general, there is some laws giving part of the dynamics; moreover, a complex model is done often of more elementary parts, describing the interactions inside some subsystems of the system, and involving a limited number of variables. These parts or subsystems are often added with some weights describing the importance of the dynamic of the subsystem in the whole dynamic. The model can be linear (cf. the example below) or not.

The discrete model can be also the result of the discretisation of some continuous model, with the goal of making it simpler or more easily implementable on a computer. For example, a dynamical model written as an ordinary differential equation with continuous time needs to be discretised in some way to be simulated on a computer; a numerical integration method (Euler, Runge-Kutta, ...) is needed to do that in the most accurate way. Partial differential equations, having continuous variables in time and space, for example, need also to be discretised in time and space to be implemented on a computer. The model obtained after discretization is often of large dimension, and the solutions should be compared to the solutions of the original continuous model: the aim being that, for, in general, a small step size for the discretization, the two kind of solutions are very similar. We enter here the large domain of numerical analysis.

1.2 The state space; basic vocabulary

Consider the general system (1); it can be written in the more concise form

$$x(k+1) = f(x(k)) \tag{2}$$

where f is some function associating an n -vector to another. Given an initial vector condition $x(0) = x_0$, the solution will be some vector $(x_1(k), x_2(k), \dots, x_n(k))$ evolving with time k . The usual graphical representation of this vector is the representation with respect to time : the time is on the X-axis, and the n variables on the Y-axis. The state space is another way of seeing the system, very efficient, particularly for the low dimensions. The state space for the dimension 2 (two variables $x_1(k), x_2(k)$) is the representation in the plane of the point of coordinates $x_1(k), x_2(k)$: the time does not appear explicitly. The dynamical is clear from this figure: starting from a point (initial condition x_0), the dynamical system “jumps” to another point, and so on. This representation enables to see (with the help of a computer) a more geometrical vision of the behavior; moreover, as will be seen in the next section, a classification is possible in this space. This space is also named the phase space.

A point that does not move is called an equilibrium; it verifies $x^* = f(x^*)$; a sequence of points jumping from one to the next (given by the equation of the system) is a solution. The initial point x_0 at time $t = 0$ is called the initial condition.

In some cases, the system can be submitted to the action of external variables, that do not belong to the state variables: it could be, for example, the external temperature that will change the survival and reproduction rates in the Leslie models; these external variables are called inputs in the language of control theory (see *Basic Principles of Mathematical Modelling*). If there is some input $u(k)$ depending on the time k , the new system is

$$x(k+1) = f(x(k), u(k))$$

1.3 Linear discrete equations

Let us consider the simple example of the geometric growth (see *Classification of models*). The model is

$$x(k+1) = ax(k)$$

In particular, we wish to know if the population will decline or increase, and how it behaves for large times. This formalism and study is in fact at the basis of all the models we will write

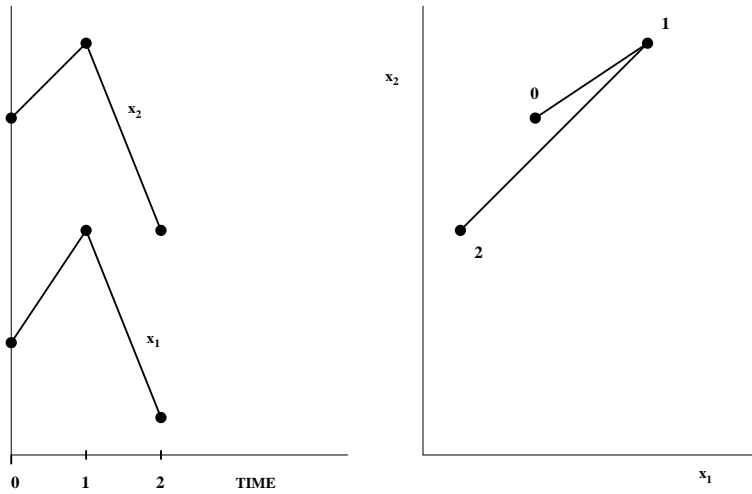


Figure 1: Time (left) and phase (right) representation in dimension two

in the following. The model describes how the variables determining the state of the system at time k will evolve at next time ($k + 1$). The initial condition gives the value of the state variables at time 0. We wish to study the behaviour of a solution starting from the initial condition, and describe it for any time.

For the above example, the answer is simple, because the solution is

$$x(k) = a^k x(0)$$

and therefore:

- if $a > 1$, then the solution grows without limits (if $x(0)$ is not zero)
- if $a = 1$, then the state stays always at the initial value $x(0)$
- if $a < 1$, then the solution goes to zero: the population goes to extinction.

Even in this very simple discussion, we have used our knowledge of the physical meaning of the parameter a : we know that a is positive because it represents a number of cells.

Now we can consider the more general case (several variables) of a linear discrete system, also called difference equations. It plays a prominent role in the study of mathematical dynamic discrete models (similarly to its continuous analog: the linear differential equation).

The system is supposed to be described by n state variables $x_1(k), x_2(k), \dots, x_n(k)$ at instant k . We list first the variations around linear models. The simplest case is the case of a linear square constant matrix A with n rows and n columns.

1.3.1 The homogeneous constant linear system

It is written

$$x(k + 1) = Ax(k)$$

The matrix A is given by

$$A = \begin{pmatrix} a_{11} & a_{12} & a_{13} & \dots & a_{1n} \\ a_{21} & a_{22} & a_{23} & \dots & a_{2n} \\ \vdots & \vdots & \vdots & & \vdots \\ a_{n1} & a_{n2} & a_{n3} & \dots & a_{nn} \end{pmatrix}$$

To define a solution, we must give us an initial condition $x(0) = x_0$. As an example, consider the Leslie model (see *Classification of Models*):

$$x(k + 1) = Ax(k)$$

with

$$A = \begin{pmatrix} 0 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix}$$

1.3.2 The homogeneous time-varying linear system

It is written

$$x(k + 1) = A(k)x(k)$$

The matrix $A(k)$ depends on the time k . Of course, it is a generalization of the above constant case.

As an example, let us imagine that the parameter of survival and reproduction and the Leslie model vary with the time (let us say the year) because of the variation of climate.

1.3.3 The non-homogeneous linear system

It is written

$$x(k + 1) = A(k)x(k) + b(k)$$

where $b(k)$ is some forcing vector of dimension n depending (possibly) on time.

As an example, in the Leslie model, the vector

$$b = \begin{pmatrix} 0 \\ b_2 \\ 0 \end{pmatrix}$$

could represent the immigration of individuals coming from outside in the second age class.

1.3.4 The controlled linear system

The above vector $b(k)$ can be seen as an input, and can be written to make explicit the connection between the actual inputs of the system $u(k)$ of dimension m , and the evolution equation. Thus we define a matrix $B(k)$ of n lines and m columns, and write:

$$x(k + 1) = A(k)x(k) + B(k)u(k)$$

This system is now relevant for Control Theory (see *Basic Principles of Mathematical Modelling, Controllability, Observability, Sensitivity and Stability of mathematical models*); we may also add outputs, describing the available measurements:

$$y(k) = C(k)x(k)$$

1.3.5 Conversion to matrix linear form

The model can sometimes be described by an equation involving the state variable at different times k . Let us take the example of the linear difference equation:

$$y(k + n) + a_{n-1}y(k + n - 1) + \dots + a_0y(k) = u(k)$$

The model depend on the variable y taken at times between k and $k + n$, n is a given integer.

Define the new state variable $x(k)$ of dimension n by:

$$\begin{aligned}x_1(k) &= y(k) \\x_2(k) &= y(k+1) \\&\vdots \\x_n(k) &= y(k+n-1)\end{aligned}$$

then the system is a linear homogeneous system

$$x(k+1) = Ax(k) + Bu(k)$$

with

$$A = \begin{pmatrix} 0 & 1 & 0 & \dots & 0 \\ 0 & 0 & 1 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \dots & 1 \\ -a_0 & -a_1 & -a_2 & \dots & -a_{n-1} \end{pmatrix} \quad B = \begin{pmatrix} 0 \\ 0 \\ \vdots \\ 0 \\ 1 \end{pmatrix}$$

1.4 Basic study of the homogeneous constant linear system

This case is the simplest one, but also the most important as a basis for the study of dynamical systems, either linear or nonlinear (the linear system being obtained by linearisation of the nonlinear one, see below).

The considered system is

$$x(k+1) = Ax(k)$$

with an initial condition $x(0) = x_0$. The explicit solution is easily written as:

$$x(k) = A^k x_0$$

We suppose that the matrix $A - I$ is bijective for simplicity, then the origin is the only equilibrium, because the equation $x = Ax$ has only one solution.

The following theorems give the basic behaviors of such systems: they are based on the notions of eigenvalue and eigenvectors.

Theorem 1 *Case 1 (asymptotic stability): if all the eigenvalues of the matrix A are strictly less than 1 in modulus, then the solution goes to zero.*

Case 2 (instability): if one eigenvalue of the matrix is greater than one (in modulus), then the solution is not bounded for almost any initial condition.

It is possible also to classify the behaviour in the phase space (the space of the state variables) into some cases giving a good and intuitive view of the situation. In the case of two variables, we obtain (we have concentrated on generic cases for simplicity):

Proposition 1 *Classification of behaviour in the plane:*

- *stable node: if the two eigenvalues are real of modulus lower than one, the solution converge toward the origin with two principal directions (the two eigenvectors).*
- *stable focus: if the two eigenvalues are complex and conjugated with a real part lower than one, the solution converges along a kind of spiral towards the origin.*
- *unstable node: if the two eigenvalues are real and of modulus greater than one, the solution becomes unbounded with two principal directions (the two eigenvectors).*

- *stable focus*: if the two eigenvalues are complex and conjugated with a real part greater than one, the solution converges along a kind of spiral towards the origin.
- *saddle* : if one eigenvalue is real and greater than one in modulus, and the other real and lower than one in modulus, then the phase space has one attractive direction, and one repulsive, along two lines (the two eigenvectors).

There exists algebraic tests to study the location of the eigenvalues, and conclude concerning the stability. In dimension two, they are simple:

Proposition 2 *The second order matrix A is asymptotically stable if*

$$|\text{trace}(A)| < 1 + \text{determinant}(A), \quad \text{determinant}(A) < 1$$

1.5 Basic study of the non homogeneous constant linear system

The basic equation is:

$$x(k+1) = Ax(k) + b$$

where the vector b is constant also. In fact, the study of this system amounts to the study of a translated linear homogeneous system.

Proposition 3 *Consider the unique equilibrium x^* such that*

$$x^* = Ax^* + b$$

then the new variable $y = x - x^$ is solution of the system:*

$$y(k+1) = Ay(k)$$

This system is studied as above.

1.6 Basic study of the homogeneous time-varying linear system

We consider again the system

$$x(k+1) = A(k)x(k) \tag{3}$$

It is easy to solve recursively

$$x(k+1) = A(k)x(k)$$

to obtain the solution

$$x(k) = A(k-1)A(k-2) \dots A(0)x_0$$

but it is often of little utility because we are more interested in obtaining qualitative results such as the limit behaviour for large k .

Except the fact that the solution belongs to a linear space, it is difficult to obtain specific results for this kind of systems: the difficulties coming from the fact that we do not know how the matrices $A(k)$ are varying.

One pertinent hypothesis can be that the matrices $A(k)$ are varying periodically, with period q , i.e. $A(k+q) = A(k)$ for all time. In fact, if we consider the variable $x(0), x(q), x(2q)$ (each period of time), we obtain a constant matrix $C = A(q-1)A(q-2) \dots A(0)$ and a new time-invariant system

$$x((p+1)q) = Cx(pq)$$

that we studied above.

1.7 Positive linear systems

The class of positive linear systems constitutes an important subclass of the linear systems. Its importance comes from the fact that, very often, the variables of the model are constrained to be positive, or nonnegative, because they represent numbers, or concentrations (numbers per volume unit for example). Therefore one desirable property of the model is to contain such a property in its dynamical formulation, i.e. “if the initial condition of a variable is nonnegative, it will stay nonnegative”. It is easy to see that an equivalent property (in the linear case) is that the matrix $A(k)$ (of dimension n) is nonnegative for all k .

Proposition 4 *If the matrix $A(k)$ is nonnegative for all k , for all nonnegative initial conditions, the variables $x(k)$ of*

$$x(k+1) = A(k)x(k) \quad (4)$$

stay nonnegative for all k .

1.7.1 Basic properties of positive linear constant systems

As before, it is simpler to take the matrix A constant. The system is of course a particular case of linear system, and the properties above apply. But the positivity of the matrix implies some important characteristics of the dominant eigenvalue. These properties are the consequences of the theorem of Perron-Frobenius, that has many subtleties. We give here the main lines.

The simplest case is for a positive matrix A , i.e. each term of the matrix is strictly positive.

Theorem 2 *If the matrix A is positive, then the system (4) has a positive real eigenvalue λ (called the dominant eigenvalue) strictly greater in modulus than the others, and a unique positive eigenvector v_λ associated to this eigenvalue.*

This theorem enables to deduce the limit behaviour of the system, which is very similar to a geometrical law along the dominant eigenvector.

Proposition 5 *For large times (large k), the solution $x(k)$ of the system (4) behaves as $\lambda^k v_\lambda$.*

If the matrix is nonnegative only (some of the elements can be zero), the results are more involved. They use often the graph associated to the matrix, offering a very visual way to illustrate the interactions between the variables of the model. This graph is constituted with n points (or vertices) linked with (oriented) edges between point i and j if the element a_{ji} is positive. The figure shows the graph associated with the matrix:

$$A = \begin{pmatrix} 0 & * & * \\ * & 0 & 0 \\ 0 & * & 0 \end{pmatrix}$$

The matrix is irreducible if there is a path joining two arbitrary points. This property can easily be seen on the graph.

Proposition 6 *The matrix A is irreducible if and only if the graph is strongly connected.*

Proposition 7 *If the matrix A is irreducible, then the system (4) has a positive real eigenvalue λ (called the dominant eigenvalue) greater in modulus than the others, and a unique positive eigenvector v_λ associated to this eigenvalue.*

Let us remark that the dominant eigenvalue can be non unique ; in this case, the h dominant eigenvalues are of the same modulus, and the system is said to be cyclic of index h . This index of cyclicity can also be read on the influence graph.

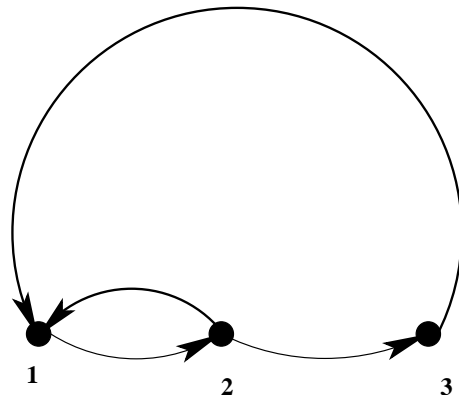


Figure 2: Graph associated with the matrix A ; compare with the graph for the Leslie matrix in *Classification of models*

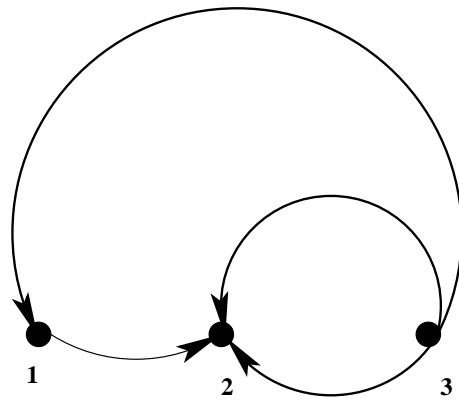


Figure 3: Graph associated with a non irreducible matrix; the graph is not strongly connected because it is not possible to go from the node 2 to another node.

Proposition 8 *Let A be an irreducible matrix, then the index of cyclicity h is the greatest common divisor of all the lengths of the circuits (closed loops) in the graph.*

If this index of cyclicity is greater than one, the system is said to be cyclic, and the behaviour can be periodical. If the index h is equal to one, the system is said primitive. Let us remark that these properties depend only on the structure of the matrix A , and not upon the exact values of the elements.

Proposition 9 *Let A be an irreducible and primitive matrix, then its limiting behaviour is similar to a positive matrix, i.e. for large k , $v_\lambda \lambda^k$. There is no periodic behaviour.*

If the matrix is not primitive, the behaviour can be periodic; as an example, we take the Leslie matrix (see *Classification of models*) with only three elements.

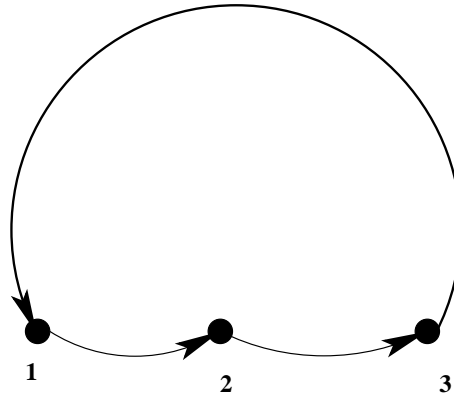


Figure 4: Graph associated with a non primitive matrix; the index of cyclicity is three

The Leslie matrix models (see *Classification of models*) can be studied with this theory, and the result has a nice interpretation : the final population structure is fixed (it is the eigenvector v_λ), and the final growth rate is a geometrical law with parameter λ .

1.7.2 Basic properties of non-homogeneous positive linear systems

We consider the forced system:

$$x(k+1) = Ax(k) + b \quad (5)$$

Because the variables are assumed to be positive, we take a positive vector b . But one question arises: does there exist a positive equilibrium to the system (5) ? The following property exhibits an intriguing connection between equilibrium and stability, under a slight hypothesis of excitability.

Definition 1 *Let us consider the graph of the system (5) (the influence of b is represented by the node 0); the system is said excitable if there exists at least one path from the node 0 to any other node.*

Proposition 10 *For an excitable system (5), there exists a positive equilibrium if and only if it is asymptotically stable.*

We can apply this theorem to Leslie models with immigration (cf. figure).

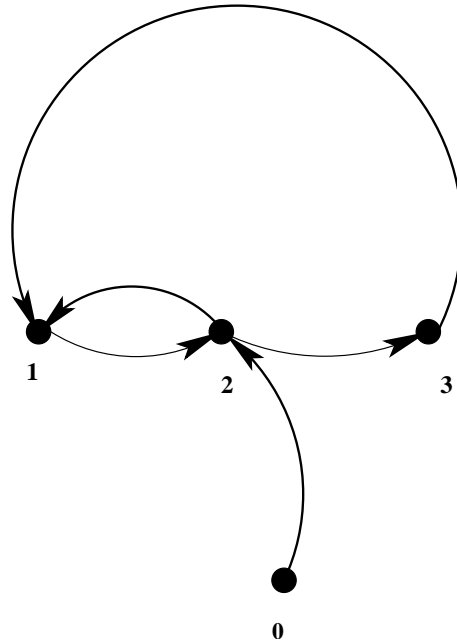


Figure 5: Graph associated with a forced excitable system; there is an input in the second variable.

1.7.3 Various properties of positive linear systems

The first interesting property is a property of comparison between systems. When modelling a real system, it happens often that some parameters are not well known, so that we obtain for examples two systems with two matrices A^- and A^+ such that we know the actual matrix A is (term by term) between the two:

$$A^- \leq A \leq A^+$$

It is very interesting that, for positive systems, the dominant eigenvalues, characterizing the asymptotic behaviour, are also ranked:

Proposition 11 *If for positive matrices $A^- \leq A \leq A^+$, then the dominant eigenvalues verify $\lambda(A^-) \leq \lambda(A) \leq \lambda(A^+)$.*

For example, if the upper matrix A^+ is stable, we deduce the stability of all the matrices A lower than A^+ .

The second property states the intuitive fact that λ is the dominant eigenvalue

Proposition 12 *If $\alpha x \leq Ax \leq \beta x$, with x positive, then $\alpha \leq \lambda \leq \beta$.*

1.8 Nonlinear discrete systems

As stated in the introduction, a general discrete dynamical system is expressed as:

$$x(k+1) = f(x(k))$$

Given an initial condition $x(0) = x_0$, we want to study the behaviour of the solution starting at x_0 . The behaviour of such a system can be very complex, even for low dimension: it can have periodic behaviour, limit cycles, or even chaotic motion. There are a few general methods of study, but it is often necessary to take advantage from the specificities of the system. One general but local method is the linearisation around some point or trajectory. The Liapunov functionals

are often of great utility if you are able to find one; the monotonicity of the system can also be used. Endly, it is also interesting to study the qualitative variations of stability of the system with respect to one important parameter, and to draw, if possible, the bifurcation diagram.

1.8.1 Useful elements of the study

An equilibrium is described by the equation

$$x^* = f(x^*)$$

it is a nonlinear algebraic equation (called a fixed point equation) that can be itself very difficult to solve.

An invariant region is a domain of the space with the property that, if the initial condition starts in this region, it will stay in the region for all times. Such regions are very useful to separate the state into several parts.

A solution may converge towards an equilibrium x^* , but also towards a periodic solution of period T such that $x(k + T) = x(k)$ for all k . It could also have a more complicated behaviour (e.g. chaos....).

1.8.2 Stability

Concerning the behaviour with respect to an equilibrium, one can define the notions of stability, or a stronger notion of asymptotic stability. Intuitively, it says that a solution starting near an equilibrium point will stay near in the future. The precise definition use the concept of neighborhood - and is also called Liapunov stability. These notions can be local (in a neighborhood of an equilibrium for example) or more global (in the whole state space for example).

Definition 2 *An equilibrium point x^* is stable if, for a neighborhood V_2 of x^* , there exist a smaller neighborhood V_1 such that, if $x(0)$ belongs to V_1 , then the solution $x(k)$ belongs to V_2 for all k .*

Definition 3 *An equilibrium point x^* is attractive if the solution initiated at $x(0)$ converges towards x^* .*

Definition 4 *An equilibrium point x^* is asymptotically stable if it is stable and attractive.*

As an important example, we can give the two theorems on linear systems of a preceding section. We consider again the linear system

$$x(k + 1) = Ax(k)$$

Theorem 3 *Case 1 (asymptotic stability): if all the eigenvalues of the matrix A are lower than 1 in modulus, then the zero equilibrium is asymptotically stable.*

Case 2 (instability): if one eigenvalue of the matrix is greater than one (in modulus), then the equilibrium is unstable.

1.8.3 Local study around an equilibrium

A very general and useful method giving local indications on the behaviour around an equilibrium consists in linearizing the system. Of course, there can be several different equilibria for the nonlinear system, leading to several different linearizations.

Proposition 13 *The linearized system associated to $x(k+1) = f(x(k))$ around one of the equilibria $x^* = f(x^*)$ is the linear system:*

$$y(k+1) = A^*y(k)$$

with

$$y(k) = x(k) - x^*$$

and

$$A^* = Df(x^*)$$

(A^* is the Jacobian matrix of the partial derivatives of f evaluated at the point x^*)

Recall the expression of the Jacobian matrix:

$$Df(x) = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \cdots & \frac{\partial f_1}{\partial x_n} \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} & \cdots & \frac{\partial f_2}{\partial x_n} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial f_n}{\partial x_1} & \frac{\partial f_n}{\partial x_2} & \cdots & \frac{\partial f_n}{\partial x_n} \end{pmatrix}$$

In general, the nonlinear system and this linear system behaves locally in a similar way. The study of the linearized system gives us (roughly) the local behaviour around the equilibrium of the nonlinear system, and, in particular, the classification of linear systems given above applies. One can obtain also theorems on the local stability:

Theorem 4 *If the Jacobian matrix around x^* has all its eigenvalues with moduli strictly lower than one, then the equilibrium of the nonlinear system is locally asymptotically stable.*

Theorem 5 *If one eigenvalue (at least) has a modulus greater than one, the equilibrium around x^* is unstable.*

As an example, we take the Nicholson-Bailey model (see *Classification of models*).

$$\begin{aligned} x_1(k+1) &= \lambda x_1(k) e^{-ax_2(k)} \\ x_2(k+1) &= cx_1(k)(1 - e^{-ax_2(k)}) \end{aligned}$$

We can analyze this model by determining first its steady states. We solve the system:

$$\begin{aligned} x_1 &= \lambda x_1 e^{-ax_2} \\ x_2 &= cx_1(1 - e^{-ax_2}) \end{aligned} \tag{6}$$

and obtain two solutions : the trivial solution $(0, 0)$ and the positive equilibrium:

$$\begin{aligned} x_1^* &= \frac{\lambda \ln(\lambda)}{(\lambda-1)ac} \\ x_2^* &= \ln(\lambda)/a \end{aligned} \tag{7}$$

We observe that we have to suppose $\lambda > 1$ in the model so that the second coordinate is positive.

To study the local behavior around the positive equilibrium, we write the linearized system around the second equilibrium, obtaining the matrix

$$\begin{pmatrix} 1 & -ax_1^* \\ c(1 - 1/\lambda) & cax_1^*/\lambda \end{pmatrix} \tag{8}$$

Because the conditions for the stability of the system are violated (the determinant is greater than one), we conclude that the nonlinear system is locally unstable.

1.8.4 Liapunov functionals

There is a more global, more powerful, and yet very clear, method for computing the stability of an equilibrium x^* . It consists in finding a scalar function $V(x)$, positive for $x \neq x^*$ and equal to zero only for $x = x^*$; intuitively, this function should be similar to a cone smoothed at the extremity (cf figure 6). Moreover, this function $V(x(k))$ for $x(k)$ verifying $x(k+1) = f(x(k))$ should decrease for each iteration, i.e. $V(x(k+1)) < V(x(k))$. Such a function will be called a Liapunov function. Then, intuitively, the solution goes towards the bottom of the cone, to the equilibrium point. This method is powerful and global, but there is no indication on how to find a Liapunov function; some classes are known (for linear system, one knows it is possible to take quadratic Liapunov functions $V(x) = xPx$), but in general it is an open problem.

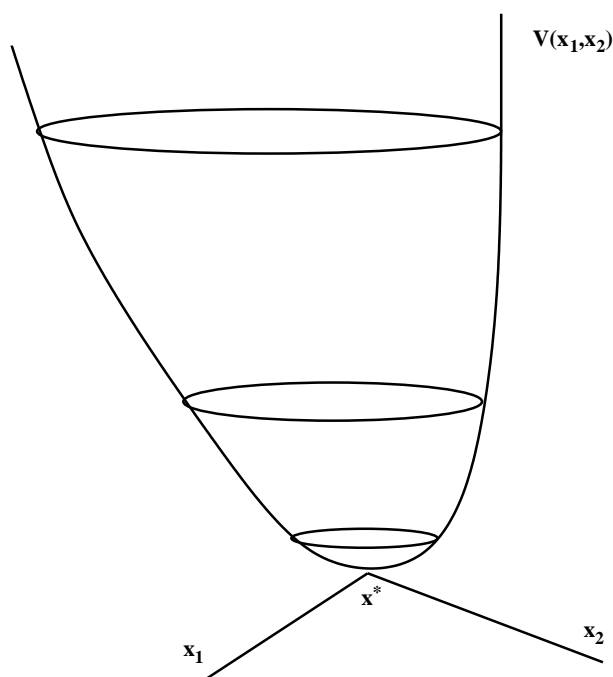


Figure 6: The Liapunov function V ; the equilibrium x^* is at the bottom.

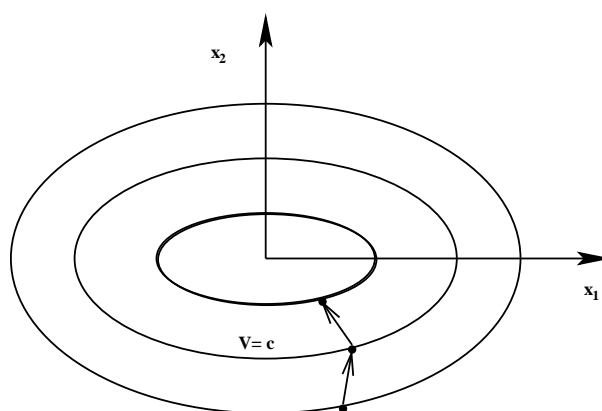


Figure 7: Level curves of V illustrating Liapunov stability.

1.8.5 The one-dimensional example

The general problem in the discrete case is rather well illustrated by the case of a real variable $x(k)$ with a real function $f(x)$; one famous example being given by the logistic function $rx(1-x)$, r being a positive parameter (see *Complexity, pattern recognition and neural models*).

The system is

$$x(k+1) = rx(k)(1-x(k))$$

and the behaviour is well seen on a graph. Now, depending on the precise value of the parameter r , it can be seen that the solution can converge towards the equilibrium or towards a periodic solution of period 2, or 4, 8, This cascade of bifurcation by period doubling leads to a chaotic behaviour, where there are simultaneously solutions of any period, and where the behaviour is complicated and very sensitive to the initial conditions: a very small initial difference in the initial conditions will lead to two very different solutions; for example, the successive iterates computed simultaneously by two different computers, starting at the same initial conditions, will give two solutions very dissimilar after some time.

1.8.6 Bifurcation with respect to a parameter

Consider the geometric growth in one dimension $x(k+1) = rx(k)$. When r increases from below one to above one, the qualitative behaviour of the equations changes totally: before $r = 1$, the solution goes to zero, and after it goes to infinity. The value $r = 1$ plays a special role; this is one of the simplest (and rudimentary) examples of a bifurcation value for the parameter r . More generally, one can study the behaviour (local or global) of a nonlinear system with respect to a parameter; we have seen already the bifurcation of the solution of the logistic equation with respect to a parameter, leading to chaotic behaviour. A classification of the types of the bifurcations is useful, and gives normalized answers for the possible cases. A famous case of the classification is called the Hopf bifurcation, and gives the standard conditions for the apparition of a small attractive periodic solution when an equilibrium loses its stability.

2 Continuous time models

2.1 The concept of differential system

We consider in this section the continuous models which describe a phenomenon varying in time. Assume that we have selected the state variables $x(t)$ at time t .

$$\dot{x}(t) = f(t, x(t)) \tag{9}$$

In general $x(t)$ is a vector of n real variables $x(t) = (x_1(t), \dots, x_n(t))$, so that, the above equation is a set of differential equations or a differential system

$$\begin{aligned} \dot{x}_1(t) &= f_1(t, x_1(t), \dots, x_n(t)) \\ &\dots \\ \dot{x}_n(t) &= f_n(t, x_1(t), \dots, x_n(t)) \end{aligned} \tag{10}$$

where $f_1(t, x(t)), \dots, f_n(t, x(t))$ are the components of the vector $f(t, x(t))$. The functions f_i are defined on some open subset D of $\mathbb{R} \times \mathbb{R}^n$ and are assumed to be continuously differentiable in all variables.

2.1.1 Solutions of differential equations

A solution of the differential system (9) or (10) is a map

$$t \mapsto x(t) = (x_1(t), \dots, x_n(t))$$

from some interval I into \mathbb{R}^n such that $x(t)$ is differentiable and satisfy, for all $t \in I$, $(t, x(t)) \in D$ and

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

The domain D is called the *extended phase space*. The subspace of variables (x_1, \dots, x_n) is called the *phase space*. Equation (9) determines a *vector field* on D defined in the following way : at every point (t, x) of the domain D is attached a vector $(1, f(t, x))$. The graph of a solution $x(t)$ may be interpreted geometrically as a curve in D which is tangent to this vector field at every one of its points $(t, x(t))$. The graph of a solution is called an *integral curve* (or a *trajectory*). A *phase curve* (or *orbit*) is the projection of an integral curve on the phase space along the t -axis.

An *initial condition* is the specification of the position at some given time. The *Cauchy problem* consists in determining the solutions of system (9) satisfying the initial condition

$$x(t_0) = x_0 \tag{11}$$

where t_0 is the initial value of time, x_0 is a given initial value of the unknown function $x(t)$ and (t_0, x_0) belongs to D . We can find in every textbook on differential equations the theorem of the existence and uniqueness of solutions, which states that *under local Lipschitz condition, for every initial condition there exists a unique solution to the Cauchy Problem* (9,11). The corresponding solution will usually be denoted by $x(t, t_0, x_0)$. Let us note that a solution need not be defined for all times as it is shown in the following example.

Example 1 If x is scalar and $f(t, x) = x^2$ then the solution are given by the formula

$$x(t, t_0, x_0) = \frac{x_0}{1 + x_0(t_0 - t)} \tag{12}$$

Notice that the solution (12) is defined on interval $-\infty < t < t_0 + x_0^{-1}$ if $x_0 > 0$; it is defined on interval $-\infty < t < +\infty$ if $x_0 = 0$; it is defined on interval $t_0 + x_0^{-1} < t < +\infty$ if $x_0 < 0$.

Example 2 Consider the Cauchy problem

$$\dot{x} = 3|x|^{2/3}, \quad x(0) = 0 \tag{13}$$

There exists an infinite number of solutions of (13) which are defined on \mathbb{R} . For any $\alpha \leq 0$ and $\beta \geq 0$, the function $x_{\alpha, \beta}$ defined by

$$x_{\alpha, \beta}(t) = \begin{cases} (t - \alpha)^3 & \text{if } t < \alpha \\ 0 & \text{if } \alpha \leq t \leq \beta \\ (t - \beta)^3 & \text{if } t > \beta \end{cases}$$

is a solution of problem (13).

This example shows that something more than the continuity of the vector field f is required in order to guarantee that a solution passing through a given point is unique. The Lipschitz condition imply uniqueness. The function f is said to be locally Lipschitzian in x on the domain D if for every point $(t_0, x_0) \in D$ there exists a cylinder R of type

$$R = \{(t, x) \in \mathbb{R}^{n+1} : |t - t_0| \leq s, \|x - x_0\| \leq r\}$$

such that $R \subset D$, and a constant $k \geq 0$ such that for every (t, x_1) and (t, x_2) in R

$$\|f(t, x_1) - f(t, x_2)\| \leq k\|x_1 - x_2\|$$

The constant k is called the Lipschitz constant. If f has continuous partial derivatives on D with respect to x , then it is locally Lipschitzian in D .

2.1.2 Continuous dependence of solutions, stability

The solution $x(t, t_0, x_0)$ depends continuously (and even differentiably) on all its arguments. Roughly speaking, this means that if $x(t, t_0, x_0)$ is restricted to a closed interval $I = [a, b]$, then for t_1 close to t_0 , and x_1 close to x_0 , the solution $x(t, t_1, x_1)$ exists at least on the interval I and remains close to $x(t, t_0, x_0)$ on this interval. In general, nothing can be said about the proximity of the solutions $x(t, t_0, x_0)$ and $x(t, t_1, x_1)$ when t tends to the extremities of the interval of definition of the solution $x(t, t_0, x_0)$. An even more important concept is the concept of stability which is the continuous dependence on initial conditions on infinite intervals of time.

A solution $p(t)$ of system (9) which is defined for all $t \geq 0$ is said to be *stable* (in the sense of Liapunov) if, given any $\varepsilon > 0$, there exists a $\delta > 0$ such that $\|x_0 - p(0)\| < \delta$ implies $\|x(t, 0, x_0) - p(t)\| < \varepsilon$ for all $t \geq 0$. Intuitively this property means that any solution which passes infinitely close to $p(0)$ at time $t = 0$ will remain infinitely close to $p(t)$ at any time $t \geq 0$. The solution $p(t)$ is said to be *asymptotically stable* if, in addition to being stable, there is $b > 0$ such that $\|x_0 - p(0)\| < b$ implies $\|x(t, 0, x_0) - p(t)\| \rightarrow 0$ as $t \rightarrow +\infty$. Intuitively this property means that any solution which starts in a suitable neighborhood of $p(0)$ becomes infinitely close to $p(0)$ for any infinitely large time $t \geq 0$.

2.2 Linearisation

2.2.1 Linear systems

The basic characteristic property of linear systems of the form

$$\dot{y} = A(t)y + b(t) \quad y \in \mathbb{R}^n \quad (14)$$

is the *principle of superposition*: If $y_1(t)$ is a solution of (14) corresponding to the *forcing term* (or *input*) $b_1(t)$ and $y_2(t)$ is a solution corresponding to the forcing term $b_2(t)$ then $\lambda_1 y_1(t) + \lambda_2 y_2(t)$ is a solution corresponding to the forcing term $\lambda_1 b_1(t) + \lambda_2 b_2(t)$. This property implies that if $y_0(t)$ is a particular solution of (14), then any solution $y(t)$ of (14) is of the form

$$y(t) = x(t) + y_0(t)$$

where $x(t)$ is a solution of the homogeneous system

$$\dot{x} = A(t)x \quad (15)$$

If the functions $A(t)$ and $b(t)$ are defined on an interval I , then the solutions of (14) and (15) exist on all the interval I .

Except in the autonomous case, there is no general method to compute the solutions of the linear homogeneous system (15). Let $X(t)$ be a matrix solution, that is, $X(t)$ is a square matrix of order n , and each column of $X(t)$ is a solution. Then the determinant $W(t) = \det X(t)$ satisfies the scalar equation $\dot{w} = [\text{tr}A(t)]w$ where the trace $\text{tr}A(t)$ of $A(t)$ is the sum of its diagonal elements. Hence we have the Liouville formula

$$W(t) = W(t_0) \exp \left(\int_{t_0}^t \text{tr}A(s) ds \right) \quad (16)$$

For homogeneous systems with constant coefficients

$$\dot{x} = Ax \quad (17)$$

the solution $x(t, x_0)$ of (17) passing through x_0 at time 0 is given by

$$x(t, x_0) = e^{tA} x_0 \quad (18)$$

where the exponential matrix e^{tA} is given by

$$e^{tA} = I + tA + \frac{1}{2!} t^2 A^2 + \cdots + \frac{1}{n!} t^n A^n + \cdots \quad (19)$$

A complex number λ is said to be an *eigenvalue* of the matrix A if and only if λ is a solution of the *characteristic equation*

$$\det(A - \lambda I) = 0$$

The characteristic equation is a polynomial equation of order n in λ and, therefore, has s distinct solutions $\lambda_1, \dots, \lambda_s$ with algebraic multiplicities $m(\lambda_i)$ satisfying $m(\lambda_1) + \dots + m(\lambda_s) = n$. The eigenvalues of A can be real or complex: in the later case, they occur in conjugate pairs. The coefficients $x_i(t)$ of the solution (18) are linear combinations, with constant coefficients, of the following functions:

1. $e^{t\lambda}$ where λ is a real eigenvalue of A ;
2. $e^{ta} \cos bt$ and $e^{ta} \sin bt$, i.e. the real and the imaginary part of $e^{t\mu}$, where $\mu = a + ib$ is a complex eigenvalue of A .
3. $t^j e^{t\lambda}$, $t^j e^{ta} \cos bt$ or $t^j e^{ta} \sin bt$, with $0 < j < m$, if the eigenvalue λ or μ occurs with multiplicity m .

The origin is obviously an equilibrium of (17). It is asymptotically stable if and only if all eigenvalues of A have real parts < 0 . The solution $y(t, t_0, x_0)$ the non-homogeneous system

$$\dot{y} = Ay + b(t) \tag{20}$$

passing through x_0 at time t_0 is given by the so called *variation of constant formula*

$$y(t, t_0, x_0) = e^{(t-t_0)A}x_0 + \int_{t_0}^t e^{(t-s)A}b(s)ds$$

2.2.2 Stability in the linear approximation

In this section we consider perturbations of linear systems of the form

$$\dot{x} = A(t)x + f(t, x)$$

where the nonlinear terms $f(t, x)$ are assumed to be small. Assume that $f(t, 0) = 0$, so that $x = 0$ is an equilibrium.

Theorem 1 *Let A be a constant matrix with all eigenvalues having negative real parts. Let $f(t, x)$ be continuous and*

$$\lim_{x \rightarrow 0} f(t, x)/\|x\| = 0$$

Then the solution $x = 0$ of $\dot{x} = Ax + f(t, x)$ is asymptotically stable.

Suppose that the autonomous system

$$\dot{x} = f(x) \tag{21}$$

has the origin as an equilibrium. According to Taylor's formula we have $\dot{x} = Ax + g(x)$ where $A = \partial f/\partial x(0)$ and $g(x) = o(\|x\|)$. The following result is an immediate consequence of Theorem 1.

Theorem 2 *If all the eigenvalues of $\partial f/\partial x(0)$ have negative real parts then the origin of (21) is asymptotically stable.*

2.2.3 The Chemostat with two competing species

The Chemostat was described in *Classification of Models*. The system of two competing microorganism in a Chemostat is

$$\begin{aligned}\dot{S} &= (S^{(0)} - S)D - \frac{m_1 x_1 S}{a_1 + S} - \frac{m_2 x_2 S}{a_2 + S}, \\ \dot{x}_1 &= x_1 \left(\frac{\gamma_1 m_1 S}{a_1 + S} - D \right), \\ \dot{x}_2 &= x_2 \left(\frac{\gamma_2 m_2 S}{a_2 + S} - D \right),\end{aligned}\tag{22}$$

For the mathematical study of this system it is more convenient to use the non-dimensional variables

$$\bar{S} = \frac{S}{S^{(0)}}, \quad \bar{x}_i = \frac{x_i \gamma_i}{S^{(0)}}, \quad \bar{t} = \frac{t}{D}$$

We obtain the differential equations

$$\begin{aligned}\frac{d\bar{S}}{d\bar{t}} &= (1 - \bar{S}) - \frac{\bar{m}_1 \bar{x}_1 \bar{S}}{\bar{a}_1 + \bar{S}} - \frac{\bar{m}_2 \bar{x}_2 \bar{S}}{\bar{a}_2 + \bar{S}}, \\ \frac{d\bar{x}_1}{d\bar{t}} &= \bar{x}_1 \left(\frac{\bar{m}_1 \bar{S}}{\bar{a}_1 + \bar{S}} - 1 \right), \\ \frac{d\bar{x}_2}{d\bar{t}} &= \bar{x}_2 \left(\frac{\bar{m}_2 \bar{S}}{\bar{a}_2 + \bar{S}} - 1 \right).\end{aligned}\tag{23}$$

where $\bar{m}_i = m_i/S^{(0)}$ and $\bar{a}_i = a_i/S^{(0)}$. Dropping the bars we obtain the system

$$\begin{aligned}\dot{S} &= (1 - S) - \frac{m_1 x_1 S}{a_1 + S} - \frac{m_2 x_2 S}{a_2 + S}, \\ \dot{x}_1 &= x_1 \left(\frac{m_1 S}{a_1 + S} - 1 \right), \\ \dot{x}_2 &= x_2 \left(\frac{m_2 S}{a_2 + S} - 1 \right).\end{aligned}\tag{24}$$

Let $\Sigma(t) = 1 - S(t) - x_1(t) - x_2(t)$ and rewrite the system as

$$\begin{aligned}\dot{\Sigma} &= -\Sigma \\ \dot{x}_1 &= x_1 \left(\frac{m_1(1 - \Sigma - x_1 - x_2)}{a_1 + 1 - \Sigma - x_1 - x_2} - 1 \right) \\ \dot{x}_2 &= x_2 \left(\frac{m_2(1 - \Sigma - x_1 - x_2)}{a_2 + 1 - \Sigma - x_1 - x_2} - 1 \right)\end{aligned}\tag{25}$$

One has that

$$\lim_{t \rightarrow \infty} \Sigma(t) = 0.$$

On the set $\Sigma = 0$, the system reduces to

$$\begin{aligned}\dot{x}_1 &= x_1 \left(\frac{m_1(1 - x_1 - x_2)}{a_1 + 1 - x_1 - x_2} - 1 \right) \\ \dot{x}_2 &= x_2 \left(\frac{m_2(1 - x_1 - x_2)}{a_2 + 1 - x_1 - x_2} - 1 \right)\end{aligned}\tag{26}$$

The first step of the analysis is to compute the stability of the equilibria of (26) by finding the eigenvalues of the Jacobian matrix evaluated at each of these equilibria. Suppose that $m_i > 1$, $i = 1$ and 2 , and that $0 < \lambda_1 < \lambda_2 < 1$, where $\lambda_i = a_i/(m_i - 1)$. Then any solution of (24) with $x_i(0) > 0$ satisfies

$$\lim_{t \rightarrow \infty} x_1(t) = 1 - \lambda_1, \quad \lim_{t \rightarrow \infty} x_2(t) = 0\tag{27}$$

The system (26) has three equilibria

$$E_0 = (0, 0), \quad E_1 = (1 - \lambda_1, 0), \quad E_2 = (0, 1 - \lambda_2)$$

At E_0 the Jacobian matrix takes the form

$$\begin{bmatrix} \frac{(m_1-1)(1-\lambda_1)}{1+a_1} & 0 \\ 0 & \frac{(m_2-1)(1-\lambda_2)}{1+a_2} \end{bmatrix}$$

Both eigenvalues are positive since $\lambda_1 < 1$ and $\lambda_2 < 1$. The origin is unstable. At E_1 the Jacobian matrix

$$\begin{bmatrix} \frac{(\lambda_1-1)(a_1 m_1)}{(\lambda_1+a_1)^2} & \frac{(\lambda_1-1)(a_1 m_1)}{(\lambda_1+a_1)^2} \\ 0 & \frac{(m_2-1)(\lambda_1-\lambda_2)}{\lambda_1+a_2} \end{bmatrix}$$

Both eigenvalues are negative since $\lambda_1 < \lambda_2 < 1$ and $m_2 > 1$. Thus E_1 is locally asymptotically stable. At E_3 the Jacobian matrix is

$$\begin{bmatrix} \frac{(m_1-1)(\lambda_2-\lambda_1)}{\lambda_2+a_1} & 0 \\ \frac{(\lambda_2-1)(a_2 m_2)}{(\lambda_2+a_2)^2} & \frac{(\lambda_2-1)(a_2 m_2)}{(\lambda_2+a_2)^2} \end{bmatrix}$$

One eigenvalue is negative since $\lambda_2 < 1$ and one is positive since $\lambda_1 < \lambda_2$. Thus E_2 cannot be a global attractor. Since E_1 is a local attractor, to prove (27) it remains only to show that it is a global attractor. The proof of this last result is more delicate and make use of sophisticated tools of dynamical systems theory. We will not give it there.

2.3 Autonomous Systems

Of particular interest are the *autonomous* or *time-independent* differential systems

$$\dot{x} = X(x) \tag{28}$$

Here, the right-hand side, does not depend on t . If $x(t)$ is a solution of (28) on an interval (a, b) , then for any number τ , $x(t - \tau)$ is a solution of (28) on the interval $(a + \tau, b + \tau)$. For any point initial condition x_0 , there is a unique solution $x(t, 0, x_0)$ of (28) passing through x_0 at $t = 0$. This solution is simply denoted by $x(t, x_0)$ or by $X_t(x_0)$.

Example 3: Verhulst or Logistic growth. The logistic equation is

$$\dot{x} = rx(1 - x/K)$$

then

$$x(t, x_0) = \frac{x_0 e^{rt}}{1 + x_0 (e^{rt} - 1)/K}$$

For $x_0 = 0$ or $x_0 = K$, the population number $x(t, x_0)$ does not change. For $0 < x_0 < K$, it increases, and for $x_0 > K$, it decreases.

The phase curve or orbit of a point $x \in \Omega$ is the set

$$\gamma(x) = \{X_t(x) : t \in I(x)\}$$

Where $I(x)$ is the maximal open interval for which the solution $X_t(x)$ exists. The positive semi-orbit $\gamma^+(x)$ is obtained by taking $t \geq 0$ in this definition. There is a unique orbit through a given x in Ω . This property does not hold for non-autonomous systems.

In an important case, the solution is defined for all times t : if there is some compact set in the domain of definition of the vector field X that $X_t(x)$ does not leave, then $I(x) = (-\infty, +\infty)$.

If there exists a set D in the domain of definition of X such that for all $x \in D$ and all $t \in \mathbb{R}$, the solution $X_t(x)$ is defined and lies in D , then the differential system (28) determines a *continuous dynamical system* on D .

An *equilibrium point* or (*singular point*) of a vector field $X(x)$ is a point p such that $X(p) = 0$. The trajectory of a singular point p is the straight line in $\mathbb{R} \times \Omega$ given by $x(t) = p$ and the orbit of p is the set $\{p\}$. A *regular point* is a point which is not singular.

An orbit γ is said to be *closed* (or to be a *cycle*) if it is a *Jordan curve*, that is to say, a homeomorphic image of a circle. An orbit is closed if and only if it corresponds to a nonconstant periodic orbit. This property does not hold for non-autonomous systems.

If $t \mapsto x(t, x_0)$ is injective, then the orbit never intersects itself: topologically it looks like a line.

2.3.1 Lotka-Volterra Equations for Predator-Prey Systems

The Lotka Volterra equations for predators and preys (see *Classification of Models*) are

$$\begin{aligned}\dot{x} &= x(a - by) \\ \dot{y} &= y(-c + dx)\end{aligned}\tag{29}$$

Since populations densities have to be nonnegative, we shall only consider the restriction of this system to the positive cone

$$\mathbb{R}_+^2 = \{(x, y) \in \mathbb{R}^2 : x \geq 0, y \geq 0\}$$

We may write four solutions :

1. $x(t) = y(t) = 0$,
2. $x(t) = 0, y(t) = y(0)e^{-ct}$ (for any $y(0) > 0$),
3. $y(t) = 0, x(t) = x(0)e^{at}$ (for any $x(0) > 0$),
4. $x(t) = c/d, y(t) = a/b$.

To these solutions correspond four orbits : (1) the origin $(0,0)$, which is a rest point, (2) the positive y -axis, (3) the positive x -axis, (4) the equilibrium $S = (c/d, a/b)$. Together, the three orbits (1), (2) and (3) form the boundary of the positive cone \mathcal{C} . This set is invariant. Indeed, as we have seen, the boundary of \mathcal{C} is an union of orbits. Since no orbit can cross another, the interior

$$\text{int } \mathbb{R}_+^2 = \{(x, y) \in \mathbb{R}^2 : x > 0, y > 0\}$$

is also invariant. The orbit S is the unique equilibrium in $\text{int } \mathcal{C}$. This equilibrium is surrounded by periodic orbits. Indeed from system (29) we obtain

$$(c/x - d)\dot{x} + (a/y - b)\dot{y} = 0$$

Thus $V(x(t), y(t)) = \text{const}$ where

$$V(x, y) = c \ln x - dx + a \ln y - by$$

The constant level sets

$$\{(x, y) \in \mathcal{C} : V(x, y) = \text{const}\}$$

are closed curves around S . The orbits, therefore, are periodic. The densities of predator and prey will oscillate periodically, with both amplitude and period of the oscillations depending on the initial conditions.

Let $(x(t), y(t))$ be a periodic solution of period T . From (29) we deduce that

$$\ln x(T) - \ln x(0) = aT - b \int_0^T y(t) dt$$

$$\ln y(T) - \ln y(0) = -cT + d \int_0^T x(t) dt$$

Since $x(T) = x(0)$ and $y(T) = y(0)$, this implies that

$$\frac{1}{T} \int_0^T x(t) dt = \frac{c}{d}, \quad \frac{1}{T} \int_0^T y(t) dt = \frac{a}{b}.$$

Thus, the time average of the densities will remain constant and equal to their values corresponding to the equilibrium S .

Taking into account the competition within the prey and within the predator, system (29) is replaced by

$$\begin{aligned} \dot{x} &= x(a - bx - cy) \\ \dot{y} &= y(-d + ex - fy) \end{aligned} \tag{30}$$

with positive constants a to f . The positive orthant \mathbb{R}_+^2 is invariant. Its boundary consists of five orbits: two equilibria $(0, 0)$ and $(a/b, 0)$, the two intervals $(0, a/b)$ and $(a/b, +\infty)$ of the x -axis and the positive y axis. The lines

$$bx + cy = a, \quad ex - fy = d$$

eventually intersect in $\text{int}\mathbb{R}_+^2$. Let $S = (\bar{x}, \bar{y})$ be the intersection. The Jacobian matrix at S is

$$A = \begin{bmatrix} -b\bar{x} & -c\bar{y} \\ e\bar{x} & -f\bar{y} \end{bmatrix}$$

The determinant $\det A = (ec + bf)\bar{x}\bar{y}$ is positive and the trace $\text{tr} A = -b\bar{x} - f\bar{y}$ is negative. Thus both eigenvalues are of negative real part and the equilibrium S is locally asymptotically stable. Actually, all the solutions are attracted by S and not only the solutions starting in a small neighborhood of S .

2.3.2 Limit sets

A set M is called an *invariant set* of (28) if for any x in M , the orbit $\gamma(x)$ lies in M . A set M is called *positively invariant* if for each x in M , the positive semi-orbit $\gamma^+(x)$ lies in M . If M is a positively invariant set of (28) and M is homeomorphic to the closed n -ball, there is at least one equilibrium point in M . This result is a consequence of Brouwer's fixed point theorem. As a consequence we obtain the following result

Theorem 3 *In a two dimensional system any closed orbit must surround a singular point.*

An invariant set M is said to be *stable* if for any $\varepsilon > 0$, there is a $\delta > 0$ such that $\text{dist}(x_0, M) < \delta$, implies $\text{dist}(x(t, x_0), M) < \varepsilon$. An invariant set M is said to be *asymptotically stable* if in addition of being stable there is $b > 0$ such that $\text{dist}(x_0, M) < b$, implies $\text{dist}(x(t, x_0), M) \rightarrow 0$ as $t \rightarrow +\infty$.

A nonconstant periodic solution can never be asymptotically stable. To see this, note that for any periodic solution $p(t)$ of (28), $p(t + \tau)$ is also a solution of (28). By taking τ small enough $p(0)$ and $p(\tau)$ can be made arbitrarily close. Nevertheless, $\|p(t + \tau) - p(t)\|$ does not tend to 0 as $t \rightarrow +\infty$, so that asymptotic stability does not prevail. Another concept of stability is of great importance in this case. A periodic solution is said to be *orbitally stable* if the corresponding orbit is stable. A periodic solution is said to be *asymptotically orbitally stable* if the corresponding orbit is asymptotically stable.

A point q belongs to the ω -*limit set* (or *positive limit set*) $\omega(\gamma)$ of an orbit $\gamma(p)$ if there is a sequence a real number (t_k) , $t_k \rightarrow +\infty$ as $k \rightarrow +\infty$ such that $X_{t_k}(p) \rightarrow q$ as $k \rightarrow +\infty$. Similarly a point q belongs to the α -*limit set* (or *negative limit set*) $\alpha(\gamma)$ of an orbit $\gamma(p)$ if there is a sequence a real number (t_k) , $t_k \rightarrow -\infty$ as $k \rightarrow +\infty$ such that $X_{t_k}(p) \rightarrow q$ as $k \rightarrow +\infty$.

Intuitively the positive limit set is the set of points in Ω which are approached along γ with increasing time. A limit set is *invariant*, that is, if it contains a point x , it contains also its orbit $\gamma(x)$. If an orbit γ is positively bounded, that is γ^+ remains in a compact subset of Ω , then its positive limit set $\omega(\gamma^+)$ is nonempty compact and connected.

2.3.3 Poincaré-Bendixon theory

For two dimensional systems the limit sets are well described.

Theorem 4 (Poincaré-Bendixon Theorem) *If γ^+ is a bounded positive semi orbit and $\omega(\gamma^+)$ does not contain a critical point, then $\omega(\gamma^+)$ is a periodic orbit.*

If $\omega(\gamma^+) \neq \gamma^+$, γ^+ actually spirals around $\omega(\gamma^+)$ in a certain sense and the periodic orbit $\omega(\gamma^+)$ is called a *limit cycle*. This result is often used to prove the existence of periodic solutions. Indeed, a closed region which is free from singular points and contains a semi-orbit contains also a closed orbit. Suppose that γ_1 and γ_2 are closed orbits bounding an annular region free from singular points or other closed orbits. We say then that γ_1 and γ_2 are *adjacent*.

Theorem 5 *Two adjacent closed orbits cannot both be asymptotically stable in the region between the two orbits.*

The nonexistence of cycles is guaranteed by the following criterion.

Theorem 6 (Criterion of Dulac-Bendixon) *If $\text{div}X = \partial X_1/\partial x_1 + \partial X_2/\partial x_2$ has a fixed sign (zero excluded) in a region Ω of the plane, then Ω contains no periodic orbits.*

For suppose that there is a cycle γ in Ω and let it bound a region $S \subset \Omega$. Applying Green's formula we have

$$\int \int_S (\partial X_1/\partial x_1 + \partial X_2/\partial x_2) dx_1 dx_2 = \oint_{\gamma} (X_1 dx_2 - X_2 dx_1) = 0$$

Hence $\text{div}X$ cannot have a fixed sign in S , nor a fortiori in Ω .

As a corollary, one obtains: if there is a positive function B on Ω such that $\text{div}BX$ has fixed sign on Ω , then $\dot{x} = X(x)$ admits no periodic orbit in Ω . Indeed X differs from BX only by a change in velocity, which does not affect the orbits. Such a function B is said to be a Dulac function. We have also the following sufficient condition for orbital stability.

Theorem 7 *If the Poincaré index*

$$\int_0^T \text{div}X(p(t))dt$$

of the T -periodic orbit $p(t)$ is negative then $p(t)$ is orbitally asymptotically stable.

The difficulty in applying this result is to localize the periodic orbit C corresponding to the periodic solution and evaluate its Poincaré index.

2.3.4 The Gause predator prey model with Holling-type interaction

The predator prey model of Gause with logistic growth and Holling-type interaction is (see *Classification of Models*)

$$\begin{aligned} \dot{x} &= rx(1 - x/K) - axy/(b + x), \\ \dot{y} &= cxy/(b + x) - dy, \end{aligned} \tag{31}$$

where all parameters are positive. If either $c \leq d$ or $K \leq \frac{bd}{c-d}$, then all solutions of (31) in the positive orthant \mathbb{R}_+^2 converge to the steady state $(K, 0)$, that is, the predator tends to extinction and the prey converges to the carrying capacity K .

If $c > d$ and $K > \frac{bd}{c-d}$, then (31) admits a steady state $S = (\bar{x}, \bar{y})$ with

$$\bar{x} = \frac{bd}{c-d}, \quad \bar{y} = \frac{r}{aK}(K - \bar{x})(b + \bar{x}).$$

If $K \leq b + 2\bar{x}$, then all solutions of (31) in the positive orthant \mathbb{R}_+^2 converge to the steady state S . For the proof consider the Dulac function

$$B(x, y) = \frac{b+x}{x} y^{\alpha-1}, \quad \text{where } \alpha = \frac{r}{c-d} \left(1 - \frac{b}{K}\right)$$

Denoting the right hand side of (31) by X and Y we obtain

$$\frac{\partial BX}{\partial x} + \frac{\partial BY}{\partial y} = \frac{y^{\alpha-1}}{x} \left[r \left(1 - \frac{b}{K} \right) \left(1 - \frac{b+2\bar{x}}{K} \right) - \frac{2r}{K} \left(x - \frac{K-b}{2} \right)^2 \right] \leq 0$$

Hence periodic orbits are excluded.

If $K > b + 2\bar{x}$, then the point S is a repeller and there must be a limit cycle around S . The attractivity of this limit cycle follows from the computation of its Poincaré index. This is a formidable task since it is very difficult to localize this cycle in the plane. Thus all the solutions of (31) in the positive orthant \mathbb{R}_+^2 converge to a periodic solution.

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