CLASSIFICATION OF MODELS

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Contents

Glossary

- continuous: the value taken by the time belongs to $\mathbb{R}$, the set of real numbers
- discrete: the value taken by the time are isolated: $0, h, 2h, ...$
- eigenvalues: roots of the characteristic equation $\det(\lambda Id - A) = 0$, they are complex numbers λ such that $Ax = \lambda x$
- equilibrium point: a point at which the dynamical system remains at rest
- linear: the dynamics of the system is described by a function which is linear in the state, e.g. the multiplication by a matrix
- matrix: a rectangular array of numbers; represents a linear system
- periodic solution (cyclic behavior): a solution that reproduces identically after some period T.
- phase space: the same as state space
- state variables: variable describing the state of the system, that is the quantities required to describe the motion (in time) to the next step
- stability: describes the behavior near an equilibrium point

Summary

We give the description and motivations of some mathematical models arising in biology, in discrete and continuous time.

1 Discrete time models

We will consider in this section models describing a phenomenon varying with time: the time will be discrete, but the variables of the model will be continuous (real numbers). We will give some examples, mainly taken from biological models. The basic methods for studying these models will be given in the next section.

1.1 A model for cell division

The simplest model for this category is maybe the model of the division of a cell into a daughter cells, at each generation. Let us suppose that the number of cell is $x(k)$ at the k^{th} generation (the initial generation is taken as 0). Then, the number of cells at the next generation will be:

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

The number of cells will be successively

$$x(0),\ ax(0),\ a^2x(0), \dots,\ a^nx(0)$$

These numbers follow a geometrical law. If a is greater than one, the population will grow over successive generation, and become unbounded.

This situation is not very realistic, because from a biological point of view the population will be submitted to limitations of the resources. Some models describe the limitations to be proportional to the square x^2 of the population, because of the competition between individuals. The model becomes:

$$x(k+1) = ax(k) - bx^2(k)$$

where b is a positive parameter describing the strength of the competition. It is called the logistic equation, and has become one of the most famous simple nonlinear model; it has a wide spectrum of behavior, from stability to chaos (see *Complexity, pattern recognition and neural models*). There are many other discrete models for a single population (see *Mathematical Models of Biology and Ecology*).

1.2 Matrix and Leslie models

Biologist wish often to model the life cycle of a population in a more structured way. The Leslie matrices describe the transitions between the categories, or stages, determining the life cycle. The most simple model describes the transition between age classes, with the hypothesis that all the individuals in an age class either die or go to the next class. Let us take the example of three age classes; the life cycle can be represented in an intuitive way on a graph with nodes (the age classes) and arrows (the possible transitions). In Figure 1, the transitions are possible from age 2 and 3 towards the first age class; that means that the ages 2 and 3 are fertile.

The set of equations describing the growth for the time k is:

$$\begin{array}{rcl} x_1(k+1) & = & F_2x_2(k) + F_3x_3(k) \\ x_2(k+1) & = & P_1x_1(k) \\ x_3(k+1) & = & P_2x_2(k) \end{array}$$

or in matrix form

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

with

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

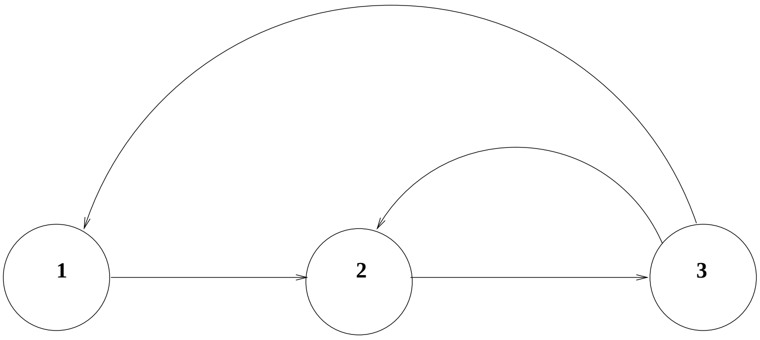

Figure 1: A life cycle

The parameters F_i are the fertility coefficients, and P_i are the probabilities of survival. This kind of matrix is called a Leslie matrix, and has particular mathematical properties linked with Perron-Froebenius theorem (see next section). The model itself is a linear matrix model, with constant coefficients. The mathematical study shows that the solutions of this model have a dominant behavior, that can be characterized by a dominant growth rate (called dominant eigenvalue) playing a role quite similar as the growth rate of our geometrical law in one dimension. If this dominant eigenvalue λ_1 is greater than one, then the numbers of individuals in every age class grow and become unbounded. If λ_1 is smaller that one (λ_1 is nonnegative), then the population goes extinct. Cyclic behavior is possible, as can be seen by taking $F_2 = 0$ (case when the second age class is not fertile), and the other parameters equal to one; if the population starts with some number in the first age class and nothing in the second and third age classes, then this number simply jumps from one age class to the next, without alteration (see *Basic Methods of the Development and Analysis of Mathematical Models*).

The Leslie models, or, more generally, the life cycle models are very appealing to represent complex transitions in the life of organisms; but they cannot incorporate nonlinear effects that appear frequently in the biological processes.

1.3 Nonlinear discrete models

Let us consider the equation giving the number of the first age class:

$$x_1(k+1) = F_2 x_2(k) + F_3 x_3(k)$$

The linear relation between the older age classes and the first one is not very realistic; a more refined model could be to suppose (and to justify with experimental data) that the relation is nonlinear, and that the number of young decreases when the total number $s(k) = x_1(k) + x_2(k) + x_3(k)$ increases. A possible model is:

$$x_1(k+1) = F_2 x_2(k) e^{-bs(k)} + F_3 x_3(k) e^{-bs(k)}$$

where the function $e^{(-bs)}$ is introduce to represent the decreasing of fertility when the density increases. We obtain a density-dependent nonlinear model; the behaviour (and the mathematical study...) can be complicated.

One can also build nonlinear models with no matrix structure; let us cite, among many others, the Nicholson-Bailey model which describe the interaction between hosts and parasitoids. This is a simplified description for the complex and interlaced life cycles of the two species. The parasitoid deposit its eggs in an host (this host being at some stage of its life, often larval or pupal), that becomes a parasited host; the eggs develop at the expense of the host, eventually killing him. Let x_1 the density of host and x_2 the density of parasitoids, then the model is:

$$\begin{array}{rcl} x_1(k+1) & = & \lambda x_1(k) f(x_1(k), x_2(k)) \\ x_2(k+1) & = & c x_1(k)(1 - f(x_1(k), x_2(k))) \end{array} \tag{1}$$

The parameter λ is the host reproductive rate, c is the average number of eggs laid by the parasitoid in the host. The function $f(x_1(k), x_2(k))$ is the fraction of hosts non parasited, and is chosen to be $e^{-ax_2(k)}$, given the hypotheses that the encounters are random, and choosing a Poisson probability distribution to describe the first encounter. This leads to the model:

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

It can be shown (see *Basic Methods of the Development and Analysis of Mathematical Models*) that this model has an equilibrium, and that this equilibrium is unstable: an initial condition near the equilibrium results in diverging oscillations.

2 Continuous time models

We consider in this section the continuous models which describe a phenomenon varying in time. The time will vary continuously. Assume that we have selected the state variables $x(t)$ at time t. It remains to write the equations giving the state variables at time $t + \Delta t$ where Δt is a very short interval of time. Let us denote by $f(t, x(t))\Delta t$ the variation of $x(t)$ during time Δt :

$$x(t + \Delta t) - x(t) = f(t, x(t))\Delta t$$

This equation can be rewritten as

$$\frac{x(t + \Delta t) - x(t)}{\Delta t} = f(t, x(t))$$

Let us postulate the existence of a time derivative

$$\frac{dx}{dt}(t) = \lim_{\Delta t \to 0} \frac{x(t + \Delta t) - x(t)}{\Delta t}$$

which we shall usually denote by $\dot{x}(t)$. Thus, if we go to the limit when Δt goes to 0 we can write

$$\dot{x}(t) = f(t, x(t)) \tag{2}$$

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

$$\begin{array}{c} \dot{x}_1(t) = f_1(t, x_1(t), \cdots, x_n(t)) \\ \cdots \\ \dot{x}_n(t) = f_n(t, x_1(t), \cdots, x_n(t)) \end{array} \tag{3}$$

2.1 Malthus's model and Verhulst's model

Let us begin with the well known 18th century Malthus's model of *exponential growth*. Let $x(t)$ be the population number at time t. The function $x(t)$ is integer valued and hence not differentiable, of course. Still, if the number is very large, or if we consider the density (number per volume) then the jumps caused by individual births and deaths will look negligibly small on a graph of $x(t)$. So let us postulate the existence of a time derivative $\dot{x}(t)$. The ratio $m = \dot{x}/x$ may be viewed as the growth rate of population. If the rate of growth is constant

$$\dot{x} = mx$$

then

$$x(t) = x(0)\mathrm{e}^{mt}$$

We have an exponential growth if $m > 0$ or decay if $m < 0$ of the population, which means explosive growth to infinity or extinction.

The *doubling time* in the case of growth ($m > 0$) is the length of time needed for $x(t)$ to increase from its initial value to twice its initial value. The doubling time is independent of the initial value. Call t_2 the doubling time. Since $x(t_2) = 2x(0) = x(0)\mathrm{e}^{mt_2}$ we obtain

$$t_2 = \frac{\ln 2}{m}.$$

Similarly the *half-life* in case of decay ($m < 0$) is the time required for $x(t)$ to decay to half its initial value. The half time is also independent of the initial value. Call $t_{\frac{1}{2}}$ the half-life. We have

$$t_{\frac{1}{2}} = \frac{-\ln 2}{m}.$$

The doubling of population size in fixed times eventually leads to astronomically large number. This situation is not very realistic and Malthus's model is suitable for the description of the population growth only for times of limited duration. There are various ways in which the model can be made more realistic by slowing or limiting the rate of growth. Among them

- Gompertz' model in which the rate of growth is of the form

  $$r = k\mathrm{e}^{-\alpha t},$$

  that is, it decreases exponentially at time,
- Verhulst's model in which the rate of growth is of the form

  $$r = r(1 - x/K)$$

  that is, a larger population means fewer resources and this implies a smaller rate of growth.

Gompertz's model is described by equation

$$\frac{dx}{dt} = k\mathrm{e}^{-\alpha t}x$$

where k and α are positive constants. The solution are

$$x(t) = x(0)\mathrm{e}^{\frac{k}{\alpha}(1-\mathrm{e}^{-\alpha t})}$$

For Compertz's model, $x(t)$ approaches $x(0)\mathrm{e}^{\frac{k}{\alpha}}$ as $t \to \infty$.

Verhulst or *logistic growth* is described by

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

The constant K is the carrying capacity of the environment. The constant r is the rate of growth for small population numbers. The term $-rx^2/K$ corresponds to competition within the population. The solution is as follows

$$x(t) = \frac{Kx(0)\mathrm{e}^{rt}}{K + x(0)\left(\mathrm{e}^{rt} - 1\right)}$$

The behaviour of the solution is easy to analyze. If $x(0) = 0$ or $x(0) = 0$, the population number $x(t)$ does not change. For $0 < x(0) < K$, it increases to K, and for $x(0) > K$, it decreases to K.

2.2 The Chemostat

The Chemostat, a basic piece of laboratory apparatus, occupies a central place in mathematical ecology. It consists of three connected vessels. The *feed vessel* contains the nutrients needed for growth of a microorganism. The *culture vessel* contains the microorganisms and the nutrients. Measurements are made in the *collection vessel* without disturbing the action in the culture vessel. The contents of the feed vessel are pumped at a constant rate into the culture vessel; the contents of the culture vessel are pumped at the same constant rate into the collection vessel. The differential equations of this model are easy to establish when just one organism is growing in the culture vessel. Let $S(t)$ and $x(t)$ be the concentrations of nutrient and microorganism respectively in the culture vessel at time t are. The differential equations for S and x take the form

$$\begin{aligned} \dot{S} &= (S^{(0)} - S)D - \frac{mxS}{a+S}, \\ \dot{x} &= x\left(\frac{\gamma m S}{a+S} - D\right), \end{aligned} \tag{4}$$

where $S^{(0)}$ is the concentration of the input nutrient, D is the dilution or washout rate, m the maximal growth rate, a the half saturation constant and γ a yield constant reflecting the conversion of the nutrient to organism. The formulation of the consumption term $mxS/(a+S)$ is based on experimental evidence and goes back to Monod in the middle of the 20th century. Other forms have been considered in the literature.

If one adds the two equations and defines $\Sigma = S^{(0)} - S - x/\gamma$, then one obtains

$$\dot{\Sigma} = -D\Sigma, \qquad \dot{x} = x\left(\frac{\gamma m(S^{(0)} - x/\gamma - \Sigma)}{a + S^{(0)} - x/\gamma - \Sigma} - D\right).$$

It follows at once that $\Sigma(t) \to 0$ as $t \to \infty$. At the limit $\Sigma = 0$, the growth of S must satisfy

$$\dot{x} = x\left(\frac{\gamma m(S^{(0)} - x/\gamma)}{a + S^{(0)} - x/\gamma} - D\right).$$

This equation has two steady states $x = 0$ and $x = \gamma(S^{(0)} - \lambda)$ where

$$\lambda = \frac{Da}{\gamma m - D}$$

is called the break-even concentration. If $\gamma m < D$ the organism is washing out faster than its maximal growth rate. If $\gamma m > D$ and $\lambda \geq S^{(0)}$, there is insufficient nutrient available for the organism to survive. In either case, the model predicts that $x(t)$ converges to 0 and extinction of the organism is not surprising. If $\gamma m > D$ and $\lambda < S^{(0)}$, there is sufficient nutrient available for the organism to survive and the model predicts that $x(t)$ converges to $\gamma(S^{(0)} - \lambda)$.

To study competition in the chemostat, introduce two different microorganisms into the culture vessel, labeled x_1 and x_2 with corresponding maximal growth m_i, half saturation a_i and yield constant γ_i. The system is

$$\begin{aligned} \dot{S} &= (S^{(0)} - S)D - \frac{m_1 x_1 S}{a_1 + S} - \frac{m_2 x_2 S}{a_2 + S}, \\ \dot{x}_1 &= x_1\left(\frac{\gamma_1 m_1 S}{a_1 + S} - D\right), \\ \dot{x}_2 &= x_2\left(\frac{\gamma_2 m_2 S}{a_2 + S} - D\right), \end{aligned} \tag{5}$$

For each organism we define the corresponding λ_1 and λ_2. The behaviour of the solution is described by the following result. Suppose that $\gamma_i m_i > D$, $i = 1$ and 2, and that $0 < \lambda_1 < S_2 < S^{(0)}$ then the solutions of (5) with $x_i(0) > 0$ satisfies $x_1(t) \to \gamma_1(S^{(0)} - \lambda_1)$ and $x_2(t) \to 0$. The less efficient organism is excluded by competition: for the study, see *Basic Methods of the Development and Analysis of Mathematical Models.*

2.3 Lotka-Volterra Equations for Predator-Prey Systems

During the First World War, the hostilities between Austria and Italy had disrupted fishery in the Adriatic. In the years after, the amount of Predator fishes was found to be considerably higher than in the years before. Why was the disrupted fishery more favorable to predators than to their prey? This question was posed to Volterra who denoted by x the density of the prey fishes, by y that of the predators, and came up with the differential system

$$\begin{aligned} \dot{x} &= x(a - by) \\ \dot{y} &= y(-c + dx) \end{aligned} \tag{6}$$

with positive constants a, b, c and d. The constant a is the rate of growth of preys in the absence of predators. The constant c is the rate of death of predators, in the absence of preys. By eating the prey, the predator increases its own population and obviously, decreases the population of the prey.

If $x(0) = c/d$ and $y(0) = a/b$ then we obtain $x(t) = c/d$ and $y(t) = c/d$ for all t. The state $S = (x(t) = c/d, y(t) = a/b)$ is called a *steady state* or an *equilibrium point.* We can see that the solutions are periodic. Let $(x(t), y(t))$ be a periodic solution of period T. Volterra proved that

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

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

Volterra's explanation of the increase of predator fishes during the war follows from this property. Fishing reduces the rate growth of prey and augment the rate of death of predators, that is to say, instead of a and c, we now gave some values $a - k$ and $c + m$. However, the interactions constants b and d do not change. The average density of predators is now $\frac{a-k}{b}$ and hence smaller than $\frac{a}{b}$. The average density of prey is now $\frac{c+m}{d}$ and hence larger than $\frac{c}{d}$. Thus disrupting fishing leads to an increase of predators and a decrease of preys.

Taking into account the competition within the prey and within the predator a much more realistic model can be built. System (6) is replaced by

$$\begin{aligned} \dot{x} &= x(a - bx - cy) \\ \dot{y} &= y(-d + ex - fy) \end{aligned} \tag{7}$$

with positive constants a to f. The terms $-bx^2$ and $-fy^2$ correspond to competition within each specie. Depending on the parameters, the lines

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

may or may not intersect. Since population densities have to be nonnegative, we consider the restriction of this system to the positive orthant

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

If they don't intersect in the positive orthant $\mathbb{R}^2_+$, the solutions tend to the steady state $(a/b, 0)$. The predator will therefore vanish; the prey density converges to the carrying capacity of the logistic equation $\dot{x} = x(a - bx)$. In the case of an intersection $S = (\overline{x}, \overline{y})$ in the positive orthant $\mathbb{R}^2_+$, then S is an equilibrium and every solution converge to S.

2.4 Lotka-Volterra Equations for Competing Species

Let us model the interaction of two *competing species.* If x and y denote their densities, then the differential system is

$$\begin{aligned} \dot{x} &= x(a - bx - cy) \\ \dot{y} &= y(d - ex - fy) \end{aligned} \tag{8}$$

with positive constants a to f. The constants a and d are the rate of growth one specie in the absence of the other specie.predators and. absence of preys. The terms $-bx^2$ and $-fy^2$ correspond to competition within each specie. The terms $-cxy$ and $-exy$ correspond to competition within the two species.

Depending on the parameters, the lines

$$bx + cy = a, \qquad ex + fy = d$$

may or may not intersect. If they don't intersect in the positive orthant $\mathbb{R}^2_+$, one of the species tends to extinction. In the case of an intersection $S = (\overline{x}, \overline{y})$, then S is an equilibrium and every solution converge to S in the case where

$$\frac{b}{e} > \frac{a}{d} > \frac{c}{f}.$$

2.5 The general Lotka-Volterra equation

The general Lotka-Volterra for n populations is of the form

$$\dot{x}_i = x_i \left(r_i + \sum_{j=1} a_{ij} x_j \right), \quad i = 1, \cdots, n. \tag{9}$$

The x_i denote the density of the i-th population and the r_i its intrinsic growth (or decay) rate. The a_{ij} describe the effect of the j-th upon the i-th population. The matrix $A = (a_{ij})$ is called the intersection matrix. Since population densities have to be nonnegative, we consider the restriction of this system to the positive orthant

$$\mathbb{R}^n_+ = \{x = (x_1, \cdots, x_n) \in \mathbb{R}^n : x_i \geq 0 \text{ for } i = 1, \cdots, n\}.$$

All kind of interactions can be modeled in this way: if a_{ij} is positive the j-th population enhances the growth of the i-th population, if a_{ij} is negative the j-th population inhibits the growth of the i-th population. Food chains where the first population is the prey of the second, which is the prey of the third etc... were investigated. Taking competition within each species into account, we obtain

$$\begin{aligned} \dot{x}_1 &= x_1 \left(r_1 - a_{11} x_1 - a_{12} x_2 \right) \\ \dot{x}_i &= x_i \left(-r_i + a_{i-1,i} x_{i-1} - a_{ii} x_i - a_{i,i+1} x_{i+1} \right), \quad i = 2, \cdots, n-1 \\ \dot{x}_n &= x_n \left(-r_n + a_{n,n-1} x_{n-1} - a_{nn} x_n \right) \end{aligned} \tag{10}$$

where all parameters are positive. The case $n = 2$ is just the Lotka-Volterra predator prey equation with intra-specific competition. In the general case we know also that all the solution of (10) converge to a steady state.

In general, the behaviour of (9) is much more complicated than the behaviour of (10) or the behaviour of the systems with $n = 2$ considered in the previous sections and many open questions remain. In particular, numerical simulation shows some kind of chaotic motion in which the asymptotic behaviour of the solutions consists of highly irregular oscillations.

2.6 The predator-prey model of Gause

Let x and y denote the densities of prey and predator, respectively. The differential system is

$$\begin{aligned} \dot{x} &= \varphi(x) - y p(x), \\ \dot{y} &= y(q(x) - d). \end{aligned} \tag{11}$$

In the absence of predators, the prey population evolves according to $\dot{x} = \varphi(x)$. The predator reduces the rate of increase $\dot{x}$ of the prey by $yp(x)$, where $p(x)$ is the amount of prey killed by one predator. The positive constant d corresponds to the mortality of the predator in the absence of prey and $q(x)$ is a positive function which represents the amount of prey transformed in predator.

This model is well understood in the case where $\varphi(x) = rx(1 - x/K)$ is a logistic growth and $p(x) = ax/(b + x)$, $q(x) = cx/(b + x)$ are of Holling-type. This type of interaction is associated also with the names of Michaelis-Menten. Then (11) becomes

$$\begin{aligned} \dot{x} &= rx(1 - x/K) - axy/(b + x), \\ \dot{y} &= cxy/(b + x) - dy, \end{aligned} \tag{12}$$

where all parameters are positive. If either $c \leq d$ or $K \leq \frac{bd}{c-d}$, then all solutions of (12) in the positive orthant $\mathbb{R}^2_+$ converge to the steady state $(K, 0)$, that is, the predator tends to extinction and the prey converge to the carrying capacity K.

If $c > d$ and $K > \frac{bd}{c-d}$, then (12) admits a steady state $S = (\overline{x}, \overline{y})$ with

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

If $K \leq b + 2\overline{x}$, then all solutions of (12) in the positive orthant $\mathbb{R}^2_+$ converge to the steady state S. If $K > b + 2\overline{x}$, then all solutions of (12) in the positive orthant $\mathbb{R}^2_+$ converge to a periodic solution (see *Basic Methods of the Development and Analysis of Mathematical Models*).

Gause's model (11) can be extended to more general food chains. The prey predator superpredator equation is

$$\begin{aligned} \dot{x} &= \varphi(x) - yp_y(x), \\ \dot{y} &= y(q_y(x) - d_y - zp_z(y)), \\ \dot{z} &= z(q_z(y) - d_z), \end{aligned} \tag{13}$$

where x, y and z are the densities of prey, predator and superpredator respectively, $p_y(x)$ is the amount of prey killed by one predator, $p_z(y)$ is the amount of predator killed by one superpredator, d_y and d_z correspond to the mortality of predator (in the absence of prey) and superpredator (in absence of predator) respectively, $q_y(x)$ and $q_z(y)$ are positive functions which represent the amount of prey transformed in predator and the amount of predator transformed in superpredator respectively. System (13) is not completely understood and its behaviour is much more complicated than the behaviour of (11).

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