

# Week 9-11: Nonlinear deterministic models.\*

Sergei S. Pilyugin†

## 1 Introductory notes

In constantly evolving systems, such as growing populations of organisms, determinism is understood as the property of the current state of the system to uniquely predict all future states of the system, provided of course, that the rule of evolution is known. There are at least two different ways to describe such rule of evolution:

- Using a *discrete dynamical system*, where the states of the system are observed at discrete sequential moments of time. In population models, the most natural way is to track the populations over the successive generations. If we denote the state of the population in generation  $n$  by  $\mathbf{x}_n$ , then the rule of evolution may be written as

$$\mathbf{x}_{n+1} = F(\mathbf{x}_n), \quad n = 0, 1, 2, 3, \dots$$

so that the state in a given generation uniquely determines the state in the next generation. Here, the state may refer to a combination of several numerical quantities, hence I am using the vector notation. If we define the *initial state* of the system to be  $\mathbf{x}_0$ , then all subsequent states are determined inductively as

$$\mathbf{x}_n = F^n(\mathbf{x}_0) = F(F(F(\dots F(\mathbf{x}_0))))). \quad (1)$$

Clearly, this is a deterministic process. The iterative scheme (1) is called the discrete dynamical system.

- Using a *continuous dynamical system*, or a *differential equation*. The main difference here is that the system is observed over some continuous interval of times, and the rule of evolution is prescribed by determining the *instantaneous rate of change* of the current state in terms of the state itself. If we denote the state of the system at time  $t$  as  $\mathbf{x}(t)$ , then the rule of evolution can be written as

$$\frac{d\mathbf{x}(t)}{dt} = F(\mathbf{x}(t)), \quad t \geq 0. \quad (2)$$

The continuous evolution rule (2) is called the differential equation or a system of differential equations. If we endow (2) with the initial condition  $\mathbf{x}(0) = \mathbf{x}_0$ , then the corresponding *initial value problem* will describe a unique solution  $\mathbf{x}(t)$  (provided that  $F$  depends on  $\mathbf{x}$  in sufficiently regular way).

There are more complicated types of evolution equations but they lie outside the scope of this course.

---

\*© Sergei S. Pilyugin, Department of Mathematics, University of Florida

†This course is made possible by the financial support from the Howard Hughes Medical Institute.

## 2 Examples of discrete dynamical systems

### 2.1 Geometric growth/decay

In the simplest possible case, we may assume that the population size increases/decreases by a certain factor  $a > 0$  (the reproductive ratio) over each generation. In this case, we obtain a very simple recursion

$$x_{n+1} = ax_n,$$

which has the solution  $x_n = a^n x_0$ . If  $x_0 > 0$ , the population will grow without bound for  $a > 1$ , decay to zero for  $a < 1$ , and remain constant for  $a = 1$ . If  $x_0 = 0$ , the population will remain zero for all subsequent generations. Such model is clearly oversimplified, and not very realistic, especially if  $a > 1$ . But it does illustrate several important concepts such as reproductive ratio, geometric growth and decay, and the existence of the fixed point  $x = 0$ .

Before making a more complicated model, let's in addition assume that the population is subject to immigration, that is, per each generation, a certain number  $b$  of individuals enters the population. How will this affect the dynamic behavior (or evolution) of the population? First, let's modify the dynamical system to include the immigration as follows:

$$x_{n+1} = ax_n + b.$$

We have that

$$x_1 = ax_0 + b, \quad x_2 = a(ax_0 + b) + b = a^2x_0 + (a + 1)b, \dots$$

and in general

$$x_n = a^n x_0 + (a^{n-1} + a^{n-2} + \dots + a + 1)b = a^n x_0 + b \frac{a^n - 1}{a - 1},$$

where  $a \neq 1$ . For  $a = 1$ , we have  $x_n = x_0 + nb$ .

How does the presence of immigration change the dynamics? For  $a \geq 1$ , it is clear that the population still grows without bound. This claim is obvious for  $a = 1$ , and for  $a > 1$ , we have

$$\lim_{n \rightarrow \infty} \left( a^n x_0 + b \frac{a^n - 1}{a - 1} \right) = \infty.$$

If  $a < 1$ , the situation is somewhat different. Calculating the same limit, we find that

$$\lim_{n \rightarrow \infty} \left( a^n x_0 + b \frac{a^n - 1}{a - 1} \right) = \frac{b}{1 - a},$$

regardless of the initial population size  $x_0$ . The value  $x^* = \frac{b}{1-a}$  corresponds to a fixed point of our dynamical system, because

$$ax^* + b = a \frac{b}{1-a} + b = \frac{ab + (1-a)b}{1-a} = x^*.$$

Moreover, regardless of the initial value  $x_0$ , the population size will approach this fixed point (constant population size) in the limit.

The main assumption behind geometric population growth is essentially an unlimited amount of resource that supports growth. In a more realistic scenario, the resource is limited and the individual members of the population must compete for this resource to survive and proliferate. There are different ways to modify the original simple model to

account for resource limitation. The most direct way is to assume that the reproductive ratio decreases with the population size. In other words, we can study the case where  $a = a(x)$  and  $x_{n+1} = a(x_n)x_n$ . Several classical models fit into this category. Three examples are the discrete logistic equation

$$x_{n+1} = r \left(1 - \frac{x_n}{K}\right) x_n,$$

the discrete Beverton-Holt equation

$$x_{n+1} = r \frac{x_n}{K + x_n},$$

and the Ricker equation

$$x_{n+1} = r \exp\left(-\frac{x_n}{K}\right) x_n.$$

The meaning of the parameter  $K$  in these models varies slightly, but in general  $K$  is correlated with the carrying capacity of the environment, that is, the number of individuals  $x^*$  that can be maintained at a fixed point.

### **3 Examples of continuous dynamical systems**

#### **4 Fixed points and equilibria. Notion of stability.**

#### **5 Positive/negative feedback**

#### **6 Oscillations**

#### **7 MATLAB notes**

#### **References**