Stochastic Modelling in Ecology and Evolution

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Modelling and Control of Complex Systems in Life and Physical Sciences , University of Dschang, November 2025

Modélisation Mathématique et Biodiversité

European Research Council
Established by the European Commission

Funded by the European Union

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Biodiversity

Biodiversity cannot be summerized in a unique value.

- Biological diversity at all levels of life
- Relation with environment
- Complex System

Ecosystèmes

Food chain of herring throughout its life cycle in the North Sea..

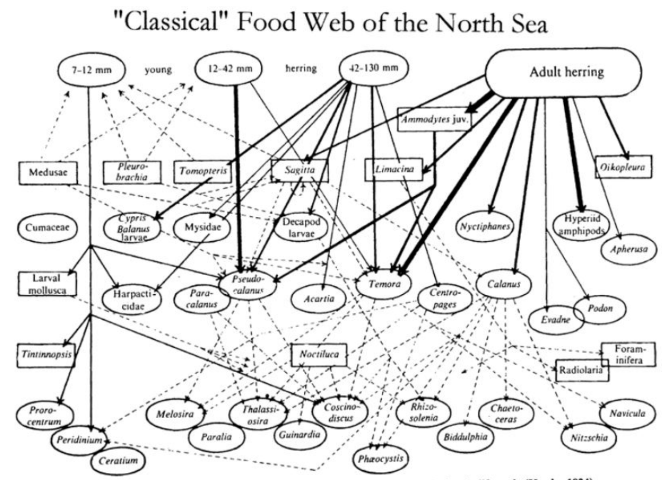
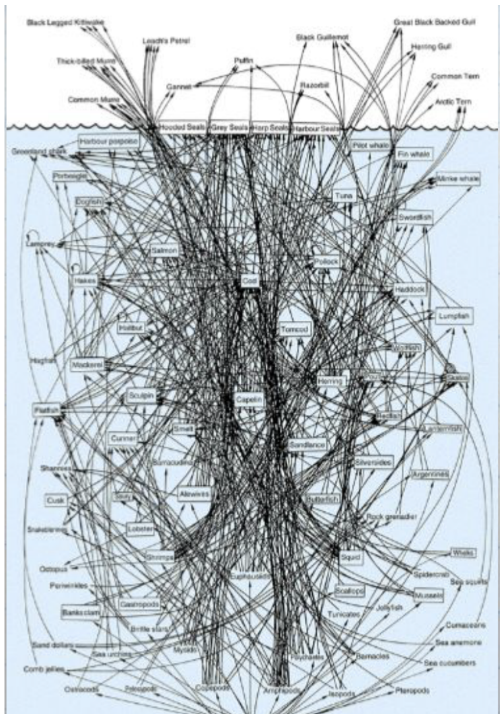


Figure 55. The food web upon which the North Sea herring depends during its life cycle (Hardy, 1924).

Food web in the North Sea.

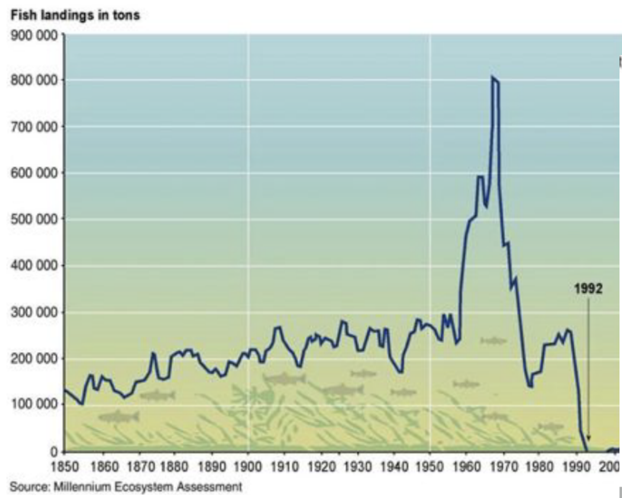

A simplified food web for the Northwest Atlantic

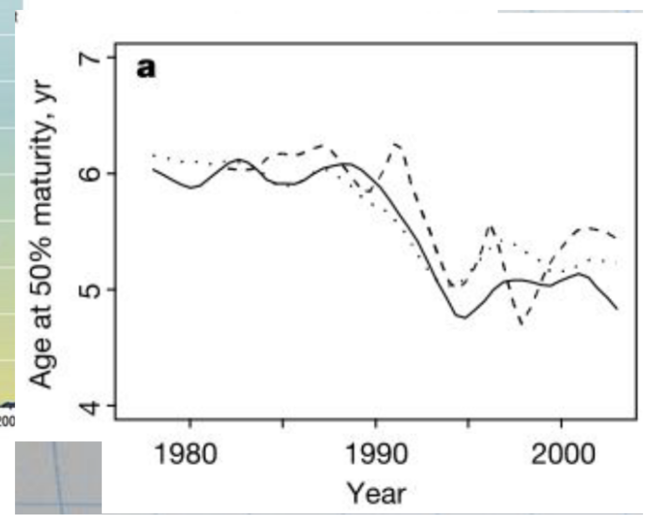
Impact environnemental, démographie et effets évolutifs

Dynamics of the number of cod caught. and age at maturity.

source: Millenium Ecosystem Assessment

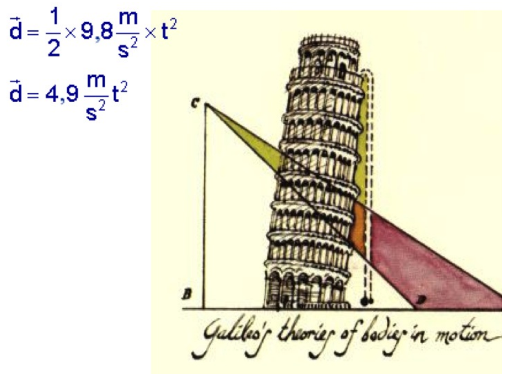
Olsen et al 2004.





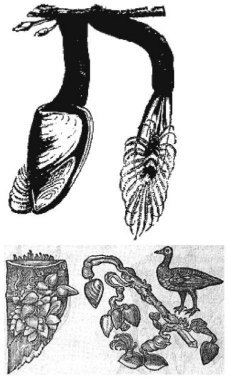
A long history to address evolution

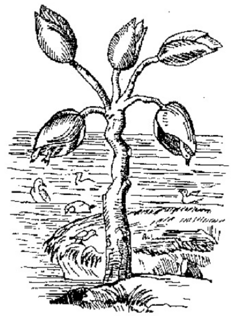
In 1604, Galilée understands the mathematical law of falling bodies.

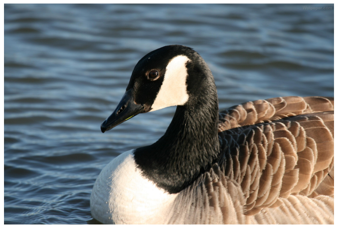


In biology, knowledge is still close to stone age....


Tiré de Duret, L'Histoire admirable des Plantes, Paris, 1605.

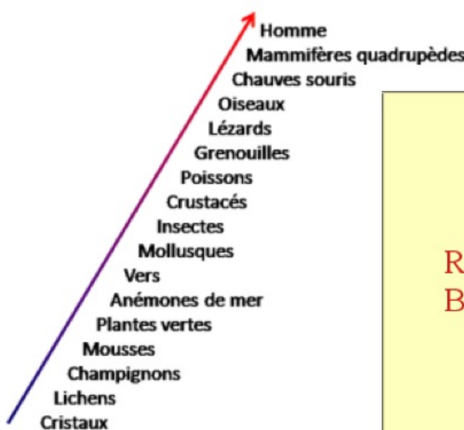


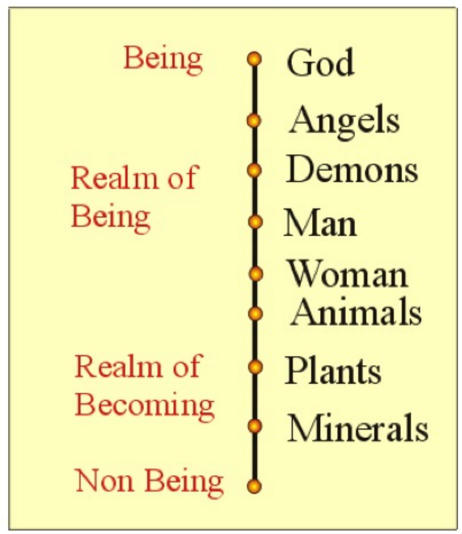

The Barnacle Tree (from Gerard's "Herball")



What is a species?

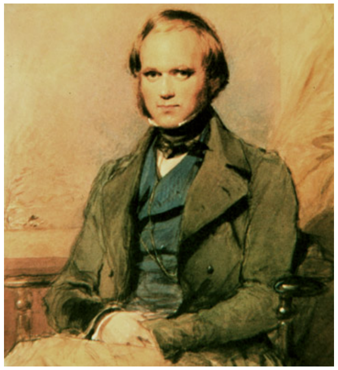
Until the end of *XVIII* century: a linear image of the great chain of living Beings.



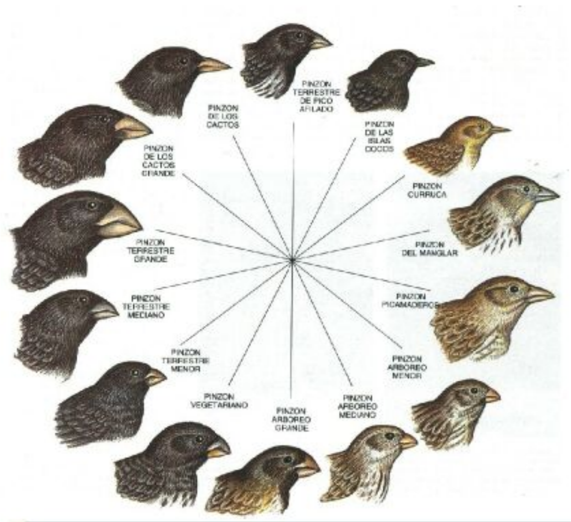


Theory of Evolution (1859)

DARWIN (1809-1882).
His work on the evolution of living species revolutionized biology.



He formulates the hypothesis that all living species have evolved over time from a single or a few common ancestors through the **natural selection process**.



Natural selection and evolution

"As many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be **naturally selected.** From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form".

Charles Darwin, On the origin of species, 1859.

Importance of randomness

3 main sources of randomness.

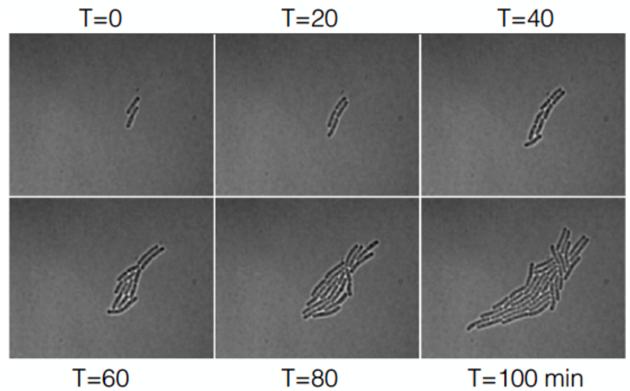
- Mutations (DNA replication).
- Individual demography (birth, death, reproduction or information exchange, movement).
- Environmental variations.

Importance of size and time scales

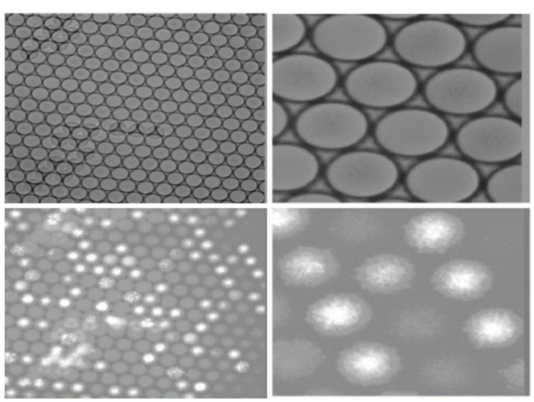
Evolution of micro-organisms

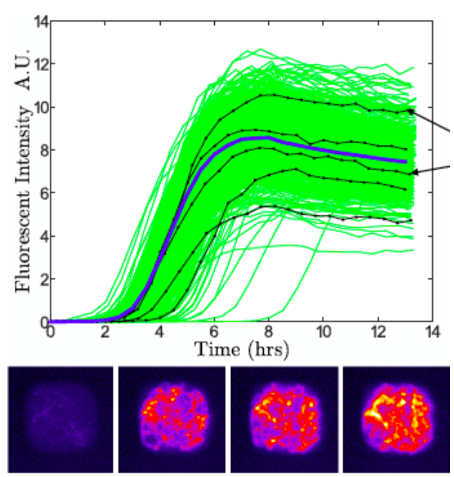
(M. El Karoui - C. Baroud - J. Harmand - L. Robert)

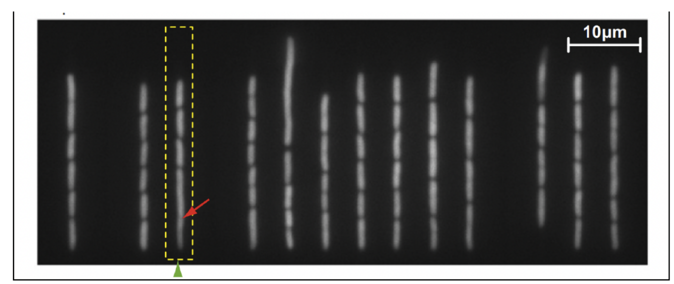
Binary division: birth and death process in continuous time.



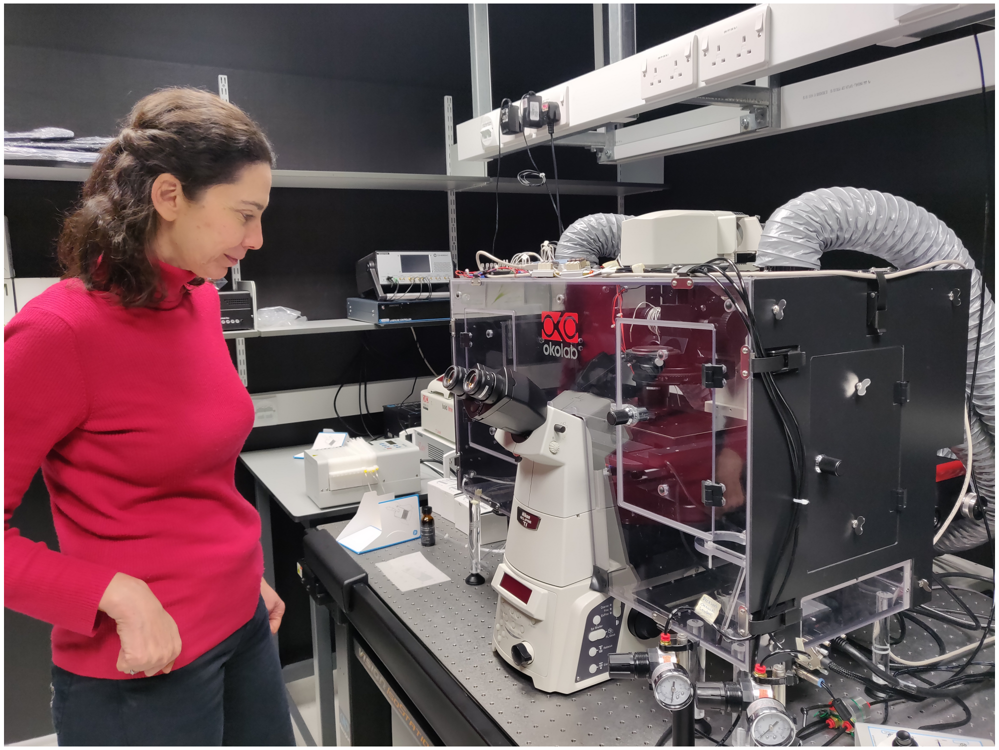
Understanding the population development. Understanding its heterogeneity.







Meriem El Karoui's microscope



I - First Models of Population Dynamics

II - Two types Population Dynamics - Horizontal Gene Transfer - Plasmids

III - Eco-Evolutionary models

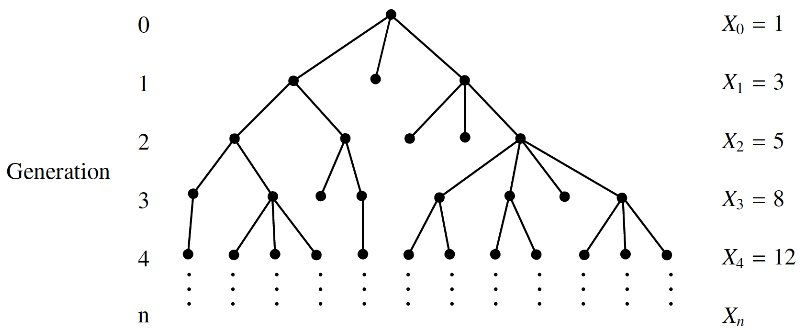
First Models of Population Dynamics

Population size dynamics in discrete time: Galton-Watson process (1845-1873)

The random variable X_n denotes the size of the population at time n.

What is the behavior of X_n when n tends to infinity?

$$X_{n+1} = \sum_{i=1}^{X_n} Z_{n;i}$$



• $Z_{n,i}$: number of offspring of the i-th individual in the generation n - independent and identically distributed random variables

$$\forall\, k \in \mathbb{N},\ \ p_k = \mathbb{P}(Z = k).$$

• Average number $m = \sum_k k\, p_k$ and generating function

$$G(s) = \sum_k p_k s^k, \forall s \in [0, 1].$$

• The mean $m = G'(1)$ is the slope of the tangent to the curve of G at 1.

Elementary properties

• Let G_n be generating function of X_n.

Then $G_1(s) = G(s)$ and one has

$$G_n(s) = \mathbb{E}(s^{X_n}) = G\big(G_{n-1}(s)\big).$$

In particular, if $X_0 = i$ and defining $g_n(s) = g \circ g ... \circ g(s)$ (n times),

$$G_n(s) = (g_n(s))^i \;\; ; \;\; \mathbb{E}_i(X_n) = \mathbb{E}(X_n | X_0 = i) = m^n \, i.$$

Proof : For $s \in [0, 1]$,

$$G_{n+1}(s) = \sum_k \mathbb{E}\Big(s^{\sum_{i=1}^k Z_{n,i}} \mathbf{1}_{\{X_n = k\}}\Big) = \sum_k (g(s))^k \, \mathbb{P}(X_n = k) \qquad \text{by independence}$$

$$= G_n(g(s)).$$

Then noting that $g_n'(s) = g'(g_{n-1}(s)) g_{n-1}'(s)$ and making $s \to 1$ in $G_n'(s) = i (g_n(s))^{i-1} g_n'(s)$, we obtain that

$$\mathbb{E}_i(X_n) = i \, m^n.$$

Extinction and Survival

Remark : if $m < 1$, then

$$\mathbb{P}_i(X_n > 0) \leq \mathbb{E}_i(X_n) = i\, m^n,$$

which tends to 0.

Extinction probability at generation n : $q_n = G_n(0)$. Then

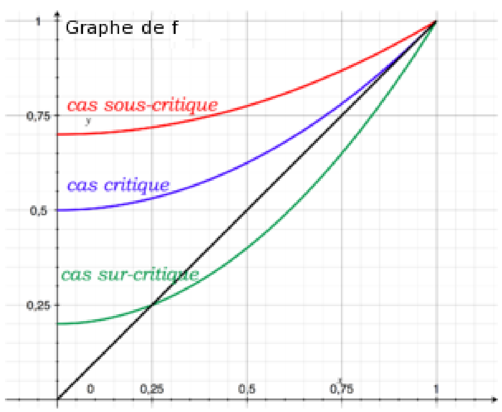
$$q_n = G(q_{n-1}).$$

Extinction probability : $q = \lim_{n \to +\infty} q_n$. It satisfies

$$q = G(q).$$

Two possible cases:

- $m \leq 1$ (subcritical or critical cases): $q = 1$. **Extinction.**
- $m > 1$ (super-critical case): $q < 1$. **Persistence with positive probability** $1 - q$**.**



Extinction of the North Atlantic right whale

(Caswell et al. 1999).

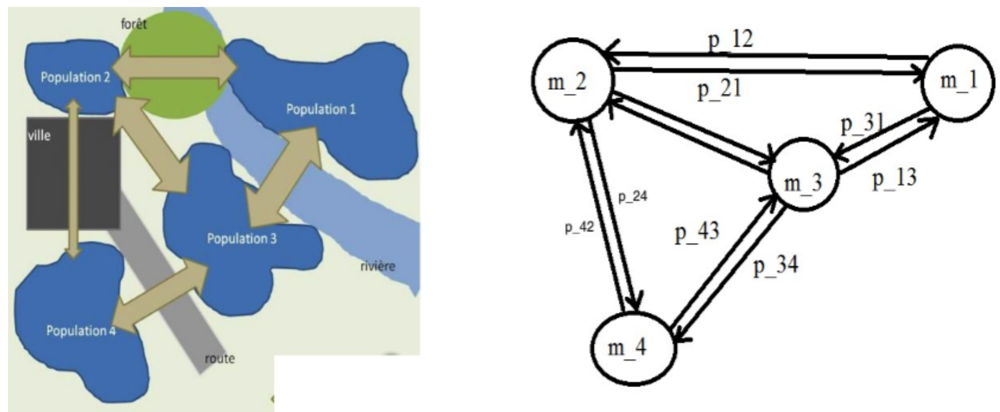
One can show that if $m < 1$ and if the initial population size is K,
$\mathbb{P}(X_n > 0) \simeq K\, m^n$.

Number of female whales in 1994:
$K = 150$.
Mean number of offspring:
$m = 0,976$.

- We are looking for n such that $\mathbb{P}($ Extinction at year $n) = 0,99$.
- $\mathbb{P}($ living whales at year $n) = 0,01$.
- $K\, m^n = 0,01 \Longleftrightarrow n = 395$.
- 99% chance of no whales remaining by 2389.

Effect of land transformation on species preservation and growth?

Applications in urban ecology, for land use planning or the creation of nature reserves.



Bansaye, Lambert 2013

Galton-Watson process on sites and random motion on the graph..

$m_i =$ average number of offspring in habitat i: ecological quality of habitat i.

p_{ij} is the probability of migration from habitat i to l'habitat j.

The probability of survival depends on the largest eigenvalue of the matrix $((m_i \, p_{ij}))$.

It is shown that the graph structure can allow the population to survive despite some very unfavourable habitats.

Population size dynamics in continuous time

The population size process $(X_t, t \geq 0)$ is indexed by the continuous time. It is a random process (random function of time) that counts the number of individuals in a population. It takes its values in $\mathbb{N}$.

X_t is the random variable denoting the number of individuals at time t.

Birth and Death Process in continuous time - Linear case

- Individuals reproduce and die independently.

- For each individual: the distribution of the first birth (or division time) follows an exponential law with parameter $b > 0$. For T_{birth} the date of the first birth event,

$$\mathbb{P}(T_{birth} \geq t) = e^{-bt} \;\; ; \;\; \mathbb{E}(T_{birth}) = \frac{1}{b}.$$

- Independently, the distribution of the first death time T_{death} follows an exponential law with parameter $d > 0$

- First time an event occurs for this individual : $T_1 = \inf(T_{birth}, T_{death})$.

$$\mathbb{P}(T_1 \geq t) = \mathbb{P}(T_{birth} \geq t; T_{death} \geq t) = e^{-(b+d)t}, \quad \textbf{by independence}.$$

The distribution of T_1 is an exponential law with parameter $b + d$.

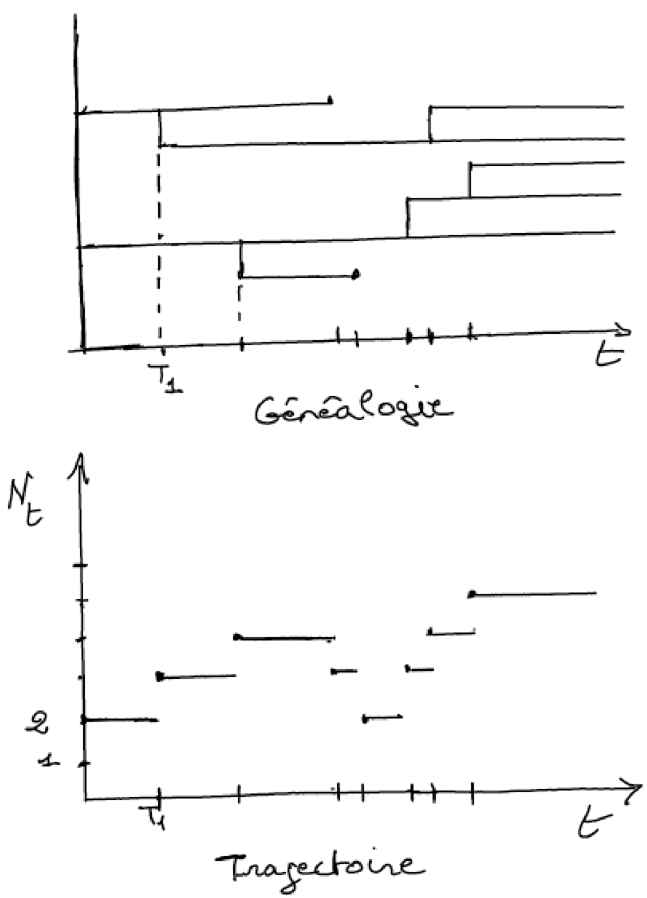
- By independence, the distribution of the first birth or death event in a population of n individuals is an exponential law with parameter $(b + d)n$.

Simulation and pictures

• If $X_0 = n$, one waits for an exponential time with parameter $(b+d)n$.

• At the first jump time T_1, with probability $\frac{b}{b+d}$ the process jumps of $+1$ and $X_{T_1} = n+1$ and with probability $\frac{d}{b+d}$ the process jumps of -1 and $X_{T_1} = n-1$.

• One reiterates the procedure.



The population process is a Markov process : for $s < t$, the distribution of X_t conditioned on $(X_v,\ v \le s)$ is equal to the distribution of X_t conditioned on X_s

Extinction ou survie

$$m = 2\,p_2 = \frac{2b}{b+d} > 1 \iff b > d.$$

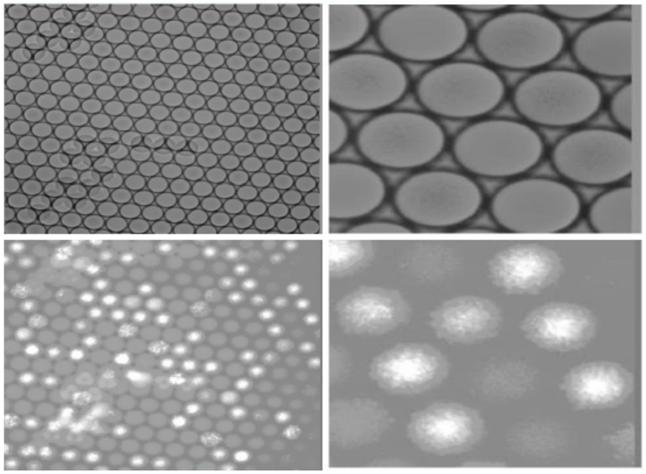
$$G(x) = \frac{d + bx^2}{b+d} = x \iff (x-1)(x - \frac{d}{b}) = 0.$$

Then,

- Extinction almost-surely if and only if $b \leq d$.
- If $b > d$, the extinction probability is $\frac{d}{b}$ and the survival probability is $\frac{b-d}{b}$.

Remark : the survival probability is never equal to 1 - The population can go to extinction by the unique effects of randomness, even though the growth rate $b - d$ is high. (Genetic drift).

Long term behaviour



• When $b > d$,

the process $(X_t\, e^{-(b-d)t})$ is a positive martingale and one can shows that

$$N_t\, e^{-(b-d)t} \longrightarrow_{t \to +\infty} W \quad p.s.$$

where, for $N_0 = 1$ and on the survival event,

$$Law(W) = \mathcal{E}xp(\frac{b-d}{b}).$$

Extinction time

One can show that $(X_t)_t$ is a semimartingale :

$$X_t = X_0 + M_t + \int_0^t (b-d)X_s ds,$$

(M_t) is a martingale with $\mathbb{E}(M_t) = 0$ and $\mathbb{E}((M_t)^2) = \int_0^t (b+d)\mathbb{E}(X_s)ds.$
It turns out that

$$\mathbb{E}(X_t) = \mathbb{E}(X_0)e^{(b-d)t}.$$

• In the subcritical case $b < d$ and if $\mathbb{E}(X_0) = k$, the dynamics will be reduced to 1 individual in average during a duration $\frac{\log K}{d-b}$.

One can prove rigorously that $\log K$ is the order of magnitude of the extinction time $T_0 = \inf\{t > 0, X_t = 0\}$.

• In the critical case $b = d$, we have seen that $T_0 < +\infty$ a.s, but one proves that $\mathbb{E}(T_0) = +\infty$.

One can also note that $X_t \to 0$ as t tends to infinity although $\mathbb{E}(X_t) = \mathbb{E}(X_0)$ for all t.

Birth and Death Process in continuous time - General case

The process $(X_t)_{t\geq 0}$ is a continuous time Markov process with values in $\mathbb{N}$.

- The process of size n increases by 1 individual at rate $\lambda_n \geq 0$.
- The process of size n decreases by 1 individual at rate $\mu_n \geq 0$.
- $\lambda_0 = \mu_0 = 0$.
- We assume that $\lambda_n \leq \bar{\lambda}\, n$, which ensures the existence of the process.
- Linear case: $\lambda_n = bn$; $\mu_n = dn$. - Yule process: $d = 0$.
- Logistic birth and death process : $\lambda_n = bn$; $\mu_n = dn + c\, n(n-1)$, where $b - d > 0$ and $c > 0$. The parameter c is often called "competition pressure".

The process can be simulated by iteration as in the linear case. At the state n, the first jump event has an exponential law with parameter $\lambda_n + \mu_n$. At this jump time, with probability $\frac{\lambda_n}{\lambda_n + \mu_n}$, the population increases by 1 individual and with probability $\frac{\mu_n}{\lambda_n + \mu_n}$, the population decreases by 1 individual.

extinction and Survival

Let $u_i = \mathbb{P}_i(T_0 < +\infty)$ be the extinction probability in finite time, for a process starting from state i. We have $u_0 = 1$.
By conditioning on the first jump $X_{T_1} - X_0 \in \{-1, +1\}$, we obtain the following recurrence relation: for all $k \geq 1$,

$$
\begin{aligned}
u_k &= \mathbb{P}_k(Extinction) \\
&= \mathbb{P}_k(Extinction|Birth)\,\mathbb{P}_k(Birth) + \mathbb{P}_k(Extinction|Death)\,\mathbb{P}_k(Death) \\
&= u_{k+1}\,\frac{\lambda_k}{\lambda_k+\mu_k} + u_{k-1}\,\frac{\mu_k}{\lambda_k+\mu_k},
\end{aligned}
$$

and then

$$\lambda_k u_{k+1} - (\lambda_k + \mu_k)u_k + \mu_k u_{k-1} = 0.$$

By resolving this equation, we prove that

If $U_\infty = \sum_{k=1}^{\infty} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k} = +\infty$, then $u_i = 1$ for any i - Almost-sure Extinction.

If $U_\infty = \sum_{k=1}^{\infty} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k} < +\infty$, then for $i \geq 1$, $u_i = (1 + U_\infty)^{-1} \sum_{k=i}^{\infty} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k}$.
The process has a positive but strictly less than 1 survival probability, for any $i \neq 0$.