Mathematical Foundations II: Dynamical Systems

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Dynamical Systems

Goal: This tutorial will serve as an introduction to nonlinear dynamics. We will cover some basic notation for describing time-varying quantities, like many we encounter in biology. We will introduce tools for graphical analysis of equations that are analytically intractable. This approach has the advantage of giving us an intuitive picture of the dynamics of complex systems before we even try to numerically simulate them.

1 What is a dynamical system?

A dynamical system is anything that changes in time. In biology, dynamics are important from the molecular to the ecological scale, and at every level in between. Often, the time evolution of a biological system is complex. This tutorial will introduce you to some basic and powerful tools for analyzing dynamics in nonlinear systems.

2 Basic notation

We begin by defining a general dynamical system with a set of n variables, x_i. The dynamics of this collection of variables is generally written as

$$(2.1)$$

where $\dot{x} = \frac{dx}{dt}$, and $\vec{x} = (x_1, x_2, \ldots, x_n) \in \mathrm{R}^n$ is called the 'phase space' or 'state space' of the dynamical system. This equation can be broken out, component-wise, so that we have an equation for each variable

$$(2.2)$$

The system is linear if all of the x_i's on the right hand side appear to first power only. Some examples of nonlinear terms are: x_1^2, $\sin x_1$, and $x_1 x_3$. Note that we can transform non-autonomous systems, those with explicit time dependence, into this form via:

$$(2.3)$$

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3   A simple pendulum is not so simple

From our first course in general physics, we learn to solve for the equation of motion of a simple harmonic oscillator, $m\ddot{x} + kx = 0$, arriving at the familiar equation, $x(t) = A\cos(\sqrt{\frac{k}{m}}t + \phi)$. We can convert this nonlinear-looking second-order equation into the above form by making the substitution $x_1 = x$ and $x_2 = \dot{x}$ to arrive at a coupled system of linear equations

$$(3.1)$$

Here we see the power of writing out the equations component-wise. In this formulation the two variables now correspond to the position and velocity of the oscillator. These equations only describe the motion of a real pendulum for small perturbations around 0. The implicit approximation made here is that $\sin x \approx x$ for small x. The true equation for a pendulum is $\ddot{x} + \frac{g}{l}\sin x = 0$, where g is the acceleration due to gravity and l is the length of the pendulum. We can also write this out component-wise

$$(3.2)$$

and we see that this is a nonlinear dynamical system that looks quite difficult (or impossible!) to solve. Oftentimes in biological systems, your equations will look like this and seem quite intractable. What can we do when faced with a problem like this?

4   Phase portraits and stability analysis

The big idea here is to run our construction in reverse. Instead of solving for the equations that govern the motion of our variables, we instead try to figure out what trajectories look like in phase space and thereby gain knowledge about those solutions. We will do that all without solving the equations! Instead, we will construct a 'phase portrait' of all of the qualitatively different trajectories in the phase space.

As an example, consider a one-dimensional version of the pendulum equation we just encountered, $\dot{x} = \sin x$, and let's try to solve for $x(t)$ in the usual way and then try to analyze the system graphically. This equation is non-linear, but it is also separable

$$(4.1)$$

We can now work with just the left-hand side of this equation to obtain

$$(4.2)$$

With initial condition, $x(0) = x_0$, we can write down an equation for t in terms of x

$$(4.3)$$

but we want x in terms of t. This equation is hard to invert and is not particularly illuminating. We can make progress, however, by instead plotting $\dot{x}$ versus x and analyzing some basic features of this phase portrait of the system.

Exercise 4.1

1. Sketch the phase portrait of this system, labeling stable and unstable fixed points.

2. Sketch $x(t)$ when $x_0 = \frac{\pi}{4}$.

5 Exponential Growth

We now consider some basic continuous growth models in population biology. Continuous growth models are especially suited for populations where reproduction can happen at any point in time.

For a discrete time model, we have:

$$(5.1)$$

meaning that the rate of increase is equal to the increase in the number of individuals $N(t + \Delta t) - N(t)$ divided by the initial number of individuals. What happens if we make the interval Δt shorter and shorter? For Δt going to zero, we obtain:

$$(5.2)$$

rearranging:

$$(5.3)$$

which is the differential equation for the exponential (Malthusian) growth you should be familiar with.

5.1   Analysis

Given the initial condition:

$$(5.4)$$

we can solve the equation. The equation is separable:

$$(5.5)$$

Integrating both sides:

$$(5.6)$$

$$(5.7)$$

$$(5.8)$$

$$(5.9)$$

$$(5.10)$$

$$(5.11)$$

The interpretation of the solution is the following: for $r > 0$ the population grows exponentially. For $r < 0$ the decay is exponential. For $r = 0$ the population is constant.

6   The Logistic Growth Model

6.1   Intraspecific Competition

We have considered a model in which populations grow without constraint. However, due to the finiteness of resources, an environment cannot sustain an infinite population. When resources start being scarce, a fierce competition among individuals of the same species begins. We call this effect intraspecific competition (i.e., within the same species).

To set the stage, let's examine some data from Gause (1932). To test the effects of intraspecific competition, Gause used brewer's yeast (*Saccharomyces cerevisiae*). His experiments were based on the growth of yeast in an environment with a limited nutrients. He started the population at some low level and then he measured the volume of the cells in time. The data is represented in Figure 1.
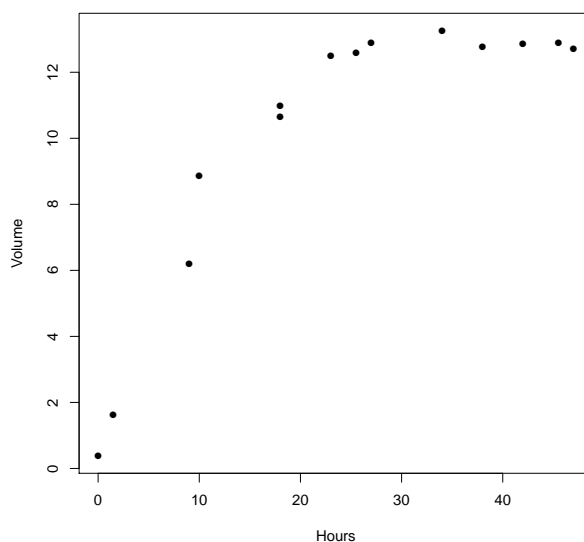

Figure 1: Data measured by Gause. Growth of brewer's yeast in an environment with limited nutrients.

Clearly, yeast does not grow to infinity. Rather, after 1 day or so the population stops growing and remains around a given volume. Suppose that a population can grow up to a certain threshold K, usually known as carrying capacity. This model can be represented by the differential equation:

$$(6.1)$$

where r can be measured as the growth rate at very low density and K is the carrying capacity for the system, i.e., the density of individuals the habitat can support. Note that $r > 0$ and $K > 0$, otherwise it does make biological sense (Why if $r < 0$ the equation does not make sense?)

6.2 Analysis

Plot $\frac{dN(t)}{dt}$ vs. $N(t)$ (see Figure 2). Using this graphical method we can count the number of equilibria and investigate their stability.

We define an equilibrium point (or steady state, or fixed point or critical point) a point in which $\frac{dN}{dt} = 0$. In this point, the growth rate is zero: left alone, the population will not grow nor decay. In the logistic growth equation we have two fixed points: $N^* = 0$, $N^* = K$. This can be seen in the graph whenever $\frac{dN}{dt}$ crosses the zero line.
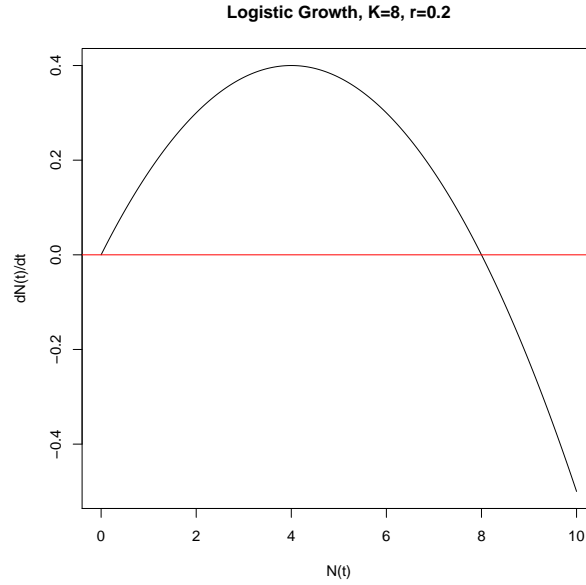
Figure 2: Graphical methods for logistic growth.

An equilibrium point N^* is stable if when we slightly perturb the system that is resting at N^*, $\lim_{t \to \infty} N(t) = N^*$. We can think about stability using the cartoon in Figure 3.

The red ball is at an unstable equilibrium point: slightly perturbing its position will set it in motion ending up at another point. The blue balls, on the other hand, will return to the same point once slightly perturbed: they are at stable equilibrium points.

For the logistic growth, we have that $N_1^* = 0$ is unstable, while $N_2^* = K$ is stable. If you start with zero bacteria, say, you will always have zero, but as soon as you have a single organism, you get exponential growth. Close to this fixed point, the system does not 'feel' the carrying-capacity. For single species dynamics, whenever growth rate is > 0 on the left of the fixed point and < 0 on the right of the fixed point we have stability. Therefore, if a species has density 0 and we slightly increase its density (decreasing it would be a biological nonsense) it will start growing until it reaches density K, when it will stop growing. It stops growing exponentially, and with the same rate that it exploded near 0.

We will now use some mathematics to get a qualitative understanding of equilibria. First, we want to find the equilibria. By definition, we want to solve the equation:

$$\tag{6.2}$$

There is a trivial solution:
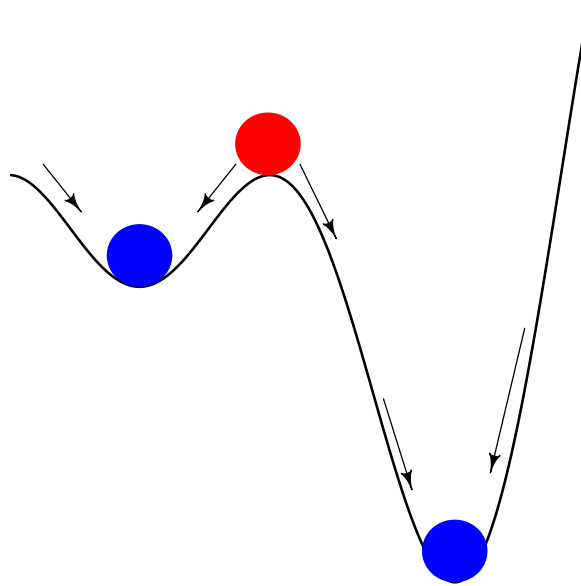
$$\tag{6.3}$$

while the other solution can be found using:

Figure 3: Stability as a metaphor.

$$\tag{6.4}$$

$$\tag{6.5}$$

$$\tag{6.6}$$

We now want to measure the growth rate in the vicinity of an equilibrium. First, let us assume that $N(0) \ll K$ (i.e., the population at time 0 is at a much lower level than the carrying capacity). Then, $(1 - N(0)/K) \approx 1$. This means that the growth rate equation is approximately:

$$\tag{6.7}$$

the population, when close to 0, will grow almost exponentially. In the same way, we can evaluate what happens when $N(0) \approx K$. In this case $(1 - N(0)/K) \approx 0$ and therefore:

$$\tag{6.8}$$

the population will remain constant.

Finally, when $N(0) \gg K$ the term $(1 - N(0)/K)$ becomes negative (say the value is some unspecified $-y$). Then the approximate growth becomes:

$$\tag{6.9}$$

the population decreases exponentially.

We want to know where the population grows at the fastest rate. To do so, we first take the derivative:

$$\tag{6.10}$$

and equate it to zero:

$$\tag{6.11}$$

$$\tag{6.12}$$

we find that when the population is half-saturated, it grows at the fastest rate. Piecing these facts together, we can draw a qualitative solution for the differential equation (Figure 4).
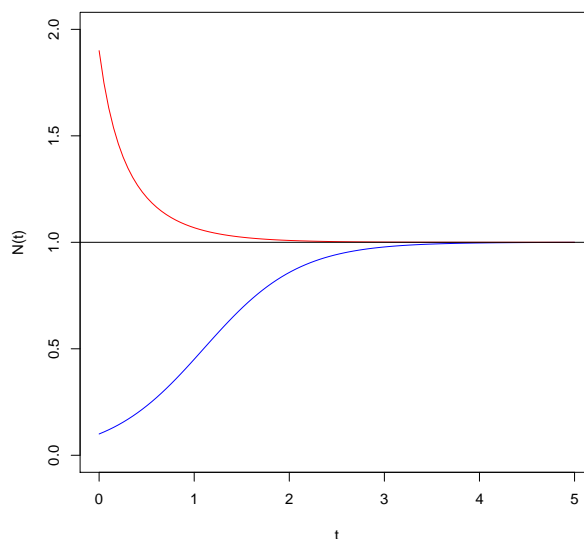

Figure 4: Logistic Growth: $K = 1$, $r = 2$. Blue: $N(0) = 0.1$, Red: $N(0) = 1.9$

This qualitative drawing captures the essential features of the solution:

8

$$(6.13)$$

7 Euler method for numerical integration

The Euler method is a very basic way to perform numerical integration on an ordinary differential equation. Suppose you wish to approximate a function, $\dot{x}(t) = f(x)$. You start at some initial condition, x_0, and want to play the dynamics forward in time. The Euler method has a simple update rule, based on the definition of the derivative from your intro calculus course. For a small step in time, Δt, update x by

$$(7.1)$$

where x_n is an approximation to $x(t_n)$.

This method is very simple to code but suffers from the fact that you need to take step sizes, Δt, much smaller than any intrinsic time scale in your system to achieve good performance. Other numerical integration methods, such as Runge-Kutta, are included in most programming packages. You should simulate a system in which you know the solution to familiarize yourself with these numerical integration schemes.

8 Further reading

Would you like to know more about nonlinear dynamics and chaos? If so, a particularly accessible set of online lectures by Steve Strogatz is available on YouTube, and a link can be found in the README for this tutorial.