Lecture 1: Introduction to Linear Population Dynamics

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Outline

Let $\mathrm{N}(t)$ be the number of individuals in a population. Probably the first model to describe the growth of a population is the model of Malthus [66] (1798), which reads as follows

$$\frac{\mathrm{dN}(t)}{\mathrm{d}t} = \underbrace{b\,\mathrm{N}(t)}_{\text{Flux of newborn}} - \underbrace{m\,\mathrm{N}(t)}_{\text{Flux of exiting or death}}, \tag{1}$$

where $b \geq 0$ is the *birth rate* and $m \geq 0$ is the *mortality rate*. Equation (1) must be supplemented by initial data

$$\mathrm{N}(t_0) = \mathrm{N}_0 \geq 0, \tag{2}$$

where $N_0 \geq 0$ is the number of individuals at time t_0.

If we integrate equation (1) over the interval $[t, t+\Delta t]$, we obtain

$$\mathrm{N}(t+\Delta t) = \mathrm{N}(t) + \int_t^{t+\Delta t} b\,\mathrm{N}(\sigma)\mathrm{d}\sigma - \int_t^{t+\Delta t} m\,\mathrm{N}(\sigma)\mathrm{d}\sigma. \tag{3}$$

When we talk about the *flux* of newborn (respectively the flux of exiting or death), we mean that by integrating in time over the interval $[t, t+\Delta t]$ we obtain

$$\int_t^{t+\Delta t} b\,\mathrm{N}(\sigma)\mathrm{d}\sigma, \quad \left(\text{respectively } \int_t^{t+\Delta t} m\,\mathrm{N}(\sigma)\mathrm{d}\sigma\right),$$

the number of newborn individuals (respectively the number of exiting or dead individuals) during the time interval $[t, t+\Delta t]$.

The *growth rate of the population* is defined as $r = b - m$ and we can rewrite the equation as

$$\frac{\mathrm{dN}(t)}{\mathrm{d}t} = r\,\mathrm{N}(t). \tag{4}$$

If we assume that $\mathrm{N}(t) > 0$ for all $t \geq t_0$, then

$$\begin{aligned}
&\frac{\mathrm{N}'(t)}{\mathrm{N}(t)} = r, \quad \forall t \geq t_0, \\
&\Leftrightarrow \int_{t_0}^{t} \frac{\mathrm{N}'(\sigma)}{\mathrm{N}(\sigma)} \mathrm{d}\sigma = \int_{t_0}^{t} r \,\mathrm{d}\sigma, \quad \forall t \geq t_0, \\
&\Leftrightarrow \ln(\mathrm{N}(t)) - \ln(\mathrm{N}(t_0)) = r\,(t - t_0), \quad \forall t \geq t_0,
\end{aligned}$$

therefore we obtain

$$\mathrm{N}(t) = \mathrm{N}_0 \exp\left(r\,(t - t_0)\right), \quad \forall t \geq t_0. \tag{5}$$

Remark 1.1

By computing the derivative of the formula obtained in (5) we deduce that this formula remains a solution whenever $N_0 \leq 0$.

In practice we fix a time step Δt (equal to one year, one month, one day etc ...) and by using (4) we obtain the formula

$$\mathrm{N}(t+\Delta t) = \mathrm{N}(t)\exp\left(r\,\Delta t\right), \quad \forall t \geq t_0 \quad \Leftrightarrow \quad \ln\left(\frac{\mathrm{N}(t+\Delta t)}{\mathrm{N}(t)}\right) = r\,\Delta t, \quad \forall t \tag{6}$$

This means that the function $t \to \ln\left(\dfrac{\mathrm{N}(t+\Delta t)}{\mathrm{N}(t)}\right)$ is constant in time, and

$$r\,\Delta t = \ln\left(\frac{\mathrm{N}(t+\Delta t)}{\mathrm{N}(t)}\right) = \ln\left(\mathrm{N}(t+\Delta t)\right) - \ln\left(\mathrm{N}(t)\right), \quad \forall t \geq t_0. \tag{7}$$

Hence r is the log variation of $\mathrm{N}(t)$ per unit of time Δt.

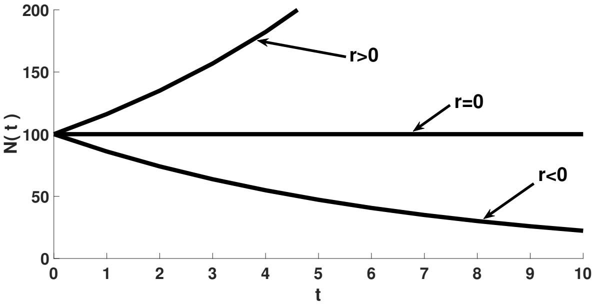

Figure: *In this figure we plot* $t \to 100\,\exp(rt)$ *over the time interval* $[0, 10]$ *and choose* $r = 0.15$, $r = 0$ *and* $r = -0.15$ *from the top to the bottom.*

This model predicts that

- If $r = 0$ the population size is stationary or constant (in time).
- If $r > 0$ the population size grows exponentially and never stops growing.
- If $r < 0$ the population size approaches 0 as the time goes to infinity. In other words, the population becomes extinct after an infinite time.

Outline

The continuous model assumes that the flux of newborns and the flux of death are constant in time. In most wild populations reproduction takes place seasonally, and mortality is also influenced by the seasons (temperature, food availability, etc...). The same is true for humans, who are more susceptible to viruses in winter (for example), so the seasons also matter for human populations. The cells in our body do not have the same activity during the day as they do at night. This is the so-called circadian rhythm. Therefore it makes sense to consider the following extended version of the Malthusian model

$$\frac{\mathrm{dN}(t)}{\mathrm{d}t} = r(t)\,\mathrm{N}(t), \quad \forall t \geq t_0 \text{ and } \mathrm{N}(t_0) = \mathrm{N}_0 \geq 0. \tag{8}$$

The time-dependent growth rate $r(t)$ can be defined by

$$r(t) = b(t) - m(t), \quad \forall t \geq t_0,$$

where $b(t)$ and $m(t)$ are respectively the time-dependent birth rate and mortality rate.

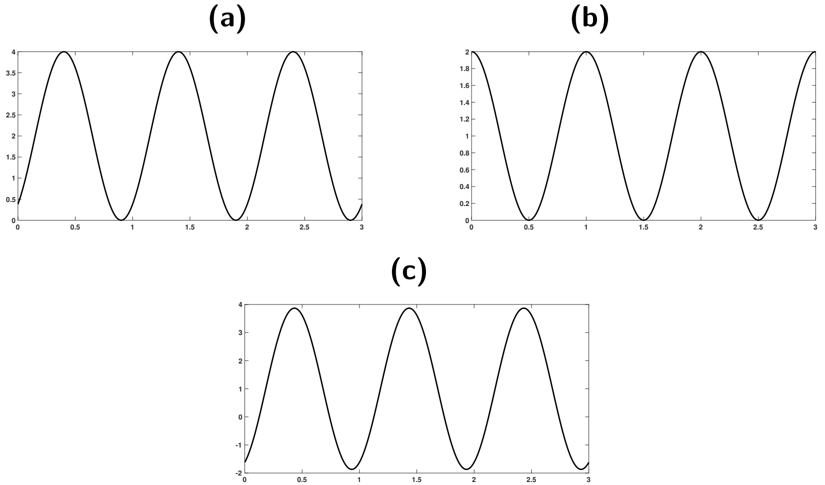

Figure: *In this figure we plot the birth rate $t \to b(t) = 2\left(\cos(2\pi(t+0.6)) + 1\right)$ in figure (a), the death rate $t \to m(t) = \cos(2\pi t) + 1$ in figure (b) and we plot the growth rate $t \to b(t) - m(t)$ in figure (c).*

In Figure 2, if the time $t_0 = 0$ corresponds to January 1, the mortality of the animals will reach a maximum and therefore it makes sense to consider a mortality rate having the following form

$$m(t) = \cos(2\pi t) + 1.$$

The births will take place mostly around June, so it makes sense to consider a birth rate having the following form

$$b(t) = 2\left(\cos(2\pi(t + 0.6)) + 1\right).$$

The birth rate $b(t)$, the death rate or mortality rate $m(t)$ and the growth rate $r(t) = b(t) - m(t)$ are represented in Figure 2 (a), (b) and (c) respectively. The solutions of the periodic Malthusian model are represented in Figure 3 and in Figure 4 with a log scale.

In Figures 3 and 4 we are using the following formula for the solution

$$\mathrm{N}(t) = \mathrm{N}_0 \mathrm{e}^{\int_{t_0}^{t} r(\sigma)\mathrm{d}\sigma}, \quad \forall t \geq t_0.$$

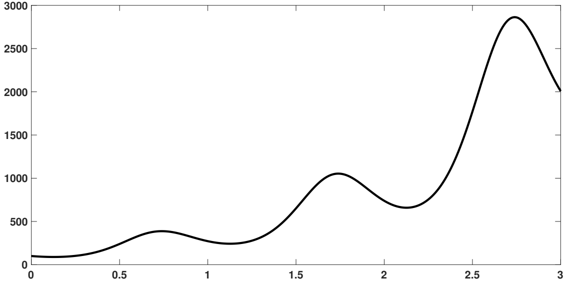

Figure: *In this figure we plot*

$$t \to \mathrm{N}(t) = 100 \times \exp\left(\int_0^t 2\left(\cos(2\pi(\sigma + 0.6)) + 1\right)\right) - \left(\cos(2\pi\sigma) + 1\right) \mathrm{d}\sigma\right).$$

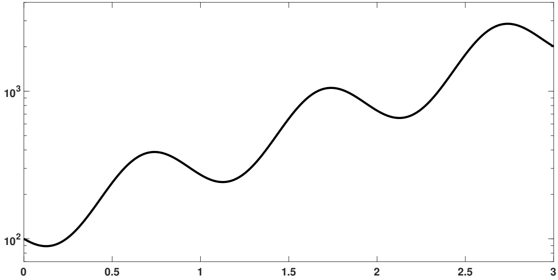

Figure: *In this figure we plot*

$$t \to \mathrm{N}(t) = 100 \times \exp\left(\int_0^t 2\left(\cos(2\pi(\sigma+0.6))+1)\right) - \left(\cos(2\pi\sigma)+1\right)\mathrm{d}\sigma\right).$$

By comparing Figure 3 and Figure 4 we can see that making some nonlinear transformation on the number of individuals may completely change our understanding of the solution. Indeed it is difficult to say anything about Figure 3, which looks complex already, while we can see that Figure 4 involves some periodic growth. The same thing could happen for data involving the seasonal growth of populations.

Outline

For the time-periodic population dynamics model, the period Δt could be one day (if we are talking about a cell growing in a dish); one year (if we are considering populations subject to seasonal changes), etc...

In periodic Malthusian models, we can take advantage of the periodicity to summarize the growth by using a single parameter over the whole period of time Δt. Remember that

$$\mathrm{N}(t) = \mathrm{e}^{\int_{t_0}^{t} r(\sigma)\mathrm{d}\sigma}, \quad \forall t \geq t_0 \text{ and } \mathrm{N}(t_0) = \mathrm{N}_0 \geq 0. \tag{9}$$

Assume that $t \to r(t)$ is Δt-periodic, that is,

$$r(t + \Delta t) = r(t), \quad \forall t \in \mathbb{R}.$$

Then

$$\frac{\mathrm{d}}{\mathrm{d}t} \int_{t}^{t+\Delta t} r(\sigma)\mathrm{d}\sigma = r(t + \Delta t) - r(t) = 0,$$

and the map $t \to \int_{t}^{t+\Delta t} r(\sigma)\mathrm{d}\sigma$ is constant.

We deduce that

$$\mathrm{N}(t+\Delta t) = R\,\mathrm{N}(t), \quad \forall t \geq t_0,$$

where

$$R = \exp\left(\int_{t_0}^{t_0+\Delta t} r(\sigma)\mathrm{d}\sigma\right).$$

Moreover, by defining

$$t_n = n \times \Delta t + t_0, \quad \forall n \in \mathbb{N},$$

and

$$U_n := \mathrm{N}(t_n), \quad \forall n \in \mathbb{N},$$

we have

$$t_{n+1} = t_n + \Delta t \text{ and } U_{n+1} := \mathrm{N}(t_n + \Delta t), \quad \forall n \in \mathbb{N}.$$

So we obtain the difference equation

$$U_n = R\,U_{n-1}, \quad \forall n \in \mathbb{N} \text{ with } U_0 = N_0. \tag{10}$$

The above equation can be rewritten equivalently as follows

$$U_n = R^n\,U_0, \quad \forall n \in \mathbb{N}, \tag{11}$$

where

$$R^n = \underbrace{R \times R \times \ldots \times R}_{\text{n times}}.$$

The qualitative behavior of the solution is completely determined by comparing R to 1:

- If $R = 1$ the population size is stationary or constant (in time).
- If $R > 1$ the population size grows exponentially and never stops growing.
- If $R < 1$ the population size approaches 0 as the time goes to infinity. In other words, the population becomes extinct in infinite time.

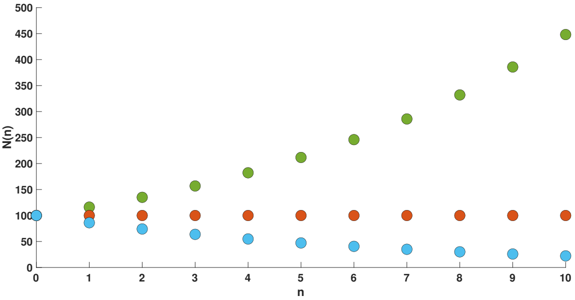

Figure: *In this figure we plot* $n \to 100 \times R^n$ *over the time interval* $[0, 10]$ *and choose* $R = \exp(0.15)$ *(green),* $R = 1$ *(orange) and* $R = \exp(-0.15)$ *(blue) from the top to the bottom.*

In vitro experiments allow the computation of r and R. For example, the above formula is used to compute the so-called growth rate in cell cultures (in a Petri dish). In vivo, exponentially growing populations can also be observed by looking at an invading population. Otherwise, after the population has become well established, some limitations (for food, space, etc...) will limit the exponential growth and another behavior (with a saturation) will occur.

A natural question to address is the following:

Does a population (without limitation) always grow exponentially?

We can also ask the following question:

Is there a unique growth rate for the population that does not depend on how much time has elapsed since the population was established?

To investigate this question, in the next section we consider a discrete-time age-structured model and we will see what can be kept from the Malthusian models.

Outline

In this section, we consider the so-called Leslie model (1945) [50, 51]. The Leslie model is a discrete-time age-structured population dynamics model. When we consider only two age classes, this model reads as follows

$$\begin{cases} \mathrm{N}_1(t+1) = \beta_1 \mathrm{N}_1(t) + \beta_2 \mathrm{N}_2(t), \\ \mathrm{N}_2(t+1) = \pi_1 \mathrm{N}_1(t), \end{cases} \tag{12}$$

for each $t \in \mathbb{N}$ (time in year) with the initial distribution

$$\begin{pmatrix} N_1(0) \\ N_2(0) \end{pmatrix} = \begin{pmatrix} N_1^0 \\ N_2^0 \end{pmatrix}. \tag{13}$$

The parameters of the system as well as the state variables are defined below.

- β_1 is the average number of offspring produced per individuals in the first age class (i.e. with age $a \in [0, 1)$);
- β_2 is the average number of offspring produced per individuals in the second age class (i.e. with age $a \in [1, 2)$);
- $\pi_1 \in [0, 1]$ is the probability to survive from the first age class to the second age class;
- $N_1(t)$ is the number of individuals in the first age class at time t. That is, the number of individuals with age $a \in [0, 1)$ at time t;
- $N_2(t)$ is the number of individuals in the second age class at time t. That is, the number of individuals with age $a \in [1, 2)$ at time t.

The total number of individuals in the population at time t is given by

$$N(t) := N_1(t) + N_2(t).$$

The diagram of flux is presented in Figure 6. The loop for the first age class corresponds to the individuals that reproduce immediately after their birth. This is possible if we consider some insects like mosquitoes, for example.

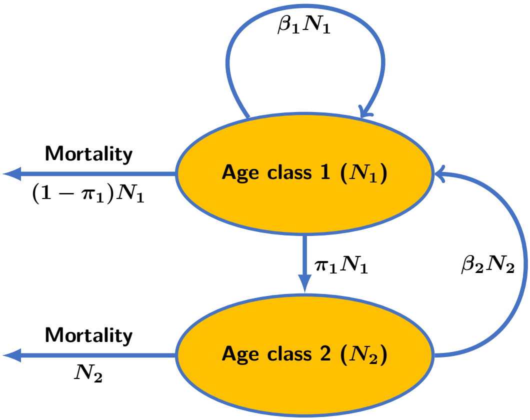

Figure: *Diagram of flux for the two age classes model* (12).

This model is obtained by using the following description

$$
\begin{aligned}
N_1(t+1) = \; & \text{number of offspring produced by the first age during the} \\
& \text{period } [t, t+1] \\
& + \text{number of offspring produced by the second age during the} \\
& \quad \text{period } [t, t+1]
\end{aligned}
$$

and

$$
\begin{aligned}
N_2(t+1) = \; & \text{number of individuals in the first age class who survived the per} \\
& \text{of time } [t, t+1].
\end{aligned}
$$

The system (12) can be rewritten in matrix form as

$$\begin{pmatrix} N_1(t+1) \\ N_2(t+1) \end{pmatrix} = \begin{pmatrix} \beta_1 & \beta_2 \\ \pi_1 & 0 \end{pmatrix} \begin{pmatrix} N_1(t) \\ N_1(t) \end{pmatrix}, \tag{14}$$

where the matrix

$$L = \begin{pmatrix} \beta_1 & \beta_2 \\ \pi_1 & 0 \end{pmatrix} \tag{15}$$

is called a *Leslie matrix*.

We observe that

$$\begin{pmatrix} N_1(2) \\ N_2(2) \end{pmatrix} = L \times \begin{pmatrix} N_1(1) \\ N_2(1) \end{pmatrix} = L \times L \begin{pmatrix} N_1(0) \\ N_2(0) \end{pmatrix}$$

therefore by using an induction argument we obtain

$$\begin{pmatrix} N_1(n) \\ N_2(n) \end{pmatrix} = L^n \begin{pmatrix} N_1(0) \\ N_2(0) \end{pmatrix}, \quad \forall n \geq 0,$$

where

$$L^n = \underbrace{L \times L \times \ldots \times L}_{n \text{ times}}.$$

The special case $\beta_1 = 0$

In the special case $\beta_1 = 0$ the Leslie matrix L has the following form

$$L = \begin{pmatrix} 0 & \beta_2 \\ \pi_1 & 0 \end{pmatrix},$$

and it follows that

$$L^2 = L \times L = \begin{pmatrix} \beta_2 \pi_1 & 0 \\ 0 & \beta_2 \pi_1 \end{pmatrix} = \beta_2 \pi_1 \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}.$$

Therefore

$$L^2 = \gamma^2 I,$$

where

$$I = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \text{ and } \gamma = \sqrt{\beta_2 \pi_1}.$$

By using this observation we deduce that

$$\begin{aligned} &L^2 = \gamma^2 I, \\ &L^3 = L \times L \times L = \gamma^2 L, \\ &L^4 = L \times L \times L \times L = L^2 \times L^2 = \gamma^4 I, \end{aligned}$$

and by induction, we deduce that for each integer $n \geq 0$

$$L^{2n} = \underbrace{L^2 \times L^2 \times \ldots \times L^2}_{n \text{ times}} = \gamma^{2n} I$$

and

$$L^{2n+1} = L^{2n} \times L = \gamma^{2n} L.$$

In this special case the population grows but the direction of the distribution $(N_1(n), N_2(n))$ may change a lot.

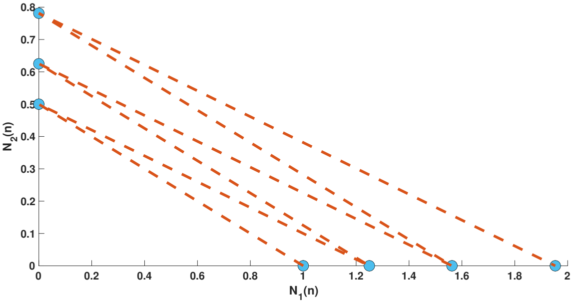

Figure: *In this figure we plot $(N_1(n), N_2(n))$ where n varies from 0 to 6.*

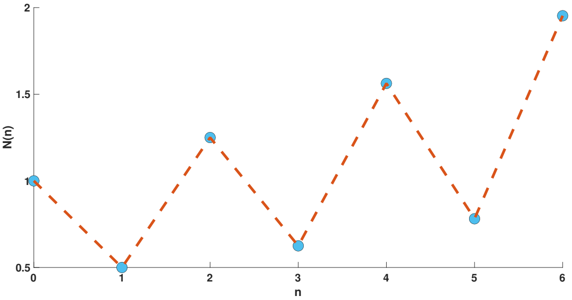

Figure: *In this figure we plot* $n \to N(n) = N_1(n) + N_2(n)$ *over the time interval* $[0, 6]$.

By using Figures 7 and 8 we obtain undamped oscillations for the direction of the population distribution. The population grows like an exponential, but with a large oscillation.

In this special case, we may try to find some initial distribution that gives a constant direction (i.e. we can look for some non-negative eigenvector). In other words, we look for a non-negative vector $(N_1^\star, N_2^\star)$ such that

$$L \begin{pmatrix} N_1^\star \\ N_2^\star \end{pmatrix} = \gamma \begin{pmatrix} N_1^\star \\ N_2^\star \end{pmatrix},$$

where $\gamma = \sqrt{\beta_2 \pi_1}$. We have

$$L \begin{pmatrix} N_1^\star \\ N_2^\star \end{pmatrix} = \gamma \begin{pmatrix} N_1^\star \\ N_2^\star \end{pmatrix} \Leftrightarrow \begin{cases} \beta_2 N_2^\star = \gamma N_1^\star \\ \pi_1 N_1^\star = \gamma N_2^\star \end{cases} \Leftrightarrow N_1^\star = \sqrt{\frac{\beta_2}{\pi_1}} N_2^\star.$$

Therefore starting from

$$N_1^\star = \sqrt{\frac{\beta_2}{\pi_1}} \text{ and } N_2^\star = 1,$$

the direction of the population distribution does not change over time.

In Figure 9 we observe that this direction is preserved.

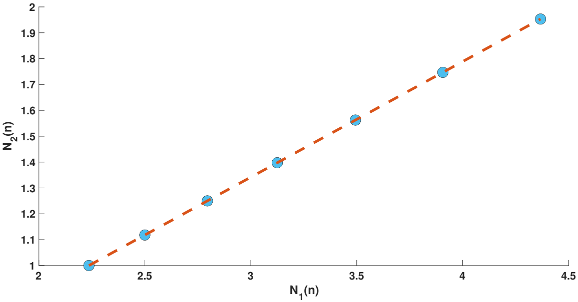

Figure: *In this figure we plot* $(N_1(n), N_2(n))$ *where* n *varies from* 0 *to* 6*. The MATLAB code uses the initial distribution* $N_1(0) = \sqrt{\dfrac{\beta_2}{\pi_1}}$ *and* $N_2(0) = 1$.

In Figure 10 we observe a Malthusian growth with no oscillations around the exponential.

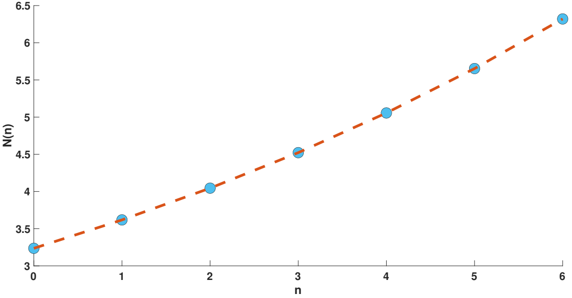

Figure: *In this figure we plot* $n \to N(n) = N_1(n) + N_2(n)$ *over the time interval* $[0, 6]$. *The MATLAB code uses the initial distribution* $N_1(0) = \sqrt{\frac{\beta_2}{\pi_1}}$ *and* $N_2(0) = 1$.

The special case $\beta_2 = 0$

In the special case $\beta_2 = 0$ the Leslie matrix L has the following form

$$L = \begin{pmatrix} \beta_1 & 0 \\ \pi_1 & 0 \end{pmatrix}$$

and it follows that

$$L^2 = \begin{pmatrix} \beta_1^2 & 0 \\ \pi_1 \beta_1 & 0 \end{pmatrix}$$

and by induction

$$L^n = \begin{pmatrix} \beta_1^n & 0 \\ \pi_1 \beta_1^{n-1} & 0 \end{pmatrix} = \beta_1^{n-1} L, \quad \forall n = 1, 2, 3, \ldots.$$

We deduce that

$$L^n \begin{pmatrix} 1 \\ 0 \end{pmatrix} = \beta_1^{n-1} \begin{pmatrix} \beta_1 \\ \pi_1 \end{pmatrix}, \text{ and } L^n \begin{pmatrix} 0 \\ 1 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}.$$

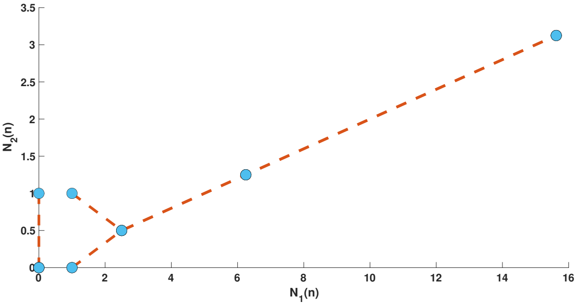

Figure: *In this figure we plot $(N_1(n), N_2(n))$ where n varies from 0 to 6. The MATLAB code uses the initial distribution $(N_1(0), N_2(0))$ is either $(1, 0)$, $(0, 1)$ or $(1, 1)$. We use $\pi_1 = 0.5$ and $\beta_1 = 2.5$.*

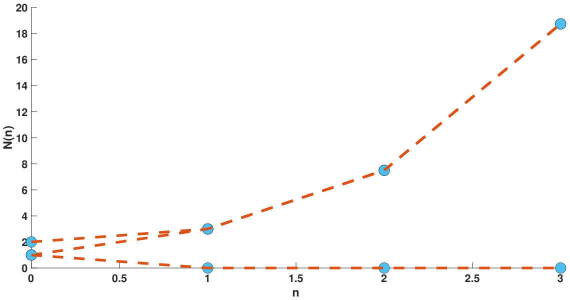

Figure: *In this figure we plot* $n \to N(n) = N_1(n) + N_2(n)$ *over the time interval* $[0, 6]$*. The MATLAB code uses the initial distribution* $(N_1(0), N_2(0))$ *is either* $(1, 0)$*,* $(0, 1)$ *or* $(1, 1)$*. We use* $\pi_1 = 0.5$ *and* $\beta_1 = 2.5$*.*

The special case $\beta_1 > 0$ and $\beta_2 > 0$

The case $\beta_1 > 0$ and $\beta_2 > 0$ is considered in Chapter 4, devoted to the so-called Perron–Frobenius theorem (see [72] and [25, 26]). Actually from this theorem, we obtain an asynchronous exponential growth result.
In Chapter 4, we will see that there exists a constant $\lambda > 0$ and two strictly positive vectors $V_r \in (0, +\infty)^2$, a right eigenvector of L (i.e. $LV_r = \lambda V_r$), and $V_l \in (0, +\infty)^2$, a left eigenvector of L (i.e. $V_l^T L = \lambda V_r^T$), with $\langle V_l, V_r \rangle = 1$ such that

$$\lim_{n \to +\infty} \frac{1}{\lambda^n} L^n U(0) = \langle V_l, U_0 \rangle V_r,$$

where $\langle \cdot, \cdot \rangle$ is the Euclidean scalar product.

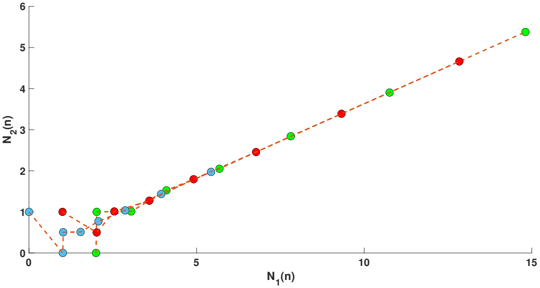

Figure: *In this figure we plot* $(N_1(n), N_2(n))$ *where* n *varies from* 0 *to* 6. *The MATLAB code uses the initial distribution* $(N_1(0), N_2(0))$ *is either* $(1, 0)$, $(0, 1)$ *or* $(1, 1)$. *We use* $\pi_1 = 0.5$ *and* $\beta_1 = \beta_2 = 1.01$.

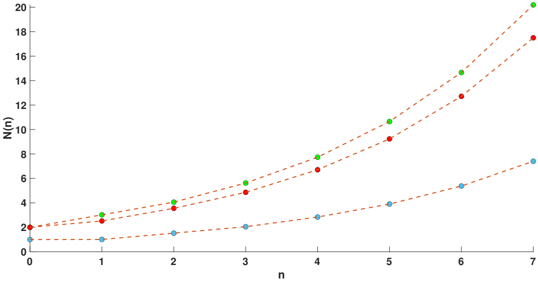

Figure: *In this figure we plot* $n \to N(n) = N_1(n) + N_2(n)$ *over the time interval* $[0, 6]$. *The MATLAB code uses the initial distribution* $(N_1(0), N_2(0))$ *is either* $(1, 0)$, $(0, 1)$ *or* $(1, 1)$. *We use* $\pi_1 = 0.5$ *and* $\beta_1 = \beta_2 = 1.01$.

Outline

Before describing the general Leslie model, let us consider the Leslie model with three age classes. By using the same notation and the same idea as the model with two age classes we can write the following model

$$\left\{\begin{array}{l} \mathrm{N}_1(t+1) = \beta_1 \mathrm{N}_1(t) + \beta_2 \mathrm{N}_2(t) + \beta_3 \mathrm{N}_3(t), \\ \mathrm{N}_2(t+1) = \pi_1 \mathrm{N}_1(t), \\ \mathrm{N}_3(t+1) = \pi_2 \mathrm{N}_2(t), \end{array}\right. \tag{16}$$

for each $t \in \mathbb{N}$ (time in year) with the initial distribution

$$\begin{pmatrix} N_1(0) \\ N_2(0) \\ N_3(0) \end{pmatrix} = \begin{pmatrix} N_1^0 \\ N_2^0 \\ N_3^0 \end{pmatrix}.$$

The Leslie system (16) can be rewritten in the following matrix form

$$\begin{pmatrix} N_1(t+1) \\ N_2(t+1) \\ N_3(t+1) \end{pmatrix} = \begin{pmatrix} \beta_1 & \beta_2 & \beta_3 \\ \pi_1 & 0 & 0 \\ 0 & \pi_2 & 0 \end{pmatrix} \begin{pmatrix} N_1(t) \\ N_2(t) \\ N_3(t) \end{pmatrix}.$$

Therefore the Leslie matrix corresponding to three age groups takes the following form

$$L = \begin{pmatrix} \beta_1 & \beta_2 & \beta_3 \\ \pi_1 & 0 & 0 \\ 0 & \pi_2 & 0 \end{pmatrix}.$$

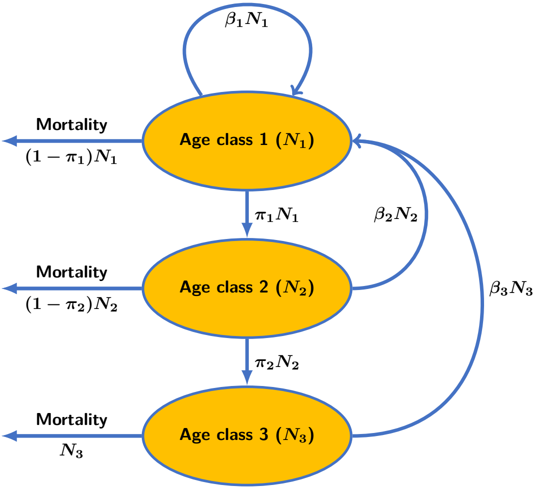

Figure: *Diagram of flux for the three age classes model. The loop for the first age class corresponds to the individuals that reproduce immediately after their birth (as in some insects, like mosquitoes).*

The Leslie model can be extended to an arbitrary number of age classes $n \geq 2$

$$\begin{cases} \mathrm{N}_1(t+1) = \beta_1 \mathrm{N}_1(t) + \beta_2 \mathrm{N}_2(t) + \cdots + \beta_n \mathrm{N}_n(t), \\ \mathrm{N}_2(t+1) = \pi_1 \mathrm{N}_1(t), \\ \vdots \\ \mathrm{N}_n(t+1) = \pi_{n-1} \mathrm{N}_{n-1}(t), \end{cases} \tag{17}$$

for each $t \in \mathbb{N}$ (time in years) with the initial distribution

$$\begin{pmatrix} N_1(0) \\ N_2(0) \\ \vdots \\ N_n(0) \end{pmatrix} = \begin{pmatrix} N_1^0 \\ N_2^0 \\ \vdots \\ N_n^0 \end{pmatrix}.$$

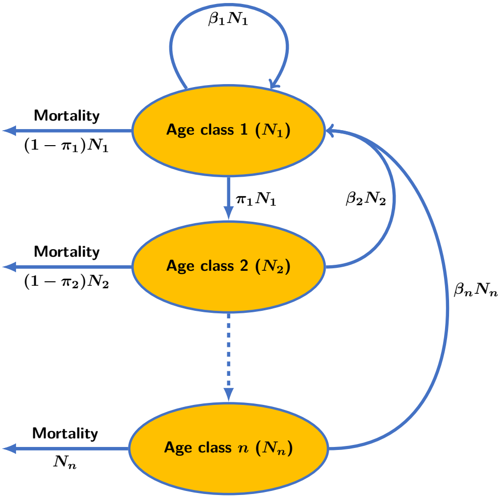

Figure: *Diagram of flux for the n age classes model. The loop for the first age class corresponds to individuals that reproduce immediately after their birth.*

The system (17) can be rewritten in matrix form as the following vector-valued difference equations

$$\begin{pmatrix} N_1(t+1) \\ N_2(t+1) \\ \vdots \\ N_n(t+1) \end{pmatrix} = \begin{pmatrix} \beta_1 & \beta_2 & \beta_3 & \dots & \beta_n \\ \pi_1 & 0 & 0 & \dots & 0 \\ 0 & \pi_2 & 0 & \dots & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \dots & 0 & \pi_{n-1} & 0 \end{pmatrix} \begin{pmatrix} N_1(t) \\ N_2(t) \\ \vdots \\ N_n(t) \end{pmatrix}, \quad \forall t = 0, 1, . \tag{18}$$

The corresponding Leslie matrix is the following

$$L = \begin{pmatrix} \beta_1 & \beta_2 & \beta_3 & \dots & \beta_n \\ \pi_1 & 0 & 0 & \dots & 0 \\ 0 & \pi_2 & 0 & \dots & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \dots & 0 & \pi_{n-1} & 0 \end{pmatrix}.$$

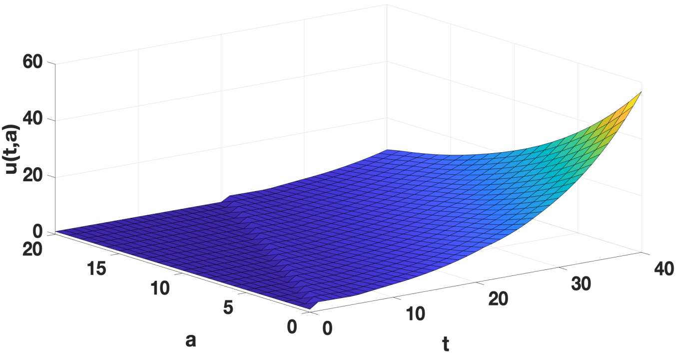

Figure: *In this figure we plot a solution* $t \to u(t,a)$ *of the Leslie model with* $a \in [0,20]$. *The reproduction function is defined by* $\beta(a) = 0.8 * \Delta a$ *if* $a > 5$ *and* $\beta(a) = 0$ *otherwise. The survival rate is* $\pi(a) = \exp(-0.1 * \Delta a)$. *The initial distribution is constant, equal to* 1. *We observe that it takes* 40 *years for the distribution of population to grow exponentially.*

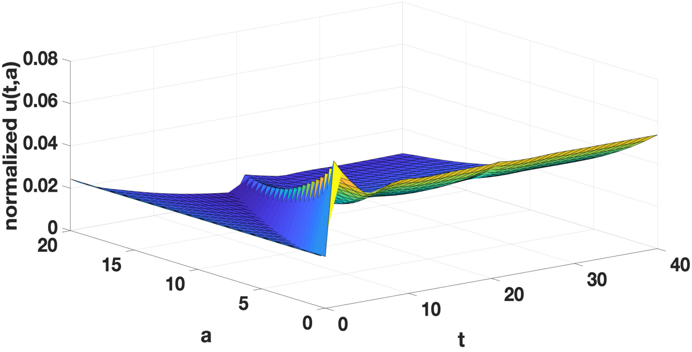

Figure: *In this figure we plot a normalized solution* $t \to u(t,a)/\Sigma_{i=0,\dots,20} u(t,i)$ *of the Leslie model* $a \in [0,20]$*. The reproduction function is defined by* $\beta(a) = 0.8 * \Delta a$ *if* $a > 5$ *and* $\beta(a) = 0$ *otherwise. The survival rate is* $\pi(a) = \exp(-0.1 * \Delta a)$*. The initial distribution is constant, equal to* 1*. We observe the convergence of the normalized distribution when the time becomes large enough.*

Remark 5.1

The above convergence result of the normalized distribution is a consequence of the Perron–Frobenius theorem. This example will be reconsidered in the lecture devoted to Perron–Frobenius theorem.

Outline

Instead of considering a discrete-time age-structured model we can also look at a continuous-time model with a discrete number of age classes as before. By using the same notations and the same model idea as the model with two age classes we can write the following model

$$\begin{cases} \mathrm{N}_1(t)' = \underbrace{\beta_1 \mathrm{N}_1(t) + \cdots + \beta_n \mathrm{N}_n(t)}_{\text{Flux of newborn}} - \underbrace{\mu_1 \mathrm{N}_1(t)}_{\text{Exit or death}} - \underbrace{\eta_1 \mathrm{N}_1(t),}_{\text{Flux going to class 2}} \\ \mathrm{N}_2(t)' = \eta_1 \mathrm{N}_1(t) - \underbrace{\mu_2 \mathrm{N}_2(t)}_{\text{Exit or death}} - \underbrace{\eta_2 \mathrm{N}_2(t),}_{\text{Flux going to class 3}} \\ \quad \vdots \\ \mathrm{N}_n(t)' = \eta_{n-1} \mathrm{N}_{n-1}(t) - \underbrace{\mu_n \mathrm{N}_n(t)}_{\text{Exit or death}} - \underbrace{\eta_n \mathrm{N}_n(t),}_{\substack{\text{Flux of individuals} \\ \text{getting older}}} \end{cases} \tag{19}$$

for each $t \in \mathbb{N}$ (time in years) with the initial distribution

$$\begin{pmatrix} N_1(0) \\ N_2(0) \\ \vdots \\ N_n(0) \end{pmatrix} = \begin{pmatrix} N_1^0 \\ N_2^0 \\ \vdots \\ N_n^0 \end{pmatrix}.$$

The system (19) can be rewritten in matrix form as

$$N(t)' = M\,N(t),$$

where the matrix of the system is the difference of two matrices

$$M = L - D,$$

where L is again a Leslie matrix defined by

$$L = \begin{pmatrix} \beta_1 & \beta_2 & \beta_3 & \dots & \beta_n \\ \eta_1 & 0 & 0 & \dots & 0 \\ 0 & \eta_2 & 0 & \dots & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \dots & 0 & \eta_{n-1} & 0 \end{pmatrix}$$

and D is the diagonal matrix

$$D = \begin{pmatrix} \mu_1 + \eta_1 & 0 & \dots & 0 \\ 0 & \mu_2 + \eta_2 & \ddots & \vdots \\ \vdots & \ddots & \ddots & 0 \\ 0 & \dots & 0 & \mu_n + \eta_n \end{pmatrix}.$$

Outline

In this section, we follow an idea of Sattenspiel and Dietz [82]. We present a patch model adapted to intercity movement. Our goal is to explain how to derive the parameters of the model in practice.
Our goal is to propose a short-term patch model to describe the movement of individuals during a few months (1–6 months). Therefore we can neglect the vital birth and death dynamic. In the case of an epidemic, we assume that the number of deaths does not significantly change the number of individuals in a given city.
To build our patch model, we make the following assumptions.

Assumption 7.1

We assume that the time spent in city 2 by visitors from city 1 follows an exponential law, and the average length of stay is $1/\rho_{21}$.

Let us start with two cities. Define

- 1) $U_{11}(t)$ the number of individuals from city 1 staying in city 1 and
- 2) $U_{21}(t)$ the number of individuals from city 1 traveling in city 2 if $i = 2$.

The total number of individuals originating from city 1 is

$$U_1 = U_{11}(t) + U_{21}(t), \tag{20}$$

which is assumed to be constant for simplicity.

The model is given by

$$\begin{cases} U_{11}'(t) = -\Gamma_{12}(t) & +\rho_{21}U_{21} \\ U_{21}'(t) = + \underbrace{\Gamma_{12}(t)}_{\substack{\text{Flux of individuals}\\ \text{traveling to city } 2\\ \text{from city } 1}} & - \underbrace{\rho_{21}U_{21}}_{\substack{\text{Flux of individuals}\\ \text{returning back home}}} \end{cases} \tag{21}$$

In our model $\rho_{21}U_{21}$ is the flux of individuals returning back home to city 1 after a trip in city 2. In order to apply our model we need to determine $1/\rho_{21}$, the average length of stay in city 2 for individuals originating from city 1. Moreover, Γ_{12} is the flux of individuals living in city 1 who are traveling in city 2.

Assumption 7.2

We assume that the number of individuals originating from city 1 who are traveling in city 2 is

$$U_{21} = f_{21} \, U_{11}, \tag{22}$$

where $f_{21} \geq 0$.

Remark 7.3

From (20) and (22) we have

$$U_1 = (1 + f_{21})U_{11} \Leftrightarrow U_{11} = \frac{1}{1 + f_{21}} U_1,$$

therefore (22) is equivalent to

$$U_{21} = \frac{f_{21}}{1 + f_{21}} U_1 = p_{21} \, U_1.$$

We observe that

$$p_{21} = \frac{f_{21}}{1 + f_{21}} \Leftrightarrow f_{21} = \frac{p_{21}}{1 - p_{21}}.$$

Therefore the parameter f_{21} in (22) can be computed by using $p_{21} \in (0, 1)$, which is the fraction of individuals living in city 1 and traveling in city 2.

By substituting $U_{21} = p_{21} U_1$ (on the left-hand side) and $U_{21} = f_{21}\, U_{11}$ (on the right-hand side) of the U_2-equation into the second equation of (21) we get

$$0 = +\Gamma_{12}(t) - \rho_{21} f_{21}\, U_{11}(t). \tag{23}$$

Therefore we obtain

$$\Gamma_{12}(t) = \rho_{21}\, f_{21}\, U_{11}(t).$$

Hence the patch model describing the movement of individuals living in city 1 must be

$$\left\{ \begin{array}{lll} U_{11}' = & -\rho_{21} f_{21}\, U_{11} & +\rho_{21}\, U_{21} \\ U_{21}' = & +\rho_{21} f_{21}\, U_{11} & -\rho_{21}\, U_{21}. \end{array} \right. \tag{24}$$

Remark 7.4

Conversely by summing the two equations of (24)*, we obtain* $U_1(t)' = 0$*. Moreover, by replacing* U_{11} *by* $U_1 - U_{21}$ *in the second equation of* (24)*, we obtain*

$$U_{21}' = +\rho_{21} f_{21} \left(U_1 - U_{21}\right) - \rho_{21} U_{21} \tag{25}$$

which is equivalent to

$$U_{21}' = +\rho_{21} f_{21} U_1 - \rho_{21} \left(1 + f_{21}\right) U_{21}. \tag{26}$$

Therefore

$$\lim_{t\to\infty} U_{21}(t) = \frac{f_{21}}{1+f_{21}} U_1 = p_{21} U_1.$$

Similarly,

$$\lim_{t\to\infty} U_{11}(t) = \left(1 - p_{21}\right) U_1.$$

The model with two cities

The movement of individuals living in city 1 with 2 cities is described by

$$\textbf{(Individuals from city 1)} \left\{ \begin{array}{rlll} U_{11}' = & -\rho_{21} f_{21} U_{11} & +\rho_{21} U_{21} \\ U_{21}' = & +\rho_{21} f_{21} U_{11} & -\rho_{21} U_{21}. \end{array} \right. \tag{27}$$

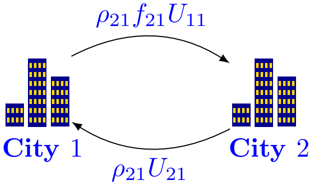

Figure: *Movement of individuals originating from city 1 with 2 cities.*

The movement of individuals living in city 2 with 2 cities is described by

$$\textbf{(Individuals from city 2)} \quad \begin{cases} U_{22}' = & -\rho_{12} f_{12} U_{22} \quad +\rho_{12} U_{12} \\ U_{12}' = & +\rho_{12} f_{12} U_{22} \quad -\rho_{12} U_{12}, \end{cases} \tag{28}$$

where U_{12} is the number of individuals originating from city 2 who are traveling in city 1 and U_{22} is the number of individuals originating from city 2 staying in city 2. The total number of individuals in city 2 is

$$U_2 = U_{12} + U_{22}.$$

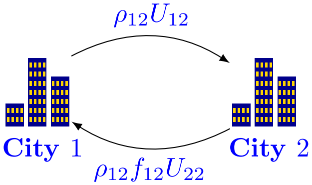

Figure: *Movement of individuals originating only from city 2 with 2 cities.*

The model with two cities and without origin distinction

The previous models (27) and (28) allow more freedom in the movement of individuals. Indeed, such models allow different behaviors for the people who originate from each city. However, to simplify the model, we may wish to reduce the number of parameters. The following reduction procedure can be helpful.

To simplify the previous models (27) and (28), we write a model without distinguishing the origin of individuals. Indeed, the total number of individuals staying in city 1 at time t is given by

$$U_{1.} = U_{11} + U_{12}$$

and the total number of individuals staying in city 2 at time t is given by

$$U_{2.} = U_{21} + U_{22}.$$

By summing the first equation of (27) and the second equation of (28) we obtain

$$U'_{1.} = -\rho_{21} f_{21}\, U_{11} + \rho_{21}\, U_{21} + \rho_{12} f_{12}\, U_{22} - \rho_{12}\, U_{12},$$

and by summing the second equation of (27) and the first equation of (28) we obtain

$$U'_{2.} = +\rho_{21} f_{21}\, U_{11} - \rho_{21}\, U_{21} - \rho_{12} f_{12}\, U_{22} + \rho_{12}\, U_{12}.$$

Assumption 7.5

Assume that $\rho_{21} f_{21} = \rho_{12}$ *and* $\rho_{21} = \rho_{12} f_{12}$.

Under the above assumption, we obtain a model with two cities without origin distinction

$$\begin{cases} U_{1.}' = & -\rho_{12}U_{1.} & +\rho_{12}U_{2.}, \\ U_{2.}' = & \rho_{12}U_{1.} & -\rho_{12}U_{2.}. \end{cases} \tag{29}$$

Outline

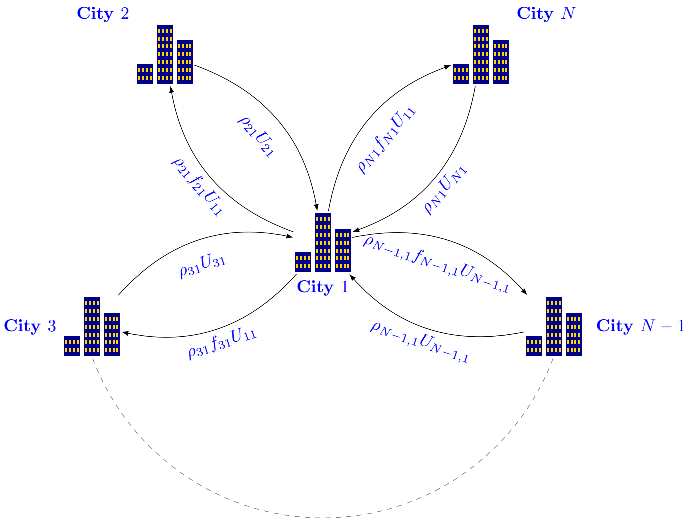

Figure: *Movement of individuals originating from city* 1.

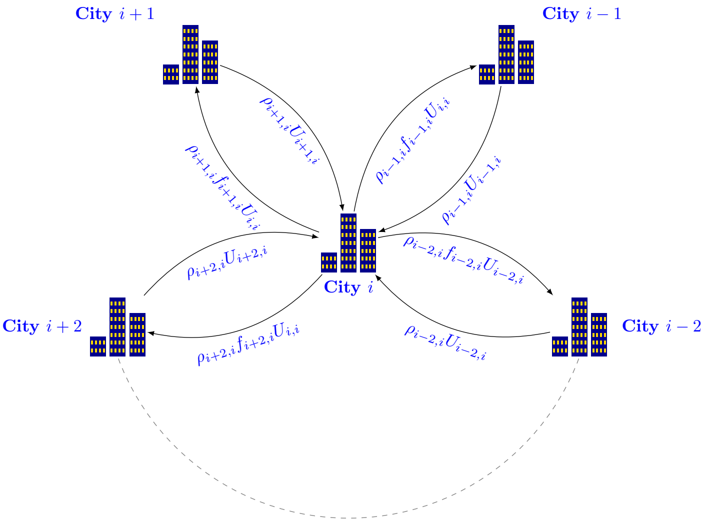

Figure: *Movement of individuals originating from city i.*

The model describing the movement of individuals originating from city 1 is

(Individuals from city 1)

$$\left\{\begin{array}{lccc} U_{11}' = & -\left(\displaystyle\sum_{i=2}^{N}\rho_{i1}f_{i1}\right)U_{11} & +\sum_{i=2}^{N}\rho_{i1}\,U_{i1} \\ U_{21}' = & +\rho_{21}f_{21}\,U_{11} & -\rho_{21}\,U_{21} \\ \vdots & \vdots & \vdots \\ U_{N1}' = & +\rho_{N1}f_{N1}\,U_{11} & -\rho_{N1}\,U_{N1}. \end{array}\right. \tag{30}$$

The model describing the movement of individuals originating from city i is

(Individuals from city i)

$$\left\{\begin{array}{rcc}
U_{1,i}' = & +\rho_{1,i} f_{1,i}\, U_{i,i} & -\rho_{1,i}\, U_{1,i} \\
\vdots & \vdots & \vdots \\
U_{i-1,i}' = & +\rho_{i-1,i} f_{i-1,i}\, U_{i,i} & -\rho_{i-1,i}\, U_{i-1,i} \\
U_{i,i}' = & -\left(\sum_{j=2,\dots,i-1,i+1,\dots,N} \rho_{j,i} f_{j,i}\right) U_{i,i} & +\left(\sum_{j=2,\dots,i-1,i+1,\dots,N} \rho_{j,i}\, U_{j,i}\right) \\
U_{i+1,i}' = & +\rho_{i+1,i} f_{i+1,i}\, U_{i,i} & -\rho_{i+1,i}\, U_{i+1,i} \\
\vdots & \vdots & \vdots \\
U_{N,i}' = & +\rho_{N,i} f_{N,i}\, U_{i,i} & -\rho_{N,i}\, U_{N,i}.
\end{array}\right. \tag{31}$$

Assumption 8.1

We assume that each city $i = 1, \ldots, N$ satisfies

$$\rho_{j,i} f_{j,i} > 0, \quad \forall j = 1, \ldots, i-1, i+1, \ldots, N.$$

Due to Assumption 8.1, by using the Perron–Frobenius theorem there exists a unique distribution $p_{1,i} > 0, \dots, p_{N,i} > 0$ such that

$$p_{1,i} + \cdots + p_{N,i} = 1$$

and satisfying

$$\left\{\begin{array}{lccc}
0 = & +\rho_{1,i} f_{1,i}\, p_{i,i} & & -\rho_{1,i}\, p_{1,i} \\
\vdots & \vdots & & \vdots \\
0 = & +\rho_{i-1,i} f_{i-1,i}\, p_{i,i} & & -\rho_{i-1,i}\, p_{i-1,i} \\
0 = & -\left(\displaystyle\sum_{j=2,\dots,i-1,i+1,\dots,N} \rho_{j,i} f_{j,i}\right) p_{i,i} & + & \left(\displaystyle\sum_{j=2,\dots,i-1,i+1,\dots,N} \rho_{j,i}\, p_{j,i}\right) \\
0 = & +\rho_{i+1,i} f_{i+1,i}\, p_{i,i} & & -\rho_{i+1,i}\, p_{i+1,i} \\
\vdots & \vdots & & \vdots \\
0 = & +\rho_{N,i} f_{N,i}\, p_{i,i} & & -\rho_{N,i}\, p_{N,i}.
\end{array}\right. \tag{32}$$

Definition 8.2

The quantity $p_{j,i}$ is the proportion of individuals moving from city i to city j.

As before we express the parameters $f_{j,i}$ as a function of $p_{j,i}$

$$\begin{cases} f_{1,i} = \dfrac{p_{1,i}}{p_{i,i}} \\ \vdots \\ f_{i-1,i} = \dfrac{p_{i-1,i}}{p_{i,i}} \\ f_{i+1,i} = \dfrac{p_{i+1,i}}{p_{i,i}} \\ \vdots \\ f_{N,i} = \dfrac{p_{N,i}}{p_{i,i}}. \end{cases} \tag{33}$$

Remark 8.3

Due to seasonal variation between business trips and personal trips the parameters of the model should vary in time. For example, the proportion $p_{j,i}$ *of individuals traveling from city* i *to city* j *and the length of stay* $1/\rho_{j,i}$ *in city* j *should both vary in time.*

Outline

In this section we consider the heat equation. This equation is commonly used in population dynamics to describe the movement of individuals. It reads as follows

$$\begin{cases} \partial_t u(t,x) = \varepsilon \partial_x^2 u(t,x), \text{ for } x \in (0,1), \\ \partial_x u(t,0) = \partial_x u(t,1) = 0, \\ u(0,\cdot) = \varphi \in L^2(0,1). \end{cases}$$

The boundary conditions mean that there is no flux at the boundary.

To write the numerical scheme for this equation (i.e. a discrete version of it) we set

$$u_i^n = u(n\Delta t, i\Delta x).$$

Then the main part of the equation may be written for $i = 2, ..., N-1$ as

$$\frac{u_i^{n+1} - u_i^n}{\Delta t} = \varepsilon \frac{1}{\Delta x^2} \left(u_{i+1}^n - 2u_i^n + u_{i-1}^n \right).$$

For $i = 1$ we obtain

$$\frac{u_1^{n+1} - u_1^n}{\Delta t} = \varepsilon \frac{1}{\Delta x^2} \left[\left(u_2^n - u_1^n \right) - \left(u_1^n - u_0^n \right) \right]$$

and the boundary condition $\left(u_1^n - u_0^n \right) / \Delta x = 0$ gives

$$\frac{u_1^{n+1} - u_1^n}{\Delta t} = \varepsilon \frac{1}{\Delta x^2} \left(u_2^n - u_1^n \right).$$

Similarly for $i = N$ we should have

$$\frac{u_N^{n+1} - u_N^n}{\Delta t} = \varepsilon \frac{1}{\Delta x^2} \left(u_N^n - u_{N-1}^n \right).$$

So we obtain the following explicit numerical scheme for the heat equation for $n \geq 0$

$$u^{n+1} = u^n + \frac{\varepsilon \Delta t}{\Delta x^2} D u^n,$$

with the initial distribution

$$u^0 = u_0 \geq 0,$$

where

$$D = \begin{pmatrix} -1 & 1 & 0 & \cdots & \cdots & 0 \\ 1 & -2 & 1 & \ddots & & \vdots \\ 0 & 1 & -2 & 1 & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & \ddots & 0 \\ \vdots & & \ddots & \ddots & -2 & 1 \\ 0 & \cdots & \cdots & 0 & 1 & -1 \end{pmatrix}.$$

The numerical scheme may be rewritten as

$$u_i^{n+1} = u_i^n + \varepsilon \frac{\Delta t}{\Delta x^2} \left(u_{i+1}^n - 2u_i^n + u_{i-1}^n \right).$$

So we obtain for $i = 2, \dots, N-1$,

$$u_i^{n+1} = \frac{p}{2} u_{i+1}^n + (1-p)\, u_i^n + \frac{p}{2} u_{i-1}^n$$

and for $i = 1$

$$u_1^{n+1} = \frac{p}{2} u_2^n + \left(1 - \frac{p}{2}\right) u_1^n$$

and for $i = N$

$$u_N^{n+1} = \left(1 - \frac{p}{2}\right) u_N^n + \frac{p}{2} u_{N-1}^n,$$

where

$$p := 2\varepsilon \frac{\Delta t}{\Delta x^2}.$$

Therefore we can interpret the discrete model as follows. An individual in city i, with $2 \leq i \leq N-1$, will move to city $i-1$ or to city $i+1$, each with probability $p/2$, or stay in city i with probability $1-p$. An individual in city 1 or N will move to city 2 or $N-1$, respectively, with probability $p/2$, or stay with probability $1-p/2$.

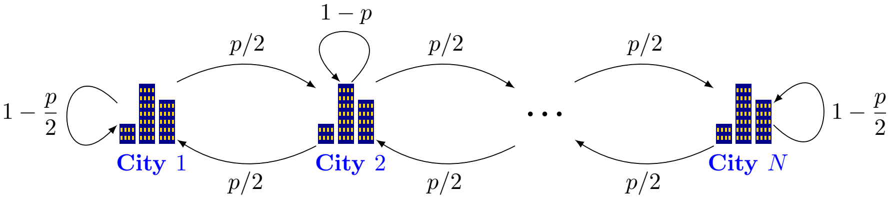

Figure: *Diagram of flux for a diffusion process between N aligned cities.*

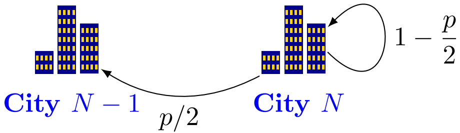

Figure: *Diagram of flux of individuals leaving city N.*

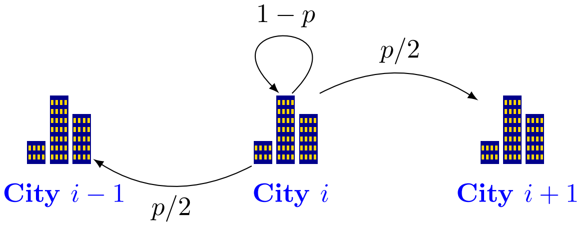

Figure: *Diagram of flux of individuals leaving city i.*

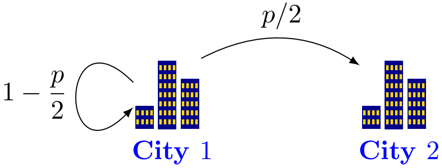

Figure: *Diagram of flux of individuals leaving city* 1.

Definition 9.1

The condition $p = 2\frac{\varepsilon \Delta t}{\Delta x^2} < 1$ is called the *Courant–Friedrichs–Lax condition* (*CFL condition* for short).

Let $\mathbb{1} := (1, \dots, 1)^T$. Then we obtain

$$D\mathbb{1} = 0 \text{ and } \mathbb{1}^T D = 0^T$$

thus

$$(I + \frac{\varepsilon \Delta t}{\Delta x^2} D)\mathbb{1} = \mathbb{1} \text{ and } \mathbb{1}^T (I + \frac{\varepsilon \Delta t}{\Delta x^2} D) = \mathbb{1}^T.$$

Therefore for each $u_0 \geq 0$,

$$\left\langle \mathbb{1}, u^{n+1} \right\rangle = \left\langle \mathbb{1}, u^n + \frac{\varepsilon \Delta t}{\Delta x^2} D u^n \right\rangle = \langle \mathbb{1}, u^n \rangle$$

and it follows that

$$\sum_{i=0}^{N} u_i^n = \sum_{i=0}^{N} u_{0i}, \quad \forall n \geq 0.$$

Moreover, as a consequence of the Perron–Frobenius theorem, we have

$$\lim_{n\to+\infty} u^n = \left(\sum_{i=0}^{N} u_{0i}\right)\begin{pmatrix} 1/N \\ 1/N \\ \vdots \\ 1/N \end{pmatrix}.$$

Figure 27 illustrates this convergence result.

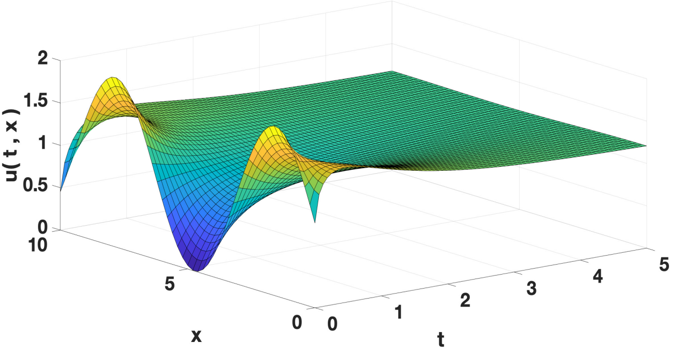

Figure: *In this figure we plot a solution of the heat equation with $x \in [0, 10]$. The diffusion coefficient is equal to $\varepsilon = 2$. The initial distribution is equal to $u_0(x) = 1 + \sin(x)$. We observe the quite rapid convergence to the constant distribution.*

Remark 9.2

The above convergence result of the distribution is a consequence of the Perron–Frobenius theorem. This example will be reconsidered in the Chapter devoted to the Perron–Frobenius theorem.

Outline

In this section we again consider the heat equation

$$\begin{cases} \partial_t u(t,x) = \varepsilon \partial_x^2 u(t,x), \text{ for } x \in (0,1), \\ u(t,0) = u(t,1), \\ u(0,\cdot) = \varphi \in L^2(0,1). \end{cases}$$

The boundary conditions mean that there is no flux at the boundary.

To write the numerical scheme for this equation (i.e. a discrete version of it) we set

$$u_i^n = u(n\Delta t, i\Delta x).$$

Then the main part of the equation may be written for $i = 2, ..., N-1$ as

$$\frac{u_i^{n+1} - u_i^n}{\Delta t} = \varepsilon \frac{1}{\Delta x^2} \left(u_{i+1}^n - 2u_i^n + u_{i-1}^n \right).$$

For $i = 1$ we obtain

$$\frac{u_1^{n+1} - u_1^n}{\Delta t} = \varepsilon \frac{1}{\Delta x^2} \left[(u_2^n - u_1^n) - (u_1^n - u_0^n) \right]$$

and the boundary condition $u_0^n = u_N^n$ gives

$$\frac{u_1^{n+1} - u_1^n}{\Delta t} = \varepsilon \frac{1}{\Delta x^2} \left(u_2^n + u_N^n - 2u_1^n \right).$$

Similarly for $i = N$ we should have

$$\frac{u_N^{n+1} - u_N^n}{\Delta t} = \varepsilon \frac{1}{\Delta x^2} \left(u_{N-1}^n + u_1^n - 2u_N^n \right).$$

So we obtain the following explicit numerical scheme for the heat equation for $n \geq 0$

$$u^{n+1} = u^n + \frac{\varepsilon \Delta t}{\Delta x^2} D u^n,$$

with the initial distribution

$$u^0 = u_0 \geq 0,$$

where

$$D = \begin{pmatrix} -2 & 1 & 0 & \cdots & 0 & 1 \\ 1 & -2 & 1 & \ddots & & 0 \\ 0 & \ddots & \ddots & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & \ddots & 0 \\ 0 & & \ddots & \ddots & \ddots & 1 \\ 1 & 0 & \cdots & 0 & 1 & -2 \end{pmatrix}.$$

The numerical scheme may be rewritten as

$$u_i^{n+1} = u_i^n + \varepsilon \frac{\Delta t}{\Delta x^2} \left(u_{i+1}^n - 2u_i^n + u_{i-1}^n \right).$$

So we obtain for $i = 2, \ldots, N-1$,

$$u_i^{n+1} = \frac{p}{2} u_{i+1}^n + (1-p)\, u_i^n + \frac{p}{2} u_{i-1}^n$$

and for $i = 1$

$$u_1^{n+1} = \frac{p}{2} u_2^n + (1-p)\, u_1^n + \frac{p}{2} u_N^n$$

and for $i = N$

$$u_N^{n+1} = \frac{p}{2} u_1^n + (1-p)\, u_N^n + \frac{p}{2} u_{N-1}^n,$$

where

$$p := 2\varepsilon \frac{\Delta t}{\Delta x^2}.$$

Therefore we can interpret the discrete model as follows. An individual in city i, with $2 \leq i \leq N-1$, will move to city $i-1$ or to city $i+1$, each with probability $p/2$, or stay in city i with probability $1-p$. An individual in city 1 will move to city 2 or city N, each with probability $p/2$, or stay in city 1 with probability $1-p$, and an individual in city N will move to city 1 or city $N-1$, each with probability $p/2$, or stay in city N with probability $1-p$.

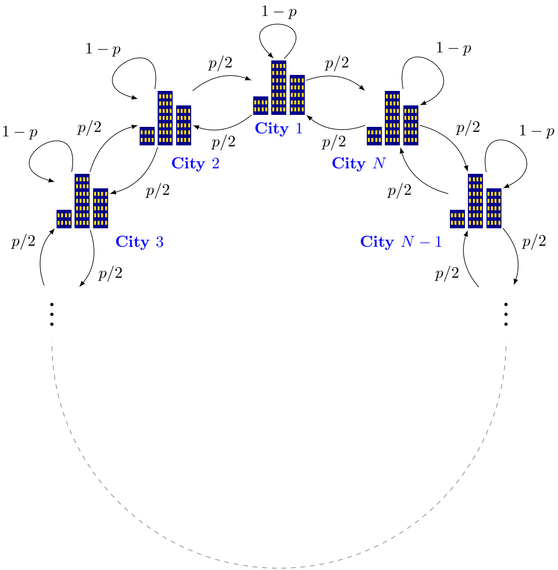

Figure: *Diagram of flux for a diffusion process between a ring of N cities.*

Let $\mathbb{1} := (1, \ldots, 1)^T$. Then we obtain

$$D\mathbb{1} = 0 \text{ and } \mathbb{1}^T D = 0^T,$$

thus

$$\left(I + \frac{\varepsilon \Delta t}{\Delta x^2} D\right) \mathbb{1} = \mathbb{1} \text{ and } \mathbb{1}^T \left(I + \frac{\varepsilon \Delta t}{\Delta x^2} D\right) = \mathbb{1}^T.$$

Therefore for each $u_0 \geq 0$,

$$\left\langle \mathbb{1}, u^{n+1} \right\rangle = \left\langle \mathbb{1}, u^n + \frac{\varepsilon \Delta t}{\Delta x^2} D u^n \right\rangle = \langle \mathbb{1}, u^n \rangle$$

and it follows that the total number of individuals is constant

$$\sum_{i=0}^{N} u_i^n = \sum_{i=0}^{N} u_{0i}, \quad \forall n \geq 0.$$

Moreover, as a consequence of the Perron–Frobenius theorem, we have

$$\lim_{n \to +\infty} u^n = \left(\sum_{i=0}^{N} u_{0i} \right) \begin{pmatrix} 1/N \\ 1/N \\ \vdots \\ 1/N \end{pmatrix}.$$

Figure 29 illustrates this convergence result.

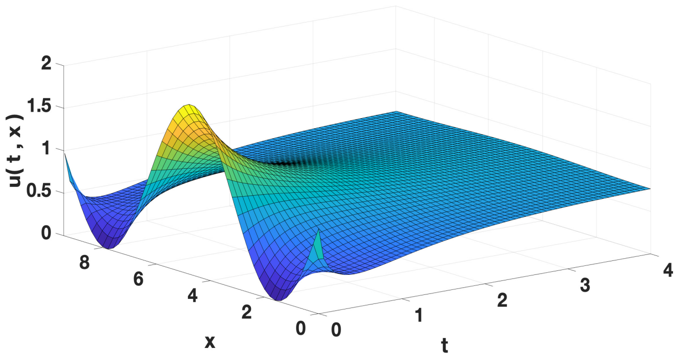

Figure: *In this figure we plot a solution to the heat equation with $x \in [0, 3\pi]$. The diffusion coefficient is equal to $\varepsilon = 2$. The initial distribution is equal to $u_0(x) = 1 + \sin(x + \pi)$. We observe the quite rapid convergence to the constant distribution.*

Remark 10.1

The above convergence result of the distribution is a consequence of the Perron–Frobenius theorem. This example will be reconsidered in the Chapter devoted to the Perron–Frobenius theorem.

Outline

In this section, we provide some references. The topics mentioned below are so rich, active, and extensive that it would be impractical to provide an exhaustive list. Instead, we have chosen an illustrative selection.

Population dynamics has a long history which starts with Fibonacci in 1202 who, in his book entitled *Liber Abaci* (Book of Calculation) [17], introduced his famous sequence

$$P_1 = 1, \quad P_2 = 2, \quad P_{n+1} = P_n + P_{n-1}, \quad \forall n \geq 0.$$

This turned out to be a special case of the Leslie model with two age classes, introduced in 1945.

As we will see several times in this book, in 1760 Daniel Bernoulli [4] proposed a mechanistic model and a phenomenological model to describe the epidemic of smallpox. We already mentioned the work of Malthus [66] in this chapter. In 1838 Verhulst rediscovered Bernoulli's generalized logistic equation [92].

The so-called Bernoulli–Verhulst equation is a scalar ordinary differential equation that takes the following form

$$N'(t) = \lambda N(t) \left(1 - (N(t)/\kappa)^{\alpha}\right), \quad \forall t \geq 0, \text{ and } N(0) = N_0 \geq 0,$$

where $\lambda > 0$, $\alpha > 0$, and $\kappa > 0$. The Bernoulli–Verhulst equation is studied in Chapter 5, as well as some n dimensional extensions of it.

Ronald Ross was awarded a Nobel prize for his famous work on malaria in 1911 [78, 79, 80, 81]. His work is partly based on the following system of two differential equations. The first equation for $H(t)$, the number of infected humans, is the following

$$H'(t) = \alpha \underbrace{(N_H - H(t))}_{\text{number of non-infected humans}} M(t) - \beta H(t),$$

which is coupled with an equation for $M(t)$, the number of infected mosquitoes,

$$M'(t) = \gamma \underbrace{(N_M - M(t))}_{\text{number of non-infected mosquitoes}} H(t) - \eta M(t).$$

Ross's model was later extended by Macdonald [59, 58, 60] in the 1950s. Therefore, nowadays this model is commonly called the Ross–Macdonald model.

The Lotka–Volterra predator-prey model is a celebrated example of a system of differential equations representing a biological system. It was first developed by Alfred Lotka in 1920 in the context of a plant-herbivorous interaction [55], although a similar system of equations had already been employed by the same author in the context of autocatalytic chemical reactions [54]. Vito Volterra developed a similar model in 1926 independently from Lotka, in the context of a predator-prey model for different species of fishes [45, 93]. The model reads as follows:

$$\begin{cases} \frac{\mathrm{d}}{\mathrm{d}t}u(t) = u(t)\big(r - \beta v(t)\big), \\ \frac{\mathrm{d}}{\mathrm{d}t}v(t) = v(t)\big(\gamma u(t) - \delta\big). \end{cases}$$

Here $u(t)$ stands for the population of prey, $v(t)$ for the population of predators; $r > 0$ is the reproduction rate of prey, $\beta > 0$ is the predation rate of a predator, $\gamma > 0$ is the prey uptake for a predator and $\delta > 0$ is the natural mortality rate of the predator.

In the second volume, we will also consider the equation introduced by Fisher [24] and discovered separately by Kolmogorov, Petrovski and Piskunov [24, 46] in 1937. This equation describes the genetic evolution of a population by using diffusion combined with a logistic equation term, and takes the following form, for $t \geq 0$ and $x \in \mathbb{R}$

$$\partial_t u(t,x) = \partial_x^2 u(t,x) + \lambda u(t,x) \left[1 - \frac{u(t,x)}{\kappa}\right], \text{ with initial value } u(0,x) = u_0($$

where $\lambda > 0$ and $\kappa > 0$.

In 1926–1927 Kermack and McKendrick [37, 38, 39] introduced the first SIR epidemic model, by combining the ideas of Bernoulli and Ross. Kermack and McKendrick's model takes the following form

$$\begin{cases} S'(t) = -\beta S(t)I(t) \\ I'(t) = \beta S(t)I(t) - \gamma I(t) \\ R'(t) = \gamma I(t). \end{cases}$$

Here $S(t)$ is the density of susceptible individuals, $I(t)$ the density of infected individuals, and $R(t)$ the density of reported individuals. The constant $\beta > 0$ is the *transmission rate*, defined as the fraction of all possible contacts between S and I that result in a new infection per unit of time; the constant $\gamma > 0$ is the *recovery rate*, meaning that $1/\gamma$ is the average duration of infection.

As we will see in the second volume, Ricker's model, which was presented in 1954 [76], takes the following form for $t \geq 0$ and $x \in \mathbb{R}$,

$$N(t+1) = \beta N(t) \exp\left(-\alpha N(t)\right), \text{ with } N(0) = N_0 \geq 0,$$

where $\beta > 0$ is the growth rate of the population and the term $\exp(-\alpha N(t))$ (with $\alpha \geq 0$) describes the intra-specific competition. This model was introduced to describe the migration of adult salmon returning back to their natal stream for reproduction.

Ricker's model is known to generate chaos. Such chaos was first described by Sharkovsky [83, 84] in 1964, with his famous order of appearance for periodic orbits. This result was also rediscovered by Li and Yorke [52] in 1975, who proved that the existence of a period three orbit implies the existence of an orbit of any period (a special case of Sharkovsky's theorem), but they prove in addition the existence of ergodic invariant measures.

Age in population dynamics

(i) *Chronological age:* The chronological age is the time since birth. This age is used by all of us to describe life history. It serves, for example, to describe the maturity of individuals, that is, the time at which individuals start to be able to produce newborns. Continuous-time chronological age will be reconsidered by using Volterra's integral equations in Chapter 2.

(ii) *Age as a clock*: Chronological age is nothing but a measure of time determined by a clock which is started at birth. It is very convenient to describe the history of a process by considering other kinds of clocks, such as the time since infection takes place (which is called the age of infection, introduced by Kermack and McKendrick [38]). It is indeed possible to extend this idea to many kinds of clocks to track the history of a process.

Leslie's matrix model was extended by Usher [91] in 1969. An application of Usher matrices to demography is presented in Gaudard et al. [28]. For models with discrete age groups, we refer Caswell [13] and Newman [70] for more results.

For continuous age-structured models, we refer to Cushing [15], Thieme [88], Smith and Thieme [87], Webb [94, 95], Iannelli [32], Inaba [34], and [21, 23, 64, 63, 65] for more results on the subject.

Age and diffusion

Since Gurtin's work [29] in the early 1970s, the interplay between the spatial motion of individuals and age structure has also been widely considered in the literature, for single populations and also for interacting species. Similar types of models (both linear and nonlinear) have been studied. We refer for instance to the papers of Gurtin and MacCamy [30], Di Blasio [18], Garroni and Langlais [27], Langlais [48, 49], and Ducrot and Magal [22].

We also refer to the monograph of Busenberg and Cooke [10], where both diffusive population models with chronological age structure and with age since infection in epidemic problems are presented. We refer to Busenberg and Iannelli [11] for the study of age-structured problems with nonlinear diffusion and to Anița [1] and the references cited therein for results on the control of age-structured problems with spatial diffusion. Let us also refer to Di Blasio [19] for epidemic problems coupling age since infection and spatial diffusion and [21, 23, 64] for some studies of the spatial spread of infection with age since infection. Population models taking into account the interplay between age structure and non-local diffusion have also been developed. We refer, for instance, to Kang and Ruan [35] and the references cited therein.

The Kermack and McKendrick model with age of infection

Let $a > 0$ be the time since the first infection of an individual in a population by a pathogen. Then the Kermack and McKendrick model with age of infection can be rewritten as follows. The number of susceptible individuals $S(t)$ satisfies the following equation

$$S'(t) = \lambda - \eta S(t) - \nu\, S(t) \int_0^\infty \beta(a) i(t,a) \mathrm{d}a, \text{ for } t \geq 0, \text{ with } S(0) = S_0 \geq 0,$$

and the distribution of population of infected $a \to i(t,a)$ at time t satisfies

$$i(t,a) = \begin{cases} \dfrac{\Pi(a)}{\Pi(a-t)} i_0(a-t), & \text{if } a > t, \\ \Pi(a)\, \nu\, S(t-a)\, B(t-a), & \text{if } t > a, \end{cases}$$

where $a \to i_0(a) \in L^1_+(0,\infty)$ is the initial distribution of population of infected.

Here *distribution of population* refers to the number of infected individuals with age of infection in between a_1 and a_2 at time $t = 0$ (respectively at time $t > 0$), that is,

$$\int_{a_1}^{a_2} i_0(a)\mathrm{d}a \quad \left(\text{respectively } \int_{a_1}^{a_2} i(t,a)\mathrm{d}a\right).$$

The function $a \to \beta(a) \in L^\infty_+(0,\infty)$ gives the fraction of infectious (i.e. capable of transmitting the pathogen to the susceptible) for individuals with infection age a, and $a \to \Pi(a)$ gives the probability of remaining infected for individuals with infection age a.

Define

$$B(t) = \int_0^\infty \beta(a) i(t,a) \mathrm{d}a,$$

then we deduce that $t \to B(t) \in C_+([0,\infty),\mathbb{R})$ is the unique solution of the Volterra integral equation for $t \geq 0$,

$$B(t) = \left[\int_t^\infty \beta(a) \frac{\Pi(a)}{\Pi(a-t)} i_0(a-t)\mathrm{d}a + \int_0^t \beta(a)\Pi(a)\, \nu\, S(t-a)B(t-a)\mathrm{d}a \right]$$

where

$$S'(t) = \lambda - \eta S(t) - \nu\, S(t)B(t),$$

or equivalently

$$S(t) = \mathrm{e}^{-\int_0^t \eta + \nu B(\sigma)\mathrm{d}\sigma} S_0 + \int_0^t \mathrm{e}^{-\int_s^t \eta + \nu B(\sigma)\mathrm{d}\sigma} \lambda \mathrm{d}s.$$

The existence and uniqueness of solutions for Volterra's integral equation will be briefly explained in Chapter 2, where it will also provide one of the motivations to consider several types of methods to prove the existence of solutions. We will reconsider the Kermack–McKendrick model with age of infection in the remarks and notes section of Chapter 8.

The global dynamics of the Kermack and McKendrick model with age of infection was first completely understood by Magal, McCluskey and Webb [62]. We also refer to Magal and McCluskey [61] for a version of this result with two groups. A more elementary presentation of such a result with Liapunov function arguments is presented in Ma and Magal [56].

Movement in space in population dynamics

(i) *Patch models:* Patches can be defined as spatial areas which are sufficiently small so that spatial effects can be neglected. Patch models have been used in population genetics since the 1940s with the introduction by Wright of the so-called "Island models" [96], which he used to study the genetic effects of isolation. Let us also mention the "Stepping stones" model, introduced by Kimura in 1953 [43] and developed in more detail by Kimura and Weiss [44]. Stepping stones are patches on which there exists a one-dimensional structure, meaning that the motion of an individual from a given node is constrained to two neighboring patches (and no other). Patch models are often used in the context of meta-populations, which are populations divided into different spatial locations. In the context of human epidemiology, patch models have been used to describe the spread of epidemics across cities [2, 42].

(ii) *Diffusion processes:* Diffusion processes and the heat equation were originally developed to describe the random motion of microscopic particles. Their use to model the behavior of living bodies can be traced back to the seminal works of Kolmogorov, Petrovski and Piskuov [46] and Fisher [24]. These two studies were published simultaneously in 1937, and are concerned with a population genetics model

$$\partial_t u(t,x) = \partial_{xx} u(t,x) + r u(t,x) \left(1 - u(t,x)\right),$$

where $u(t,x)$ stands for the proportion at time $t \geq 0$ of individuals possessing a genetic advantage measured by the rate $r > 1$, in a population structured by a space variable $x \in \mathbb{R}$.

This equation, called the Fisher–KPP equation, can be obtained in some sense as a limit of differential equations on large lattices, which will be presented in Chapter 8 of this book. Skellam [86] may have been the first biologist to use this equation in the context of a biological invasion, the invasion of the muskrat *Ondatra zibethica* L. after its introduction in central Europe in 1910. We refer to the books of Okubo [71] and Cantrell and Cosner [12] for a review.

(iii) *Lévy flight process:* To understand the laws of human displacement, a comparison between the Lévy flight process and real data was made by Brockmann et al. [9]. Since then the Lévy flight process, which is a mixture between patch model (long-distance) and daily motion (short distance), has been observed in many contexts.

(iv) *Long-short distance dispersal:* Shigesada Kawasaki [85], Bennett and Sherratt [3].

(i) *Ecology:* Iannelli and Pugliese [33], Murray [68, 69], Turchin [90], Bolker [5], Keyfitz and Caswell [41], Kot [47], Cushing [15, 16] , Tuljapurkar [89], Perthame [73, 74], Thieme [88], Smith and Thieme [87].

(ii) *Demography:* Keyfitz [40].

(iii) *Evolution:* Roff [77], Pianka [75].

(iv) *Epidemics:* Busenberg and Cooke [10], Diekmann and Heesterbeek [20] , Brauer and Castillo-Chávez [6], Brauer, Van den Driessche, Wu [8], Ma, Zhou and Wu [57], Chen, Moulin and Wu [14], Brauer, Castillo-Chavez and Feng [7], Li, Yang and Martcheva [53], Marcheva [67], Murray [68, 69], Keeling and Rohani [36], and Smith and Thieme [87].

(v) *Others:* Hofbauer and Sigmund [31].

Thank you for listening

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