Chapter 1

Phase portrait and its null-cline approximation

1.1 General ideas

Many biological systems are described by one or several differential equations. One of the most famous examples is an equation for the logistic growth of a population:

$$dx/dt = rx(1 - x/k) \tag{1.1}$$

This equation describes growth of a population x in a medium with limited resources. The parameters r and k determine the growth rate and the carrying capacity of this population.

Although the exact solution of this equation is not trivial, it can easily be studied using the qualitative method of one-dimensional phase portrait, or phase flow on a line. You have learned these methods in your previous course of mathematics. I will review them on the example of eq.(1.1). In general, to sketch a phase portrait of an equation

$$dx/dt = f(x) \tag{1.2}$$

we need to draw '$\rightarrow$' or '$\leftarrow$' arrows on the x-axis, which indicates the direction of change of x in the course of time. The '$\rightarrow$' arrow means growth of x, or $\frac{dx}{dt} > 0$. The '$\leftarrow$' arrow means decreasing of x, or $\frac{dx}{dt} < 0$. Due to eq.(1.2) the '$\rightarrow$' arrow also means $f(x) > 0$, and the '$\leftarrow$' arrow means $f(x) < 0$. Thus from the graph of $f(x)$ we can easily obtain a phase portrait and dynamics of the population as indicated in fig.1.1. We see that independent from initial conditions, the size of the population approaches the value of $n = k$.

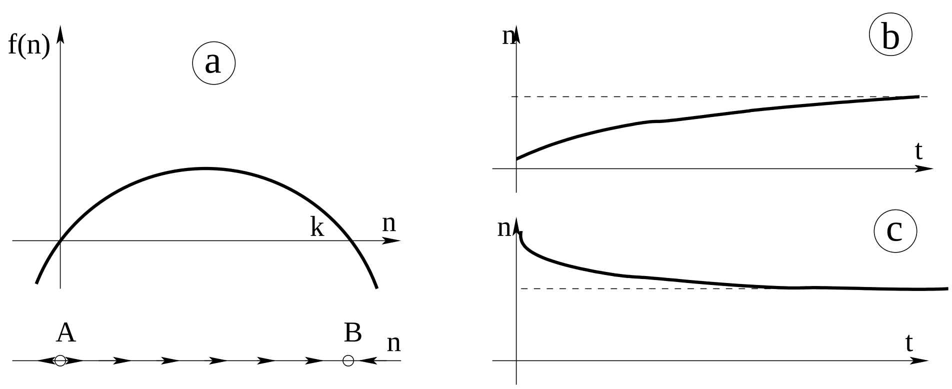

Figure 1.1:

Let us analyze the phase portrait of this equation. We see (fig.1.1) that the regions of different direction of flow (the '$\rightarrow$' and '$\leftarrow$' arrows) are separated by points A and B which are called equilibria points and which are located at $x = 0$ and $x = k$. If the population is at one of these points it will stay there forever, as there $f(x) = 0$ and the size of the population does not change in the course of time ($dx/dt = f(x) = 0$). However, the dynamics of the population around the equilibria are very different. If the initial value of x is a bit above of $x = 0$ the x will grow and it will move further and further from this equilibrium point. If, however, the initial value of x is around the point $x = k$ the x will quickly return to this equilibrium point. Thus point $x = 0$ is called an unstable and point $x = k$ is called a stable equilibrium. Stable equilibria are also called attractors and are of great importance for the dynamics of biological models as they mainly determine the qualitative dynamics of our model, as we see in fig.1.1.

The main aim of this course is to extend this description to models which are expressed in terms of systems of two differential equations. It turns out that such systems are of great interest for many biological models.

1.2 Phase portrait of system of two differential equations

The method which we will develop will work for so-called autonomous system of two differential equations which has the following general form:

$$\begin{cases} dx/dt = f(x,y) \\ dy/dt = g(x,y) \end{cases} \tag{1.3}$$

Many biological systems are described by such systems. One of the classical examples of ecological models (the predator-prey model) can be derived as follows. Let us consider the prey population x with a logistic growth given by eq.(1.1), which interacts with the predator y and let us assume that the effect of the predator on the prey population is given by the term $-bxy$. Then, if we assume that the growth of the predator population is proportional to the predator prey interaction cxy and that the death rate of the predator is given by $-dy$, we will get the following system of differential equations:

$$\begin{cases} dx/dt = rx(1-x/k) - bxy \\ dy/dt = cxy - dy \end{cases} \tag{1.4}$$

Formally system (1.4) describes the predator-prey interactions with competition in the prey population. It has several parameters, which account for the specific properties of the populations. Let us study it for $r = 3, k = 1, b = 1.5, c = 0.5, d = 0.25$:

$$\begin{cases} dx/dt = 3x(1-x) - 1.5xy \\ dy/dt = 0.5xy - 0.25y \end{cases} \tag{1.5}$$

Let us first solve this system on a computer. For that we need to choose some initial sizes of the predator and of the prey populations and find their dynamics in the course of time using a numerical integrator. Solutions for $x(0) = 2, y(0) = 1.5$ are shown in fig.1.2. We see, that in the course of time, x and y approach the stationary values $x = 0.5; y = 1$.

Let us introduce the concept of phase portrait for this system. For one dimensional eq.(1.2) we presented the dynamics in terms of a one-dimensional phase portrait using only the x-axis. Because in two dimensions we have two variables, we need to use two axes to represent the dynamics. Let us consider a two dimensional coordinate system Oxy with the x-axis for the variable x and the y-axis for the variable y. Such a coordinate system is called **a phase space**. Let us represent the trajectory from fig.2.1 on the Oxy-plane. The initial sizes of the populations were $x(0) = 2, y(0) = 1.5$, thus we put this point $(2, 1.5)$ on the Oxy-plane. At the next moment of time we get other values for x and y and we also put them on the Oxy-plane, etc. Finally, we will get the line shown in fig.1.3a. To show the direction

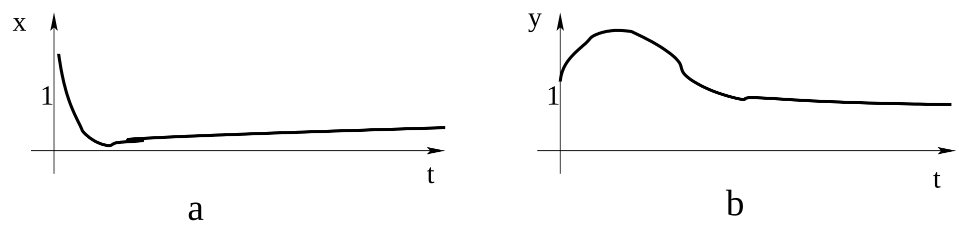

Figure 1.2:

of the x and y change in time we draw the arrows as in fig.1.3a. This trajectory is the first element of the phase portrait. If we start many trajectories from different initial conditions we will get the complete phase portrait of system (1.5) (fig.1.3b). Note, that each trajectory represents a certain type of dynamics

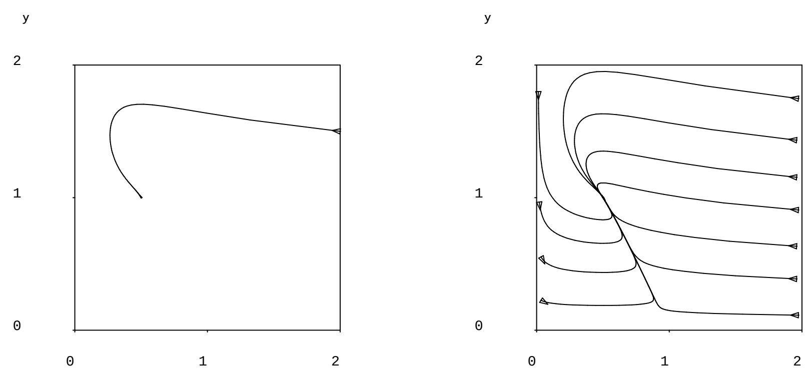

Figure 1.3:

of $x(t),y(t)$, which can be easily shown on time plots similar to fig.1.2.

The main aim of our course is to develop the procedure of drawing a phase portrait of a general system of two differential equations without using a computer. In 1D case the phase portrait included two main elements: equilibria points and flows (trajectories) between them. As we will see similar elements also compose the phase portrait of a system of two differential equations (1.3). Let us start with the first question and understand what are the equilibria points in that case.

1.3 Equilibria

In 1D case the equilibria were the points where our system is stationary: placed at equilibrium point system will stay there forever. Mathematically equilibria for eq.(1.2) were determined as the points where $dx/dt = 0$, i.e. where $f(x) = 0$. Similar condition of stationarity in 2D case should require that both variables x and y are stationary at equilibria points, i.e. both $\frac{dx}{dt} = 0$ and $\frac{dy}{dt} = 0$. Because these derivatives can be expressed in terms of system (1.3) as $\frac{dx}{dt} = f(x,y)$ and $\frac{dy}{dt} = g(x,y)$, it yields the following definition of equilibria in 2D:

Definition 1 *A point (x^*,y^*) is called an equilibrium point of a system (1.3) if*

$$f(x^*,y^*) = 0, \quad g(x^*,y^*) = 0 \tag{1.6}$$

Equilibria in two dimensions are also stationary points, i.e. if system is placed to the equilibrium it will stay there forever. Thus this trajectory will contain just one point.

Example. Find the equilibria of the system (1.5):

Solution To find the equilibria we need to solve a system of algebraic equations (1.6) which in our case becomes:

$$\begin{cases} 3x(1-x) - 1.5xy = 0 \\ 0.5xy - 0.25y = 0 \end{cases} \tag{1.7}$$

From the second equation we find $y(0.5x - 0.25) = 0$, which can be either when $y = 0$ or when $x = 0.5$. Substitution of $y = 0$ to the first equation yields $3x(1-x) - 0 = 0$. This equation has two solutions $x = 0$ and $x = 1$. Substitution of the other case $x = 0.5$ to the first equation gives $3*0.5*(1-0.5) - 1.5*0.5y = 0$, or $y = 1$. Thus we have found three equilibria points: $(0,0), (1,0)$ and $(0.5,1)$.

We see in fig.1.3 that point $(0.5,1)$ is indeed an important attractor of our system which determines the final state of the populations. The other two points are not apparent in fig.1.3, however, as we will see later they also account for important changes of trajectories of our system.

Thus we have defined equilibria for 2D systems. Our next step is to understand what is 2D analog of flows, which on 1D phase portrait were represented by the '$\rightarrow$' or $\leftarrow$ arrows.

1.4 Vector field

In 1D flows were visualizations of the direction of change of the variable x expressed via the sign of its derivative dx/dt. In 2D both variables can change and the rate of their change is given by the derivatives dx/dt and dy/dt. In 1D we were able to find the direction of flow at any point x from the right hand side function of the equation $dx/dt = f(x)$. Similarly in 2D we can find dx/dt and dy/dt at any point (x,y) from the right hand sides of system (1.3) (functions $f(x,y)$ and $(g(x,y))$. For example for system (1.5) at a point $x = 1, y = 1$ we find $dx/dt = f(x,y) = 3x - 3x^2 - 1.5xy = 3 - 3 - 1.5 = -1.5$, and $dy/dt = g(x,y) = 0.5xy - 0.25y. = 0.5 - 0.25 = 0.25$. However, what do these two numbers show? They tell us that if the size of the prey population $x = 1$ and the size of the predator population is $y = 1$, then the prey population decreases with the rate of -1.5 and the predator population grows with the rate of 0.25. On the phase plane x,y this will result in a shift of a point representing populations from point (1,1) (point A in fig.1.4a) to some point B which is to the left and upward from point A. Let us make it more quantitative. We know that rate of change of x in our case is $1.5/0.25$ times larger than the rate of change of y. This determines the direction of shift of point B relative to point A. The easiest way to represent it is to draw from point $(1,1)$ a horizontal arrow heading to the left with the length of 1.5 and a vertical arrow heading upward with the length of 0.25. The direction of the overall shift will be given by the well known rule of the parallelogram fig.1.4b. More precisely the resulting vector will give us the direction tangent to the trajectory which goes through the given point. We can generalize this result as:

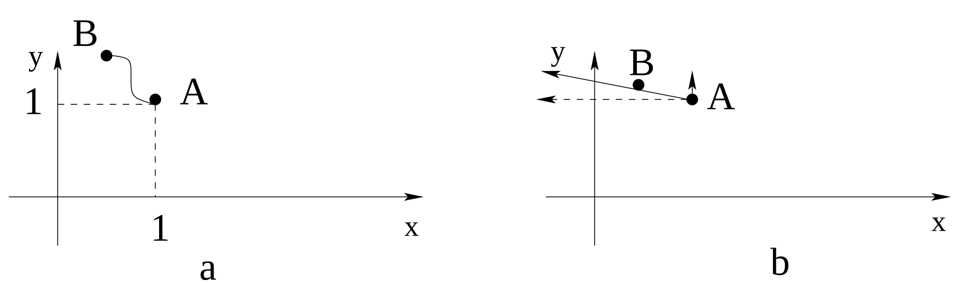

Figure 1.4:

Conclusion 1 *At any point (x,y) of a phase space for an autonomous system (1.3), we can define the vector $\vec{V}$ with the components $(f(x,y), g(x,y))$. Such vectors will be tangent to the trajectories of our*