Discrete-Time Models

Discrete delay models and age structured population

Computational Biology

Adérito Araújo (alma@mat.uc.pt)
May 29, 2024

Leonardo of Pisa (1170 – c. 1250)

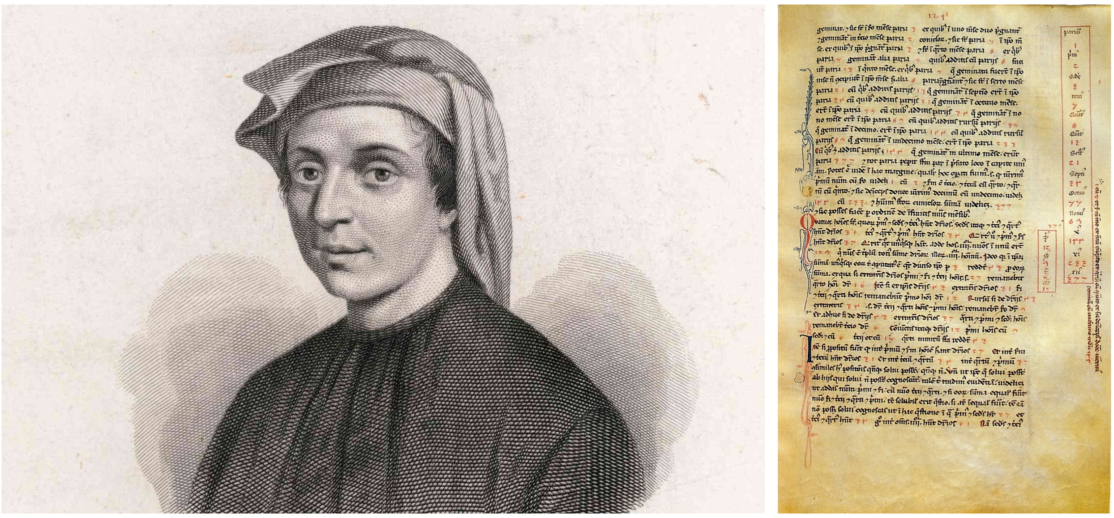
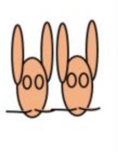
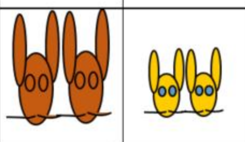
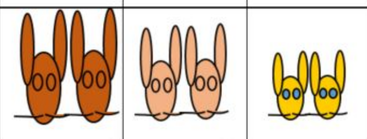
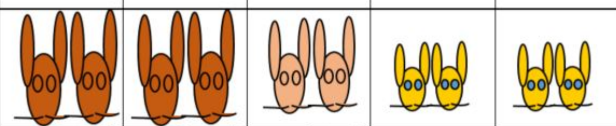
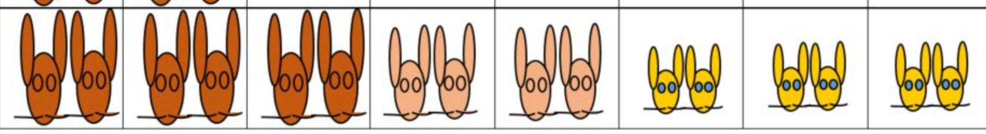


Figure: Left: Leonardo of Pisa (Fibonacci after the 18th century); Right: A page of the Liber Abaci (1202) from the National Central Library. The list on the right shows the numbers 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, 233, 377 (the Fibonacci sequence). The 2, 8, and 9 resemble Arabic numerals more than Eastern Arabic numerals or Indian numerals.

The rabbit problem

- Starting at the beginning of the breeding season with a pair of immature rabbits, male and female.
- After a reproductive season they produce another pair of immature rabbits.
- Their offspring pairs then do exactly the same and so on.
- Suppose that the rabbits never die.
- Question: Determine the number of pairs of rabbits at each reproductive period.

The rabbit problem

Months	Pairs and stages of growth	Numbers
0		1
1		1
2		2
3		3
4		5
5		8

Fibonacci sequence

- Let N_n be the number of pairs of (male and female) rabbits at the n-th reproductive stage.
- Normalising the reproductive period to 1 we have

$$N_0 = 0, \ N_1 = 1, \quad N_{n+1} = N_n + N_{n-1}, \quad n = 1, 2, 3, \ldots,$$

- Fibonacci sequence: $1, 1, 2, 3, 5, 8, 13, \ldots$.
- With $N_0 = 1$, $N_1 = 1$ the solution of $N_{n+1} = N_n + N_{n-1}$, is

$$N_n = \frac{1}{\sqrt{5}} \left(\frac{1}{2}(1+\sqrt{5}) \right)^{n+1} - \frac{1}{\sqrt{5}} \left(\frac{1}{2}(1-\sqrt{5}) \right)^{n+1}.$$

- For large n,

$$N_n \simeq \frac{1}{\sqrt{5}} \left(\frac{1}{2}(1+\sqrt{5}) \right)^{n+1}.$$

- Golden number/ratio: for n large,

$$\frac{N_n}{N_{n+1}} \simeq \frac{1}{2}(1+\sqrt{5}) = \varphi.$$

Fibonacci sequence

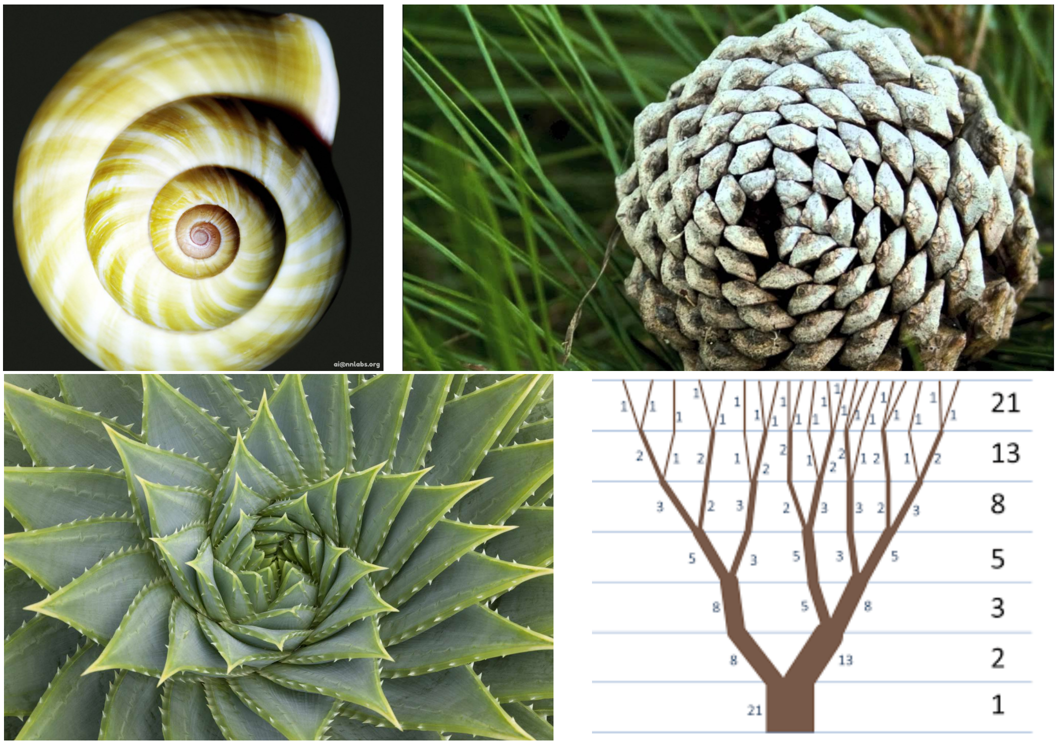


Figure: Pine cones, sunflower heads, daisy florets, angles between successive branching in many plants and many more.

Fibonacci sequence

Figure: On a sunflower head, it is possible to see sets of intertwined spirals emanating from the centre (you can see them on pine cones starting at the base). It turns out that the number of spirals varies but are always a number in the Fibonacci sequence. On the daisy head there are 21 clockwise and 34 anticlockwise spirals, which are consecutive numbers in the Fibonacci series.

Fibonacci sequence: immature/mature rabbits

- Discrete age structured population model are used in real-world-applications (Fibonacci-numbers are a toy model).
- In the Fibonacci model we can distinguish the immature rabbits from the mature (able to reproduce) rabbits.
- Let $z_{1,n}$ be the number of immature pair of rabbits at time n and $z_{2,n}$ number of mature pair of rabbits at time n. Then

$$z_{1,n+1} = z_{2,n}, \quad z_{2,n+1} = z_{1,n} + z_{2,n}.$$

- In matrix form, we have,

$$\begin{bmatrix} z_{1,n+1} \\ z_{2,n+1} \end{bmatrix} = \underbrace{\begin{bmatrix} 0 & 1 \\ 1 & 1 \end{bmatrix}}_{\text{Leslie matrix}} \begin{bmatrix} z_{1,n} \\ z_{2,n} \end{bmatrix}.$$

Age structured population and Leslie matrix

The Leslie matrix is used in ecology to model the changes in a population of organisms over a period of time. In a Leslie model, the population is divided into groups based on age classes.

At each time step, the population is represented by a vector with an element for each age class where each element indicates the number of individuals currently in that class.

The Leslie matrix is a square matrix with the same number of rows and columns as the population vector has elements. The (i, j)th cell in the matrix indicates how many individuals will be in the age class i at the next time step for each individual in stage j. At each time step, the population vector is multiplied by the Leslie matrix to generate the population vector for the subsequent time step.

Age structured population and Leslie matrix

To build a matrix, some information must be known from the population:

- $z_{i,n}$ the count of individuals of each age class i at time n;
- s_i the fraction of individuals that survives from age class i to age class $i+1$;
- f_i the fecundity, the per capita average number of female offspring reaching $z_{0,n}$ born from mother of the age class i. More precisely, it can be viewed as the number of offspring produced at the next age class b_{i+1} weighted by the probability of reaching the next age class. Therefore, $f_i = s_i b_{i+1}$.

Age structured population and Leslie matrix

This then implies the following matrix representation

$$\begin{bmatrix} z_{0,n+1} \\ z_{1,n+1} \\ z_{2,n+1} \\ \vdots \\ z_{w,n+1} \end{bmatrix} = \begin{bmatrix} f_0 & f_1 & \dots & f_{w-1} & f_w \\ s_0 & 0 & \dots & 0 & 0 \\ 0 & s_1 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & s_{w-1} & 0 \end{bmatrix} \begin{bmatrix} z_{0,n} \\ z_{1,n} \\ z_{2,n} \\ \vdots \\ z_{w,n} \end{bmatrix},$$

where w is the maximum age attainable in the population.

This can be written as

$$Z_{n+1} = LZ_n \quad \Rightarrow \quad Z_n = L^n Z_0.$$

Dominant eigenvalue and long time behaviour

- Theorem: For any Leslie matrix L there exists one real positive eigenvalue λ_1 that is strictly greater in magnitude than any other eigenvalue.
- λ_1 is called the dominant eigenvalue and is a simple root of the characteristic polynomial.
- Corollary: The associated right eigenvector, w_1, and left eigenvector, v_1, are both real and the only strictly positive right and left eigenvectors of L.
- Corollary: λ_1 determines the long time properties:
  - if $\lambda_1 > 1$ then $Z_n \sim c\lambda_1^n w_1$;
  - if $\lambda_1 < 1$ then $Z_n \to 0$ as $n \to \infty$.
- λ_1 gives the population's asymptotic growth rate (growth rate at the stable age distribution).
- w_1 is proportional to the stable age distribution; it can be rescaled to give either the proportion or the percentage of individuals in each age class.

Homework #4

Exercise 1.9:

1. Find the stable age structure and the growth rate of a baseline population with the Leslie matrix

$$\begin{bmatrix} 1 & 1 \\ 0.75 & 0 \end{bmatrix}.$$

2. Compare the speed of growth and the stable age structure of this baseline population with a population where the fecundity of each age class is increased twofold:

$$\begin{bmatrix} 2 & 2 \\ 0.75 & 0 \end{bmatrix}.$$

   Does the speed of growth also increase twofold? How does the stable age structure change if fecundity increases or decreases?

Homework #4

Exercise 1.10:

1. Compare the speed of growth and the stable age structure of the baseline population in the Exercise 1.8.1 with a population where reproduction is delayed by one year. For simplicity, assume that all individuals survive the first year such that the delay does not imply extra mortality (in reality, of course, it would):

$$\begin{bmatrix} 0 & 1 & 1 \\ 1 & 0 & 0 \\ 0 & 0.75 & 0 \end{bmatrix}.$$

2. Consider the following example: three age classes newborns (0-1 years), youngsters (1-2 years) and adults (2-3 years), after which they die. Half of the newborns become youngsters and 2/3 of youngsters grow to adulthood. The newborns have 0.5 offsprings per year, the youngsters 5 and the adult 3.
   2.1 Build the Leslie matrix.
   2.2 Find the asymptotic growth rate and stable age distribution.
   2.3 Illustrate your finding with numerical results.