Modeling Population Dynamics in Ecology and Biology

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General references :

James Murray, Mathematical Biology, 3rd edition (Springer 2003) volume 1 (basic theory) and 2 (applications)

Odo Diekmann, Hans Heesterbeek, Tom Britton, Mathematical Tools for Understanding Infectious Disease Dynamics, (Princeton University Press 2013).

Introduction

Mathematics has proven to be very useful in life sciences and in recent years mathematical modeling has been playing an increasingly important role in many areas of ecology, biology and medicine. In this course, we will be studying a few subjects among this very wast domain.

We will mostly concentrate on mathematical population dynamics and issues linked to ways of using mathematical models to control the evolution of the populations in order to satisfy particular objectives. For instance controlling the population of a pest or the vector of a disease (like dengue) or optimize cancer therapy.

Introduction to Population Dynamics

Introduction to population dynamics

We focus on the dynamics of a population of individuals (men, animals, cells, bacteria, ...) which we characterize by its density (or number) at time $t \geq 0$ denoted $N(t)$.

$N(t):$ number of individuals at time $t \geq 0$.

Introduction to population dynamics

We focus on the dynamics of a population of individuals (men, animals, cells, bacteria, ...) which we characterize by its density (or number) at time $t \geq 0$ denoted $N(t)$.

$$N(t): \text{ number of individuals at time } t \geq 0.$$

Goal : knowing the density (or number) at time $t = 0$, denoted N_0, try to predict the population dynamics for future times $t \geq 0$ depending on some observed phenomena.

Population dynamics : Malthus

One of the first important models in population dynamics was proposed by Thomas Malthus (English economist 1766-1834) in 1798 in his book *"An essay on the principle of population"*.

In this model, only two phenomena are taken into account :

- birth, with a rate $b > 0$ (mean number of individuals generated by one individual by unit of time) : for N individuals, during a time interval δt, the number of births is $bN\delta t$;
- death, with a rate $d > 0$.

$$N(t+\delta t) = N(t) + bN(t)\delta t - dN(t)\delta t.$$

Dividing by δt,

$$\frac{N(t+\delta t) - N(t)}{\delta t} = bN(t) - dN(t).$$

Taking the limit $\delta t \to 0$, we get

$$N'(t) = bN(t) - dN(t).$$

Population dynamics : Malthus

Malthus model (1798)

$$N'(t) = bN(t) - dN(t), \qquad N(0) = N_0.$$

This is a first order ODE with constant coefficients.
The solution to this Cauchy problem is given by

$$N(t) = N_0 e^{(b-d)t}.$$

This very simple model allows us to observe two phenomena :

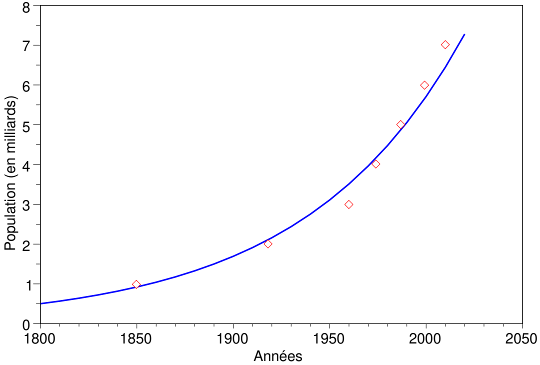
- If $b > d$, we have an **exponential growth** of the size of the population (sometimes call Malthusian growth).
- If $b < d$, we have **extinction** of the population.

$\boxed{r = b - d}$ is called the growth rate.

Population dynamics : Malthus

This model is a too simple to be realistic. Nevertheless, looking for long time scale of the world human population we have a reasonable fit :

Year	1750	1850	1918	1960	1974	1987	1999	2010
Population (in billions)	0.5	1	2	3	4	5	6	7



Population dynamics : Verhulst

In 1838, Pierre-François Verhulst (Belgian mathematician, 1804-1849) refined the Malthus model by proposing a growth rate depending on the size of the population :

- When N is small, same growth rate as for the Malthus model ;
- When the size of the population increases, the growth rate decreases until it vanishes when the size reaches an environmental capacity, denoted K. The growth rate becomes negative beyond that value.

Verhulst model (1838)

$$N'(t) = r\left(1 - \frac{N(t)}{K}\right)N(t), \qquad N(0) = N_0.$$

r : intrinsic growth rate ; K : environmental capacity.

Population dynamics : Verhulst

Verhulst model

$$N'(t) = r\Big(1 - \frac{N(t)}{K}\Big)N(t), \qquad N(0) = N_0.$$

We notice that :

- If $N \in [0, K]$, then $(1 - \frac{N}{K})N \geq 0$, thus $N' \geq 0$: The size of the population increases.
- If $N > K$, then $(1 - \frac{N}{K})N < 0$, thus $N' < 0$: The size of the population decreases.

As a consequence N is a bounded function : If $N_0 \geq 0$, $0 \leq N \leq \max\{K, N_0\}$. Moreover, it seems that the solution always converges to the stationary state K.

Population dynamics : Verhulst

Verhulst model

$$N'(t) = r\Big(1 - \frac{N(t)}{K}\Big)N(t), \qquad N(0) = N_0.$$

This Cauchy problem can actually be solved explicitly by noticing that

$$\frac{N'(t)}{N(t)(1-\frac{N(t)}{K})} = \frac{N'(t)}{N(t)} + \frac{N'(t)}{K-N(t)} = r.$$

Thus,

$$\frac{d}{dt}\Big(\ln(N(t)) - \ln(K-N(t))\Big) = r.$$

Integrating in time we obtain,

$$\ln\left(\frac{N(t)}{K-N(t)}\right) = rt + \ln\left(\frac{N_0}{K-N_0}\right).$$

Population dynamics : Verhulst

After calculation, it gives

$$N(t) = \frac{KN_0}{(K - N_0)e^{-rt} + N_0}.$$

- If $N_0 = 0$, then for all $t > 0$, $N(t) = 0$ (no autogeneration of individuals).
- If $N_0 > 0$, then $\lim_{t \to +\infty} N(t) = K$.

Verhulst model

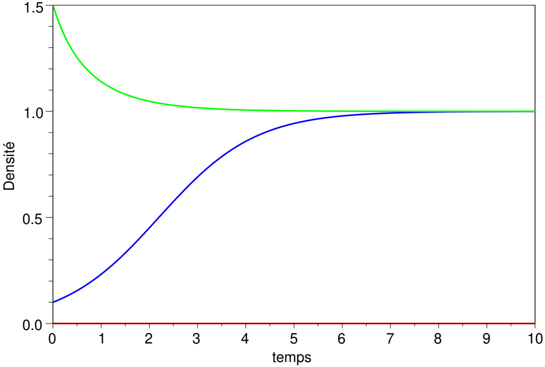
$$N'(t) = r\Big(1 - \frac{N(t)}{K}\Big)N(t), \qquad N(0) = N_0.$$

We remark that $N(t) = 0$ and $N(t) = K$ are constant solutions to this ODE.
Such solutions are called equilibria.
Except for the case where the density is initially 0, all solutions converge to the stationary state $N(t) = K$

We say that the steady state $N = K$ is stable $\Rightarrow$ monostable case.

Population dynamics : equilibria

Numerical example of solutions for $K = 1$, $r = 1$ and for 3 values of N_0 : $N_0 = 0$ (red), $N_0 = 0.1$ (blue), $N_0 = 1.5$ (green).



Allee effect, bistability

In the case of, for instance, small populations with sexual reproduction other phenomena should be taken into account : Allee effect.

There is a negative effect on growth when the population density is too low. This may be due, for example, to the scarcity effect, the consanguinity effect, the difficulty of meeting a partner for populations with low density, . . .

We choose a growth rate under the form $(1-N)(N-\theta)$, with $\theta \in (0,1)$. It is :

- negative if $0 < N < \theta$,
- positive if $\theta < N < 1$,
- negative if $1 < N$.

Denoting $N(t)$ population density at time t, the model with Allee effect is :

$$N'(t) = (1-N(t))(N(t)-\theta)N(t), \quad \theta \in]0,1[, \qquad N(0) = N_0.$$

Allee effect

$$N'(t) = (1 - N(t))(N(t) - \theta)N(t), \quad \theta \in]0,1[, \qquad N(0) = N_0.$$

Equilibria. We look for $\overline{N}$ such that

$$(1 - \overline{N})(\overline{N} - \theta)\overline{N} = 0.$$

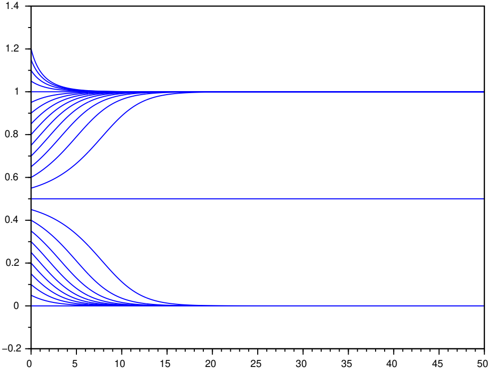
Thus, there are 3 equilibria : 0, θ and 1.

Stability.

- If $N \in]0,\theta[$, $N' < 0$ thus N decreases $\Rightarrow$ 0 is stable.
- If $N \in]\theta,1[$, $N' > 0$, thus N increases and if $N > 1$, $N' < 0$ $\Rightarrow$ 1 is stable.
- Thus, θ is unstable.

Allee effect

Allee effect : population density should be higher than a threshold to avoid extinction.



Example of a numerical simulation for the equation $y' = y(1-y)(y-0.5)$ for different initial data ranging from 0 to 1.2.

Positivity and Monotonicity

Positivity. By uniqueness, if $N_0 > 0$ then for any $t > 0$, $N(t) > 0$.
Monotonicity. Let $N_0 > 0$. Solutions are monotonous : if $R(N_0) > 0$, then $\frac{d}{dt}N(t) \geq 0$ for any $t \geq 0$; if $R(N_0) < 0$, then $\frac{d}{dt}N(t) \leq 0$ for any $t \geq 0$. (Proof left as an exercise)
In higher dimensions we can have a lot richer behaviors as we saw yesterday for the Predator-Prey model.
In some cases, like for **Cooperative or Competitive systems**, even in higher dimensions we can save some form of monotonicity in the sense of comparison between different solutions (in an appropriate partial order).

Predator-Prey model of Lotka-Volterra

In 1920, Alfred J. Lotka and Vito Volterra proposed a model to describe the dynamics of two species in interaction : preys and predators. Their model is based on several assumptions :

- The prey population finds ample food at all times.
- The food supply of the predator population depends entirely on the size of the prey population.
- The rate of change of populations is proportional to its size.
- During the process, the environment does not change in favor of one species, and genetic adaptation is inconsequential.
- Predators have limitless appetite.

Predator-Prey model of Lotka-Volterra

Denoting n the density of preys and p the density of predators. The system is

$$n' = n(\underbrace{a}_{\text{birth rate}} - \underbrace{bp}_{\text{predation}}),$$
$$p' = p(\underbrace{cn}_{\text{predation}} - \underbrace{d}_{\text{death rate}}).$$

Equilibria. We look for $(\overline{n}, \overline{p})$ solution to

$$0 = \overline{n}(a - b\overline{p}), \qquad 0 = \overline{p}(c\overline{n} - d).$$

There are two couples of solutions $(0,0)$ and $(\frac{d}{c}, \frac{a}{b})$.

Predator-Prey model of Lotka-Volterra

For the Lotka-Volterra system, there is an energy (conserved quantity). Indeed, we notice that

$$\frac{cn-d}{n}n'(t) = \frac{a-bp}{p}p'(t).$$

Integrating in time, we deduce that

$$cn(t) - d\ln(n(t)) = a\ln(p(t)) - bp(t) + \text{Cste}.$$

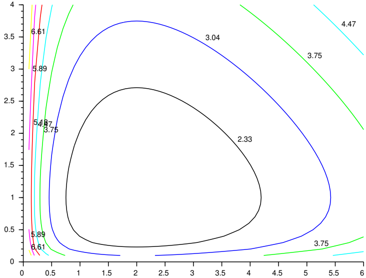
As a consequence the quantity

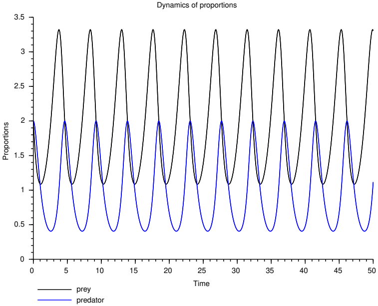
$$H(t) = cn(t) + bp(t) - d\ln(n(t)) - a\ln(p(t)),$$

is constant.

Predator-Prey model of Lotka-Volterra

As a consequence the trajectories in the phase plane (n, p) of the solutions belong to the level sets of the energy H.





The level sets of H are closed (see figure on the left and, the solutions are periodic in time (see figure on the right).

Dynamical System in Biology

Cauchy problem

Many problems in biology may be modeled by a system of differential equations.

Cauchy problem

Let $T > 0$, $f : [0, T] \times \mathbb{R}^d \to \mathbb{R}^d$, $y_0 \in \mathbb{R}^d$.
A Cauchy problem problem to give a differential system and an initial data :

$$\begin{cases} y'(t) = f(t, y(t)), & t \in [0, T], \\ y(0) = y_0. \end{cases} \tag{C}$$

- When the function f does not depend explicitely on time, the system is called *autonomous*.
- A differential equation of order n may be rewritten into a system of order 1 in dimension n by using the variable $Y(t) = (y(t), y'(t), \dots, y^{(n-1)}(t))$.

Cauchy problem : linear case

Let $A \in \mathcal{M}_n(\mathbb{R})$, $B : [0,T] \to \mathbb{R}^n$, it is easy to solve the linear problem

$$y'(t) = Ay(t) + B(t), \qquad y(0) = y_0.$$

The solution is given by

$$y(t) = \exp(tA)y_0 + \int_0^t \exp((t-s)A)B(s)\,ds,$$

where we recall that the exponential of a matrix is given by

$$\exp(A) = \sum_{k=0}^{\infty} \frac{1}{k!} A^k.$$

If the matrix A is diagonalizable : $\exists\, P \in GL_n(\mathbb{R})$ such that $P^{-1}AP = D$, then

$$\exp(tA) = P\exp(tD)P^{-1} = P \begin{pmatrix} e^{t\lambda_1} & 0 & \dots & 0 \\ 0 & e^{t\lambda_2} & \ddots & \vdots \\ & \ddots & \ddots & 0 \\ 0 & & 0 & e^{t\lambda_n} \end{pmatrix} P^{-1}.$$

Cauchy problem : existence theory

Definition

- We say that (I, y) is a *local solution* of (C) iff $I \subset [0, T]$ is an interval containing 0 and $y : I \to \mathbb{R}^d$ is differentiable and satisfies (C).
- We say that (J, z) is an *extension* of (I, y) iff $I \subset J$ and $\forall\, t \in I, \quad y(t) = z(t)$.
- We say that (I, y) is a *maximal solution* if we cannot extend it to a strictly bigger interval.
- If $I = [0, T]$, we say that the solution is *global* in $[0, T]$.

Cauchy-Lipschitz theorem

Assume f is continuous on $[0, T] \times \mathbb{R}^d$, locally Lipschitz continuous with respect to its second variable uniformly with respect to t. Then, the Cauchy problem (C) admits an unique maximal solution.
Moreover, if we denote $[0, b)$ the interval of existence of this maximal solution, if $b < T$, then $\lim_{t \to b^-} \|y(t)\| = +\infty$.

Cauchy problem : existence theory

Cauchy-Lipschitz theorem (global vesion)

Assume f is continuous on $[0,T] \times \mathbb{R}^d$ and globally Lipschitz continuous with respect to its second variable uniformly with respect to t. Then, the Cauchy problem (C) admits an unique global solution.

Remark :

- f locally Lipschitz continuous with respect to its second variable uniformly with respect to t :

$$\forall\, y \in \mathbb{R}^d, \exists\, V_y \subset \mathbb{R}^d (y \in V_y), \exists\, L_y > 0, \quad \forall\, x, \tilde{x} \in V_y, \forall\, t \in [0,T],$$
$$\|f(t,x) - f(t,\tilde{x})\| \leq L_y \|x - \tilde{x}\|.$$

- f globally Lipschitz continuous with respect to its second variable uniformly with respect to t :

$$\exists\, L > 0, \forall\, x, \tilde{x} \in \mathbb{R}^d, \forall\, t \in [0,T], \quad \|f(t,x) - f(t,\tilde{x})\| \leq L\|x - \tilde{x}\|.$$

Cauchy problem : examples

Some important examples :

- Consider the Cauchy problem

  $$y' = y^2, \qquad y(0) = y_0 > 0.$$

  The solution is given by $y(t) = \dfrac{y_0}{1 - y_0 t}$.

  It exists only on $[0, \frac{1}{y_0})$ and blows up at time $\frac{1}{y_0}$.

- Consider the Cauchy problem

  $$y' = \sqrt{y}, \qquad y(0) = 0.$$

  Then, $y(t) = \frac{t^2}{4}$ and $y(t) = 0$ are two solutions for this problem. Hence there is no uniqueness. Indeed, the locally Lipschitz assumption in the Cauchy-Lipschitz theorem is not satisfied.

Equilibrium

In this section we focus on *autonomous systems* and we assume to have existence of a *global* solution on $[0, +\infty)$.

Let $f : \mathbb{R}^d \to \mathbb{R}^d$, $f \in C^1(\mathbb{R}^d)$,

$$\begin{cases} y'(t) = f(y(t)), & t \in [0, +\infty), \\ y(0) = y_0 \in \mathbb{R}^d. \end{cases} \tag{C_0}$$

We call flow and we denote $\phi(t, y_0)$ a solution to this problem.

Equilibrium

For the above autonomous system, we introduce the following definitions :

Definitions

- An equilibrium is a stationary solution, i.e. $\overline{y} \in \mathbb{R}^d$ such that $f(\overline{y}) = 0$.
- An equilibrium is stable if $\forall\, \varepsilon > 0$, $\exists\, \delta > 0$ such that $\forall\, y \in B(\overline{y}, \delta)$, $\phi(t,y) \in B(\overline{y}, \varepsilon)$.
- An equilibrium is asymptotically stable if it is stable and $\exists\, \eta > 0$ such that $\forall\, y \in B(\overline{y}, \eta), \|\phi(t,y) - \overline{y}\| \underset{t \to +\infty}{\to} 0$.
- An equilibrium is globally asymptotically stable (GAS) if it is stable and the above implication is true for all $\eta > 0$.
- An equilibrium is unstable if it is not stable.

Stability

For general system $y' = f(y)$, with $\overline{y}$ an equilibrium. We use a Taylor expansion

$$\begin{aligned} f(y) &= f(\overline{y}) + Df(\overline{y}) \cdot (y - \overline{y}) + o(\|y - \overline{y}\|) \\ &= Df(\overline{y}) \cdot (y - \overline{y}) + o(\|y - \overline{y}\|). \end{aligned}$$

We deduce some stability results on the non-linear problem $y' = f(y)$ from a stability analysis on the linear problem $z' = Df(\overline{y})z$.

Proposition (Lyapunov stability Theorem)

Let us consider the Cauchy problem (C_0), let $\overline{y}$ be an equilibrium $(f(\overline{y}) = 0)$. Denoting $(\lambda_1, \ldots, \lambda_k)$ $(k \leq d)$ the eigenvalues of $Df(\overline{y})$. Then the equilibrium is (linearly) asymptotically stable if $\mathrm{Re}(\lambda) < 0$ for all eigenvalues $\lambda \in Sp(Df(\overline{y}))$.

Examples in one dimension

In one dimension, for the problem

$$y' = f(y), \qquad y(0) = y_0.$$

- The equilibria are the roots of f : $\overline{y} \in \mathbb{R}$ such that $f(\overline{y}) = 0$.
- The linear stability is given by the sign of the derivative :
  If $f'(\overline{y}) < 0$, then $\overline{y}$ is linearly asymptotically stable ;
  If $f'(\overline{y}) > 0$, then $\overline{y}$ is linearly unstable.

Let us come back to the Verhulst model

$$N'(t) = rN(1 - \frac{N}{K}),$$
$$N(0) = N_0.$$

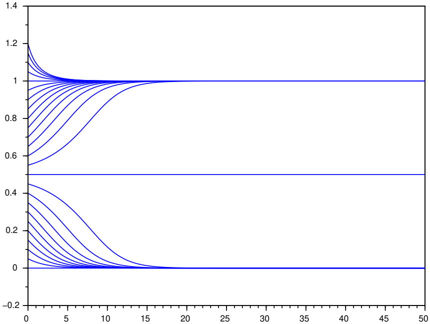
The equilibria are 0 and K. We notice that $f'(0) > 0$ and $f'(K) < 0$. Then 0 is linearly unstable and K is linearly asymptotically stable.

Examples : Allee effect

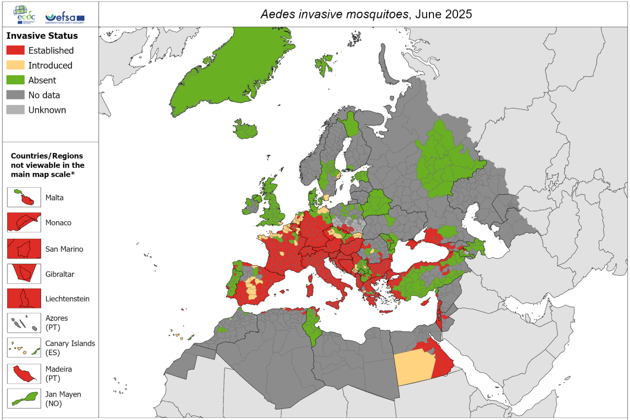
For the model with Allee effect

$$
\begin{aligned}
N'(t) &= N(1-N)(N-\theta), \qquad 0<\theta<1,\\
N(0) &= N_0.
\end{aligned}
$$

The equilibria are 0, θ and 1. We notice that $f'(0)<0$, $f'(\theta)>0$ and $f'(K)<0$. Then θ is linearly unstable and 0 and K are linearly asymptotically stable.



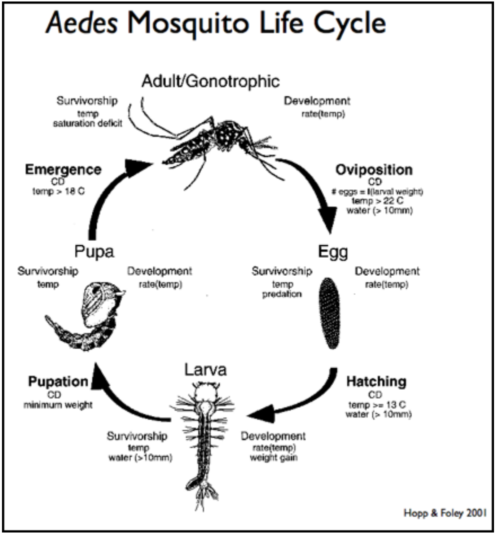
Examples : Arbovirus vector population (Tiger mosquito invasion of Europe)



Aedes invasive mosquitoes, June 2025

ECDC and EFSA, map produced on 25 Jun 2025. Data presented in this map are collected by the VectorNet project. Maps are validated by external experts prior to publication. Please note that the depicted data do not reflect the official views of the countries.
* Countries/Regions are displayed at different scales to facilitate their visualisation.The boundaries and names shown on this map do not imply official endorsement or acceptance by the European Union.Administrative boundaries © EuroGeographics, UNFAO.

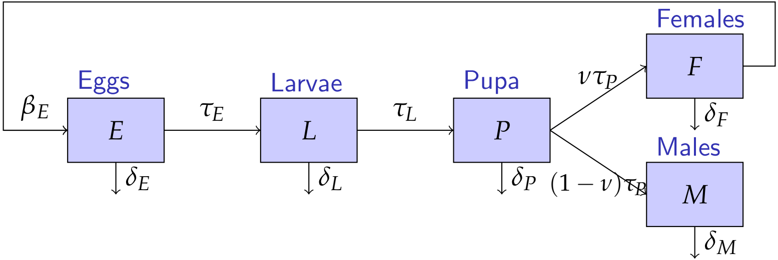
Examples : Mosquito life cycle



Aquatic phase :
egg (few days to several months)
larvae (3 days to several weeks)
pupa (1-3 days)
Adult phase ($\sim$ 1 month)

Examples : Mosquito life cycle

The life cycle for mosquitoes may be represented as follows



- $\beta_E(M)$ birth rate (per female) ;
- τ_E, τ_L, τ_P transition rates ; ν sex ratio ;
- δ_E, δ_L, δ_P, δ_M, δ_F death rates.

Mosquito life cycle

$$\frac{d}{dt}E = \underbrace{\beta_E(M)F}_{\text{birth}} \quad \underbrace{\left(1-\frac{E}{K}\right)}_{\text{intraspecific competition}} \quad - \quad \underbrace{\tau_E E}_{\text{transition to larvae}} \quad - \underbrace{\delta_E E}_{\text{death}},$$

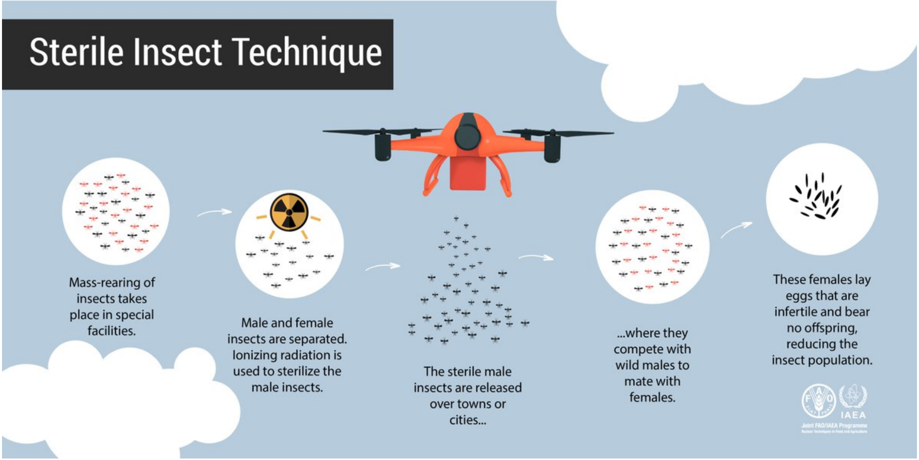
$$\frac{d}{dt}L = \tau_E E - (\quad \underbrace{cL}_{\text{competition}} \quad + \quad \underbrace{\tau_L}_{\text{transition}} \quad + \underbrace{\delta_L}_{\text{death}})L,$$

$$\frac{d}{dt}P = \tau_L L - (\tau_P + \delta_P)P,$$

$$\frac{d}{dt}F = \nu\tau_P P - \delta_F F,$$

$$\frac{d}{dt}M = (1-\nu)\tau_P P - \delta_M M.$$

Targeting sexual reproduction : SIT



Sterile Insect Technique

Mass-rearing of insects takes place in special facilities.

Male and female insects are separated. Ionizing radiation is used to sterilize the male insects.

The sterile male insects are released over towns or cities...

...where they compete with wild males to mate with females.

These females lay eggs that are infertile and bear no offspring, reducing the insect population.

Targeting sexual reproduction : SIT

Sterile Insect Technique (SIT) : releases of sterilized male mosquitoes. The release function is denoted u.
Introduce a new compartment for sterilized males, denoted M_s.
Probability for a female to meet a non-sterilized male depends on a seeking efficiency parameter, α, and a partner preference parameter, γ.

$$\frac{d}{dt}E = \beta_E F \frac{\alpha M}{1+\alpha(M+\gamma M_s)}(1-\frac{E}{K}) - (\tau_E+\delta_E)E$$

$$\frac{d}{dt}L = \tau_E E - (cL + \tau_L + \delta_L)L$$

$$\frac{d}{dt}P = \tau_L L - (\tau_P + \delta_P)P$$

$$\frac{d}{dt}F = \nu\tau_P P - \delta_F F$$

$$\frac{d}{dt}M = (1-\nu)\tau_P P - \delta_M M \qquad \frac{d}{dt}M_s = u - \delta_s M_s.$$

SIT as a general technique against pests

Widely used since the 60's and combined with other control methods, the SIT has been successful in controlling various insect pests, including

- fruit flies (Mediterranean fruit fly, Mexican fruit fly, oriental fruit fly, melon fly) ;
- tsetse fly ;
- screw worm fly (Cochliomyia hominivorax)
- moths (codling moth, pink bollworm, false codling moth, cactus moth, and the Australian painted apple moth)
- mosquitoes.

With good "return on investment" according to FAO and IAEA.

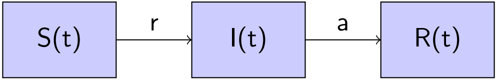
Mathematical Epidemiology

Some historical facts

- In the 18th century, London was strongly affected by an epidemic of smallpox. A controversial solution was *variolation*, which involved contacting individuals with a pustule removed from a patient. This killed the individual or gave immunity for life. Daniel Bernoulli (Swiss mathematician, 1700-1782) proposes in 1766 a mathematical model describing this epidemic and determines whether or not to practice *variolation*. He proved that by inoculating part of the population, life expectancy is considerably increased.
- In 1911, Sir Ronald Ross (Nobel prize in medicine 1902, 1857-1932) presents the first mathematical model of malaria transmission, which highlights a threshold phenomenon. This is one of the first compartmental models. He is considered one of the founding fathers of mathematical epidemiology.
- In 1927, W.O. Kermarck & A.G. Mac Kendrick use the ideas of R. Ross and propose the SIR model to study the transmission of infection between humans.

SIR model

In 1927, W.O. Kermack & A. G. McKendrick introduce the so-called compartmental models : population is divided into susceptible individuals (S), infected individuals (I), and removed/recovered individuals (R).


S(t)
r
I(t)
a
R(t)

where r is the transmission rate, a is the removal rate.

The SIR system can be written as

$$\left\{ \begin{array}{lcl} S' & = & -r\dfrac{SI}{N} \\ I' & = & r\dfrac{SI}{N} - aI \\ R' & = & aI \\ N & = & S + I + R. \end{array} \right.$$

complemented by initial data

$$S(0) = S_0, \quad I(0) = I_0, \quad R(0) = 0.$$

SIR model

- **Conservation.**

We first observe that $N = S + I + R$ is a constant. Indeed, $S' + I' + R' = 0$.

- **Equilibria.**

If we calculate the equilibria, we get

$$\begin{cases} 0 &= -r\frac{\overline{S}\,\overline{I}}{N} \\ 0 &= r\frac{\overline{S}\,\overline{I}}{N} - a\overline{I} \\ 0 &= a\overline{I} \end{cases}$$

Looking to the last equation, it gives $\overline{I} = 0$, which is the only solution. Thus, we expect that the number of infected should converge to 0 to reach the equilibrium.

However, it does not give any information about the number of individuals which has been infected (corresponding to the one in the R compartment at final time).

SIR model

$$\begin{cases} S' &= -r\frac{SI}{N} \\ I' &= r\frac{SI}{N} - aI \\ R' &= aI \end{cases}$$

Question : Knowing r, a, S_0 and I_0, can we know if an epidemic will occur or not ?

We have $I'(0) = I_0(r\frac{S_0}{N} - a)$.

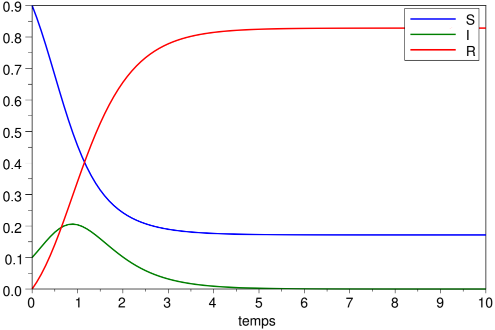
- If $rS_0 < aN$, then $I'(0) < 0$ and since $S' \leq 0$, we always have $I'(t) < 0$. Thus, the number of infected I will diminish until extinction.
- If $rS_0 > aN$, then $I'(0) > 0$. The number of infected individuals will start by increasing.

We recover the threshold phenomenon, first noticed by Sir Ronald Ross. We denote $R_0 = \dfrac{rS_0}{aN}$, called basic reproduction number.

SIR model : numerical observation

Example : In a population where 90% of individuals are susceptibles and 10% are infected ($S_0 = 0.9$, $I_0 = 0.1$).

Case : $r = 4$, $a = 2$, *thus* $R_0 = 1.8$

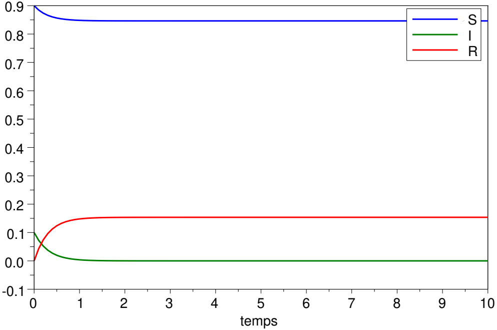


There is a peak of epidemic. At the final time, more than 80% of the population has been infected.

SIR model : numerical observation

Example : In a population where 90% of individuals are susceptibles and 10% are infected ($S_0 = 0.9$, $I_0 = 0.1$).

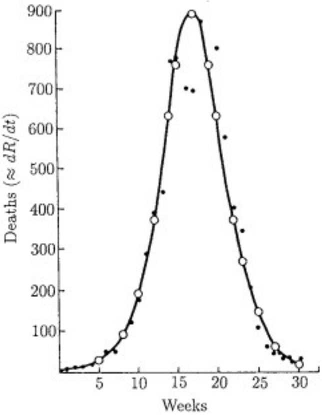
Case : $r = 2$, $a = 5$, *thus* $R_0 = 0.36$



There is no epidemic. Less than 15% of the population has been infected.

SIR model

This model has been used by Kermack and McKendrick in their seminal paper in 1927 to match the data of the Bombay plague epidemic of 1905-1906. The black dots correspond to the data, the curve is given by the theory.



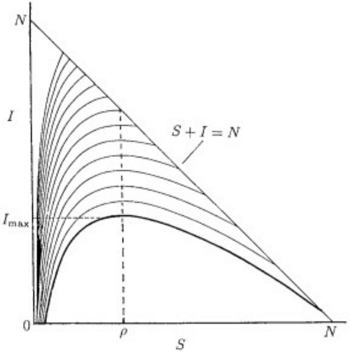
SIR model

Actually, it is possible to solve the SIR model. Indeed, we first remark from the model that

$$\frac{dI}{dS} = -\frac{rSI - aIN}{rSI} = -1 + \frac{aN}{rS}.$$

Then, we have

$$I + S - \frac{aN}{r}\ln(S) = \text{constant} = I_0 + S_0 - \frac{aN}{r}\ln(S_0).$$



Thus, recalling $R_0 = \frac{rS_0}{aN}$, and $N = S_0 + I_0$, we get

$$I(S) = N - S + \frac{S_0}{R_0}\ln(S/S_0).$$

The trajectories are given in the graph opposite.

SIR model

If an epidemic occurs (i.e. $R_0 = \frac{rS_0}{aN} > 1$), we would like to know how severe it will be. Let us denote I_{max} the maximum of I. From the equation, $I' = (\frac{r}{N}S - a)I$, we deduce that when $I = I_{\mathsf{max}}$ we have $\frac{r}{N}S = a$. Hence, $S = \frac{S_0}{R_0}$ and

$$I_{\mathsf{max}} = I_0 + S_0 - \frac{S_0}{R_0}(1 + \ln(R_0)).$$

Moreover, I is an increasing function with respect to S on $(0, \frac{S_0}{R_0})$. At equilibrium we have $I = 0$, hence it is expected that $\lim_{t\to+\infty} I(t) = 0$. It vanishes for

$$0 = N - S_\infty + \frac{S_0}{R_0}\ln(S_\infty/S_0).$$

This nonlinear equation allows to compute the value S_∞ of susceptibles which have not been infected at the end of the epidemic.

SIR model

We can proceed in the same way for the equation for R. From the system equation, we have

$$\frac{dS}{dR} = -\frac{R_0 S}{S_0}.$$

Then, integrating we get

$$\ln \frac{S}{S_0} = -\frac{R_0}{S_0} R.$$

When $t \to +\infty$, we deduce using that $S_\infty + R_\infty = N$

$$\ln \frac{S_\infty}{S_0} = -\frac{R_0}{S_0} R_\infty = -\frac{R_0}{S_0}(N - S_\infty).$$

We recover the same nonlinear equation for S_∞. We deduce $R_\infty = N - S_\infty$, which is the total number of susceptibles who catch the disease in the course of the epidemic.

Numerical value

Assuming that $N \sim S_0$, meaning that the whole population is susceptible to catch the disease, we can compute numerically the value $\frac{S_\infty}{S_0}$ for different value of R_0 : for $R_0 = 2$, we find $\frac{S_\infty}{S_0} \sim 0.2$, i.e. 80% of the population has been infected.

SIR model : summary

We have the following properties. Let

$$R_0 = \frac{rS_0}{aN}.$$

We denote by (S, I) a solution to the SIR model. The total population is denoted N and is constant.

- If $R_0 \leq 1$, then S and I are decreasing and I tends to 0 at infinity : No epidemic.
- If $R_0 > 1$, there is an epidemic : I reachs a maximum value I_{max} before going to 0 at infinity.
  The fonction S is a decreasing function and its limit S_∞ can be computed by solving the nonlinear equation :

$$0 = N - S_\infty + \frac{S_0}{R_0} \ln(S_\infty / S_0).$$

Basic reproduction number R_0

The basic reproduction number, R_0, is defined as the expected number of secondary cases produced by a single (typical) infection in a completely susceptible population.
This quantity defines the epidemic threshold of a particular infection : if $R_0 < 1$, the infection will die out ; if $R_0 > 1$, the infection will be able to spread, there is an outbreak risk.

Some examples :

Disease	R_0	Disease	R_0
Measles (Rougeole)	12-18	Coqueluche	12-17
Polio	5-7	HIV/AIDS	2-5
SRAS[1]	2-5	H1N1 (Grippe A)[2]	2-4
Influenza[3]	2-3	Coronavirus[4]	2.2 - 3.5
Ebola[5]	1.5-2.5		

1. (outbreak in China 2003)
2. (outbreak 2009)
3. (grippe espagnole 1918)
4. (China 2020)
5. (West Africa 2014)

Basic reproduction number R_0

The basic reproduction number R_0 is a dimensionless number

$$R_0 \propto \left(\frac{\text{infection}}{\text{contact}}\right) \cdot \left(\frac{\text{contact}}{\text{time}}\right) \cdot \left(\frac{\text{time}}{\text{infection}}\right)$$

In a simple model like SIR, the basic reproduction number is easy to compute. Indeed, the transmission rate is r, the mean infection time is $\frac{1}{a}$.

It becomes more tricky when we are considering infection with multiple types of infected individuals, or vector-borne disease, or sexually transmitted infections, ...

Remark : Denoting $i(t)$ the number of infected individuals at time t. If a fraction a leaves the infected compartment by unit of time, then $i'(t) = -ai(t)$, implying $i(t) = e^{-at}i(0)$. Then, the mean infection time is given by $\int_0^\infty e^{-at}dt = \frac{1}{a}$.

Basic reproduction number R_0 : example on the SIR model

Recall the SIR model

$$S' = -r\frac{SI}{N}, \quad I' = r\frac{SI}{N} - aI, \quad R' = aI, \quad N = S + I + R \text{ (constant).}$$

The equilibrium without infection is given by $(S, I, R) = (S_0, 0, 0)$ where S_0 is the (constant) number of individuals. Let us study the stability of this equilibrium. We linearize around this equilibrium, the linearized variables (s, i, r) verify

$$s' = -r\frac{S_0}{N}i, \quad i' = r\frac{S_0}{N}i - ai, \quad r' = ai.$$

Hence the Jacobian is given by $J = \begin{pmatrix} 0 & -rS_0/N & 0 \\ 0 & rS_0/N - a & 0 \\ 0 & a & 0 \end{pmatrix}$.

The eigenvalues of this matrix are $\{0, r\frac{S_0}{N} - a\}$. We deduce :

The steady state without infection is unstable if $rS_0 > aN$, i.e. $R_0 > 1$.

Hence, the basic reproduction number gives information on the stability of the equilibrium without infection.

Basic reproduction number R_0

To avoid outbreak, we may try to diminish the value of R_0. In the SIR model, we have

$$R_0 = \frac{rS_0}{aN}.$$

Then, to diminish R_0, one may :

- diminish r : quarantine, improve hygiene conditions to avoid contact with germs, ... ;
- increase a : improve treatments ;
- diminish S_0/N : vaccination campaign. We consider that to stop an outbreak, one needs to vaccine a proportion $\left(1 - \frac{1}{R_0}\right)$ of the population. Indeed if we denote p the fraction of susceptible which are vaccinated, then we replace S_0 by $(1-p)S_0$ in the previous SIR model. As a consequence the basic reproduction number for the model with vaccination is $(1-p)R_0$. And we have $(1-p)R_0 < 1$ iff $p > 1 - \frac{1}{R_0}$.

Example : for H1N1, R_0 is between 2 and 4. Thus, one needs to vaccinate between 50 and 75 % of the population.

Computation of the basic reproduction number R_0

Assume that we have a system in which there are multiple discrete types of infected individuals (e.g., mosquitoes and humans ; women and men ; or humans, dogs, and chicken). We define the next generation matrix as the square matrix G in which the ijth element of G, g_{ij}, is the expected number of secondary infections of type i caused by a single infected individual of type j, again assuming that the population of type i is entirely susceptible.
Then, the basic reproduction number is given by the spectral radius of G

$$R_0 = \rho(G) = \sup\{|\lambda|, \lambda \in \ \mathsf{Sp}\,(G)\}.$$

The next generation matrix has a number of desirable properties from a mathematical standpoint. In particular, it is a non-negative matrix and, as such, it is guaranteed that there will be a single, unique eigenvalue which is positive, real, and strictly greater than all the others. This is R_0.

Computation of the basic reproduction number R_0

A method to compute the basic reproduction number has been proposed in [Diekmann et al][6]. We assume to have a system of ODE describing the dynamics of an infection :

1. Determine the variables describing the infected states.
2. Determine the equilibrium without infection and linearize around it only the system for infected states (i.e. compute the Jacobian matrix J).
3. Split the Jacobian matrix $J = T + \Sigma$ where T is the transmission matrix (birth of infected individuals) and Σ is the transition matrix (change of state).
4. We have $R_0 = \rho(-T\Sigma^{-1})$.

Then, we have the fundamental result :

Theorem

Assume that the transmission matrix T is nonnegative, Σ is nonnegative outside the diagonal with $\sup\{ \text{Re}(\lambda), \lambda \in \text{Sp}(\Sigma)\} < 0$.
Then, the equilibrium without infection is linearly stable iff $R_0 \leq 1$.

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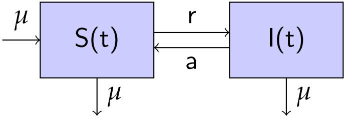
[6] O. Diekmann, J.A. Heersterbeek, J.A.J. Metz, J. Mathematical Biol. 1990

SIS model

The SIR model takes into account the fact that infected people are immune once they are cured. This may not be the case for some diseases for example for bacterial diseases like *staphylococcus aureus, streptococcus pyogenes, chlamydia pneumoniae, ...* In this situation, we use the so-called SIS model, with two compartment :

- susceptible $S(t)$;
- infected $I(t)$;
- total population $N = S(t) + I(t)$.

We assume that the birth rate and the death rate is the same and denoted μ. This dynamics is schematized with the following simple graph



where r is the transmission rate, a is the cure rate.

SIS model

The corresponding ODE system is

$$\begin{aligned} S' &= \underbrace{\mu N}_{\text{birth}} - \underbrace{r\frac{SI}{N}}_{\text{infection}} - \underbrace{\mu S}_{\text{death}} + \underbrace{aI}_{cure} \\ I' &= \underbrace{r\frac{SI}{N}}_{\text{infection}} - \underbrace{\mu I}_{\text{death}} - \underbrace{aI}_{cure}. \end{aligned}$$

The system is completed with some initial data (S_0, I_0).
As above, we have $S' + I' = 0$, then the total population is constant $N = S_0 + I_0$. Thus we can reduce the system to

$$\begin{aligned} S &= N - I \\ I' &= (r - \mu - a - \frac{r}{N}I)I. \end{aligned}$$

SIS model

Let us consider

$$I' = (r - \mu - a - \frac{r}{N} I) I, \qquad I(0) = I_0.$$

This is a logistic growth model. We have already seen this model. There are two equilibria $\{0, \frac{N}{r}(r - \mu - a)\}$. If we denote

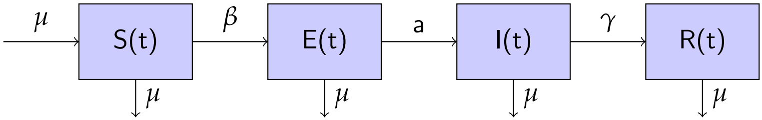
$$R_0 = \frac{r}{\mu + a},$$

then we can distinguish two cases :

- If $R_0 < 1$, then both equilibria are nonpositive, thus $\lim_{t \to +\infty} I(t) = 0$. The disease will go to extinction.
- If $R_0 > 1$, then there is a positive equilibria which is attractive. Thus $\lim_{t \to +\infty} I(t) = \frac{N}{r}(r - \mu - a)$ and $\lim_{t \to +\infty} S(t) = \frac{N}{r}(\mu + a)$. We say that the disease is endemic (*there is a non disease-free stable equilibria*).

SEIR model

We add a compartment to take into account an incubation period during which individuals are infected but not infectious. The new compartment is denoted E (exposed).



The parameters are :

- μ death rate which is assumed to be equal to the birth rate (such that the total population is constant) ;
- β rate of infection ;
- a transition rate from exposed to infected ;
- γ recovery rate.

SEIR model

The corresponding system of ODE is

$$\begin{cases} S' &=& \mu N - \mu S - \beta \dfrac{I}{N} S \\ E' &=& \beta \dfrac{I}{N} S - (\mu + a) E \\ I' &=& aE - (\mu + \gamma) I \\ R' &=& \gamma I - \mu R, \end{cases}$$

where $N = S + E + I + R$ is the total number of individuals, which is constant. We follow the strategy enumerate above

1. There are two infected states : E, I, two non infected states : S, R.
2. Equilibrium without infection is $S = N$, $E = I = R = 0$. The linearized system for infected states around the equilibrium is
$$E'(t) = \beta I - (\mu + a) E, \qquad I'(t) = aE - (\mu + \gamma) I.$$
3. Transmission and transition matrices
$$T = \begin{pmatrix} 0 & \beta \\ 0 & 0 \end{pmatrix}, \qquad \Sigma = \begin{pmatrix} -(\mu + a) & 0 \\ a & -(\mu + \gamma) \end{pmatrix}.$$

SEIR model

Finally the basic reproduction number for the SEIR model is given by

$$R_0 = \rho(-T\Sigma^{-1}) = \frac{a\beta}{(\gamma+\mu)(a+\mu)}.$$

Indeed,

$$-\Sigma^{-1} = \begin{pmatrix} \frac{1}{a+\mu} & 0 \\ \frac{a}{(\mu+\gamma)(a+\mu)} & \frac{1}{\mu+\gamma} \end{pmatrix}.$$

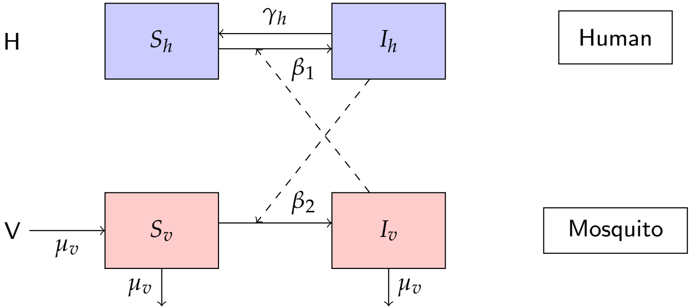
Then, we can compute

$$-T\Sigma^{-1} = \begin{pmatrix} \frac{a\beta}{(a+\mu)(\gamma+\mu)} & \frac{\beta}{\mu+\gamma} \\ 0 & 0 \end{pmatrix}.$$

It is a triangular matrix. Hence its eigenvalues are given in the diagonal.

Ross-Macdonald model

Let us consider a model based on the work of Sir Ronald Ross (Nobel prize in 1902) improved later by George Macdonald (1952) for malaria. It is a vector-borne disease, i.e. transmitted by a vector : mosquitoes (mainly of genus *Anopheles*). The dynamical system includes the mosquito dynamics and its interaction with humans.



Similar models are used for the transmission of Dengue, Chikungunya, Zika, ...

Ross-Macdonald model

The modelling assumptions are :

- Two populations : H (human), V (vector of the disease = mosquito).
- SIS model for the disease for H and V, where we assume that the total population of humans and vectors is constant.
- Parameters :
  - β_1, number of bites of an infected mosquito that are efficient in producing an infection (if the victim is a susceptiblre human) per unit of time = = proportion of bites that are efficient in producing an infection (if the victim is a susceptiblre human) x total number of bites of an infected mosquito per unit of time.
  - β_2 number of bytes of a susceptible mosquito that are efficient in making it become infected (in case it bites an infected host) = = proportion of bites giving rise to an infection of a suceptible mosquito (in case the human is infected) x number of bytes of a susceptible mosquito per unit of time ;
  - γ recovery rate for humans ;
  - μ_m death and birth rate for mosquitoes (assumed to be the same).

Ross-Macdonald model

The corresponding system of ODE is

$$\begin{aligned}
\frac{dS_h}{dt} &= -\beta_1 \frac{I_v S_h}{H} + \gamma I_h\,, \qquad H = S_h + I_h\,,\\
\frac{dI_h}{dt} &= \beta_1 \frac{I_v S_h}{H} - \gamma I_h\,,\\
\frac{dS_v}{dt} &= -\beta_2 \frac{I_h S_v}{H} + \mu V - \mu S_v\,, \qquad V = S_v + I_v\,,\\
\frac{dI_v}{dt} &= \beta_2 \frac{I_h S_v}{H} - \mu I_v\,.
\end{aligned}$$

It is clear that the number of humans, H, and of mosquitoes, V, are constant.

Ross-Macdonald model

We are now in position to compute the basic reproduction number for this system.

1. There are two infected states : I_h, I_v.
2. Equilibrium without infection : $(S_h, I_h, S_v, I_v) = (H, 0, V, 0)$.
   Linearization around this equilibrium for the infected states

$$\frac{dI_h}{dt} = \beta_1 I_v - \gamma I_h, \qquad \frac{dI_v}{dt} = \beta_2 \frac{V}{H} I_h - \mu I_v.$$

3. Transmission and transition matrices

$$T = \begin{pmatrix} 0 & \beta_1 \\ \beta_2 \frac{V}{H} & 0 \end{pmatrix} \qquad \Sigma = \begin{pmatrix} -\gamma & 0 \\ 0 & -\mu \end{pmatrix}.$$

4. Computation of R_0

$$T\Sigma^{-1} = \begin{pmatrix} 0 & \frac{\beta_1}{\mu} \\ \frac{\beta_2 V}{H\gamma} & 0 \end{pmatrix}.$$

The spectral radius for this latter matrix is then $R_0 = \sqrt{\dfrac{\beta_1 \beta_2 V}{\gamma \mu H}}$.

A model for dengue transmission

Finally, we consider a model for dengue transmission[7] This model is based on the following modeling assumption :

- The human population is assumed to be constant, i.e. the death rate for human is the same as the birth rate.
- Dengue is a SEI disease for mosquitoes.
- Dengue is a SIR disease for human.

We use the following notations :

- V, S_m, E_m, I_m denote the total number of mosquitoes, the number of susceptible mosquitoes, the number of mosquitoes exposed to the disease, the number of infected mosquitoes, respectively. We have the relation $\boxed{V = S_m + E_m + I_m}$.
- H, S_h, I_h, R_h denote the total number of human, the number of susceptible human, the number of infected human, the number of recovered humans, respectively. We have $\boxed{H = S_h + I_h + R_h}$.

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[7] From H. Hughes, N. F. Britton, *Modelling the use of Wolbachia to control dengue fever transmission*, Bull. Math. Biol. (2013).

A model for dengue transmission

With these considerations, the model is

$$\frac{dV}{dt} = bV(1-\frac{V}{K}) - dV,$$

$$\frac{dE_m}{dt} = ap(V-E_m-I_m)\frac{I_h}{H} - eE_m - dE_m, \qquad \frac{dI_m}{dt} = eE_m - dI_m,$$

$$\frac{dS_h}{dt} = \mu H - aqI_m\frac{S_h}{H} - \mu S_h, \qquad \frac{dI_h}{dt} = aqI_m\frac{S_h}{H} - cI_h - \mu I_h.$$

- Parameters are
  - a the biting rate.
  - p the probability of a blood meal leading to mosquito catching dengue from infected human.
  - q the probability of a blood meal leading to human catching dengue from infected mosquito.
  - b, d birth and death rate for mosquitoes, respectively ; e mean incubation rate.
  - μ birth and death rate (the same) ; c recovery rate.

A model for dengue transmission

We are now in position to compute the basic reproduction number for this system.

1. There are 3 infected states : $E_m,\ I_m,\ I_h$.
2. Equilibrium without infection : $(V, E_m, I_m, S_h, I_h) = (K(1-\frac{d}{b}), 0, 0, H, 0)$.
   Linearization around this equilibrium for the infected states

$$\frac{dE_m}{dt} = \frac{apK(1-\frac{d}{b})}{H} I_h - (e+d)E_m, \qquad \frac{dI_m}{dt} = eE_m - dI_m,$$
$$\frac{dI_h}{dt} = aqI_m - (c+\mu)I_h.$$

3. Transmission and transition matrices

$$T = \begin{pmatrix} 0 & 0 & \frac{apK(1-\frac{d}{b})}{H} \\ 0 & 0 & 0 \\ 0 & aq & 0 \end{pmatrix} \qquad \Sigma = \begin{pmatrix} -(d+e) & 0 & 0 \\ e & -d & 0 \\ 0 & 0 & -(c+\mu) \end{pmatrix}.$$

4. Computation of R_0 : We have

$$-\Sigma^{-1} = \begin{pmatrix} \frac{1}{d+e} & 0 & 0 \\ \frac{e}{d(d+e)} & \frac{1}{d} & 0 \\ 0 & 0 & \frac{1}{c+\mu} \end{pmatrix}.$$

A model for dengue transmission

Then, using the above approach, we compute

$$T\Sigma^{-1} = \begin{pmatrix} 0 & 0 & \frac{apK(1-\frac{d}{b})}{(c+\mu)H} \\ 0 & 0 & 0 \\ \frac{eaq}{d(d+e)} & \frac{aq}{d} & 0 \end{pmatrix}.$$

The spectral radius for this latter matrix is then $R_0 = \sqrt{\dfrac{ea^2pqK(1-\frac{d}{b})}{d(d+e)(c+\mu)H}}$.

Monotone Systems

Cooperative systems

Systems where several species will help each other

$$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 + a_1 N_1 N_2 \\ \frac{dN_2}{dt} = r_2 N_2 + a_2 N_2 N_1 \end{cases}$$

Here, unlimited growth (not realistic). Better to have logistic growth

$$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 (1 - \frac{N_1}{K_1} + b_{12} \frac{N_2}{K_1}) \\ \frac{dN_2}{dt} = r_2 N_2 (1 - \frac{N_2}{K_2} + b_{21} \frac{N_1}{K_2}) \end{cases}$$

Where $r_1, r_2, K_1, K_2, b_{12}, b_{21}$ positive constants.
b_{12}, b_{21} cooperation coefficients between species 1 and 2.

Cooperative systems

Doing a change of variables

$$u_1 = \frac{N_1}{K_1}, \quad u_2 = \frac{N_2}{K_2}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1}, \quad a_{12} = b_{12}\frac{K_2}{K_1}, \quad a_{21} = b_{21}\frac{K_1}{K_2}$$

Our system becomes

$$\begin{cases} \frac{du_1}{d\tau} = u_1(1 - u_1 + a_{12}u_2) = f_1(u_1, u_2) \\ \frac{du_2}{d\tau} = \rho u_2(1 - u_2 + a_{21}u_1) = f_2(u_1, u_2) \end{cases}$$

Critical points : $(0,0)$, $(1,0)$, $(0,1)$

Cooperative systems

Doing a change of variables

$$u_1 = \frac{N_1}{K_1}, \quad u_2 = \frac{N_2}{K_2}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1}, \quad a_{12} = b_{12}\frac{K_2}{K_1}, \quad a_{21} = b_{21}\frac{K_1}{K_2}$$

Our system becomes

$$\begin{cases} \frac{du_1}{d\tau} = u_1(1 - u_1 + a_{12}u_2) = f_1(u_1, u_2) \\ \frac{du_2}{d\tau} = \rho u_2(1 - u_2 + a_{21}u_1) = f_2(u_1, u_2) \end{cases}$$

Critical points : $(0,0)$, $(1,0)$, $(0,1)$
and a fourth one

$$u_1^* = \frac{1 + a_{12}}{1 - a_{12}a_{21}}, \quad u_2^* = \frac{1 + a_{21}}{1 - a_{12}a_{21}}$$

which is positive if $1 - a_{12}a_{21} > 0$. It corresponds to a co-existence of the two populations benefiting from each other's presence without exploding.

Cooperative systems

$(0,0)$ is unstable, $(1,0)$, $(0,1)$ are saddle points.

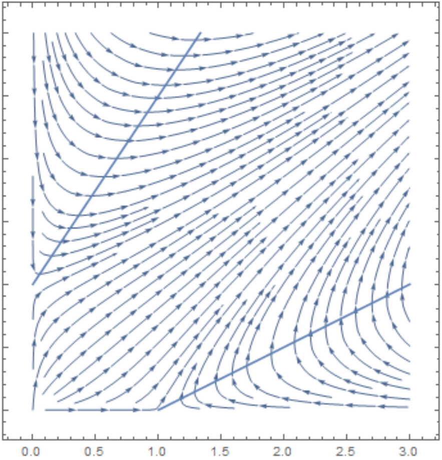

FIGURE – If $1 - a_{12}a_{21} < 0$, both explode

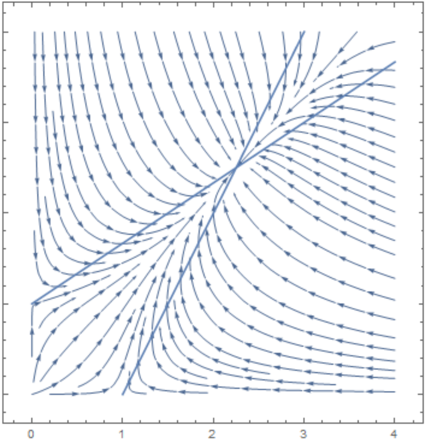

FIGURE – If $1 - a_{12}a_{21} > 0$, thanks to cooperation, both populations are beyond their isolated environmental capacity.

Competitive systems

Systems where several species compete with each other.
Principle of Mutual Exclusion (PME) : only the fittest one survives.

$$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1}\right) \\ \frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{21}\frac{N_1}{K_2}\right) = r_2 N_2 (1 - \frac{N_2 + b_{21} N_1}{K_2}) \end{cases}$$

where $r_1, K_1, r_2, K_2, b_{12}, b_{21}$ are positive constants. r_i intrinsic growth coefficient of species i. K_i carrying capacity of i (isolated). b_{12} measures the effect of species 2 on species 1.

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Change of variables :

$$u_1 = \frac{N_1}{K_1}, \quad u_2 = \frac{N_2}{K_2}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1}, \quad a_{12} = b_{12}\frac{K_2}{K_1}, \quad a_{21} = b_{21}\frac{K_1}{K_2}$$

System becomes

$$\begin{cases} \frac{du_1}{d\tau} = u_1(1 - u_1 - a_{12}u_2) = f_1(u_1, u_2) \\ \frac{du_2}{d\tau} = \rho u_2(1 - u_2 - a_{21}u_1) = f_2(u_1, u_2) \end{cases}$$

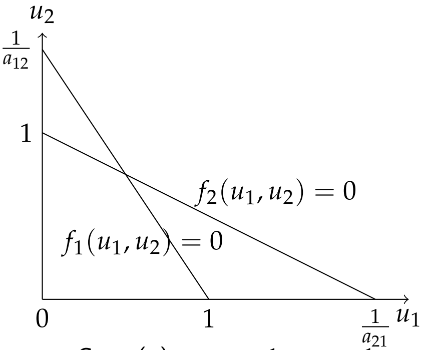
Competitive systems

Critical points (u_1^*, u_2^*) satisfy $f_1 = f_2 = 0$:
$(0,0)$, $(1,0)$, $(0,1)$ and

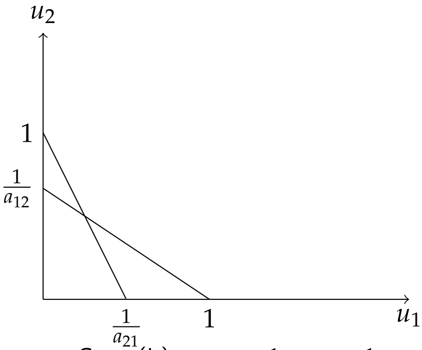
$$u_1^* = \frac{1-a_{12}}{1-a_{12}a_{21}},\ u_2^* = \frac{1-a_{21}}{1-a_{12}a_{21}}$$

Four cases depeding on values of a_{12}, a_{21} :
Case (a) : $a_{12} < 1, a_{21} < 1$ weak competition between the species ;
Case (b) : $a_{12} > 1, a_{21} > 1$ strong competition between the species ;
Case (c) : $a_{12} < 1, a_{21} > 1$ species 1 is stronger ;
Case (d) : $a_{12} > 1, a_{21} < 1$ species 2 is stronger

Competitive systems

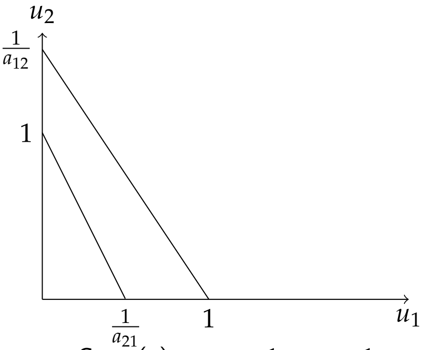


Case (a) : $a_{12} < 1, a_{21} < 1$

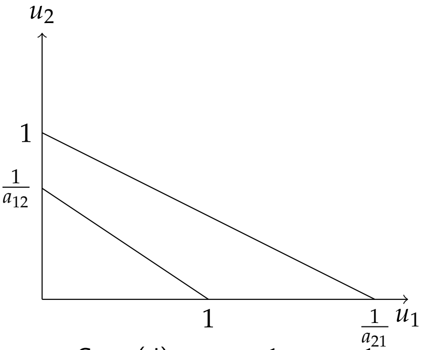


Case (b) : $a_{12} > 1, a_{21} > 1$

Competitive systems



Case (c) : $a_{12} < 1, a_{21} > 1$



Case (d) : $a_{12} > 1, a_{21} < 1$

Competitive systems

We see that in cases (c) et (d), we have only 3 critical points. Dependence on the competition coefficients a_{ij} .
For (linear) stability look at linearized system matrix :

$$A = \begin{pmatrix} \frac{\partial f_1}{\partial u_1} & \frac{\partial f_1}{\partial u_2} \\ \frac{\partial f_2}{\partial u_1} & \frac{\partial f_2}{\partial u_2} \end{pmatrix}_{u_1^*, u_2^*} = \begin{pmatrix} 1 - 2u_1 - a_{12}u_2 & -a_{12}u_1 \\ -\rho a_{21} u_2 & \rho(1 - 2u_2 - a_{21}u_1) \end{pmatrix}_{(u_1^*, u_2^*)}$$

- For $(0,0)$:

  $$|A - \lambda I| = \begin{vmatrix} 1-\lambda & 0 \\ 0 & \rho - \lambda \end{vmatrix} = 0$$

  So $\lambda_1 = 1$ and $\lambda_2 = \rho > 0$, Hence, $(0,0)$ is linearly unstable.
- For $(1,0)$:

  $$|A - \lambda I| = \begin{vmatrix} -1-\lambda & -a_{12} \\ 0 & \rho(1-a_{21}) - \lambda \end{vmatrix} = 0$$

  Hence $\lambda_1 = -1,\ \lambda_2 = \rho(1 - a_{21})$, $(1,0)$ linearly stable if $a_{21} > 1$, linearly unstable if $a_{21} < 1$.
- For $(0,1)$, $\lambda_1 = -\rho, \lambda_2 = 1 - a_{12}$. Hence, $(0,1)$ linearly stable if $a_{12} > 1$, linearly unstable if $a_{12} < 1$.

Competitive systems

For the critcal point (u_1^*, u_2^*), we have

$$A = \frac{1}{1 - a_{12}a_{21}} \begin{pmatrix} a_{12} - 1 & a_{12}(a_{12} - 1) \\ \rho a_{21}(a_{21} - 1) & \rho(a_{21} - 1) \end{pmatrix}$$

Thus,

$$\lambda_1, \lambda_2 = \frac{1}{2(1 - a_{12}a_{21})} \Bigg((a_{12} - 1) + \rho(a_{21} - 1)$$

$$\pm \sqrt{((a_{12} - 1) + \rho(a_{12} - 1))^2 - 4\rho(1 - a_{12}a_{21})(a_{12} - 1)(a_{21} - 1)} \Bigg)$$

Competitive systems

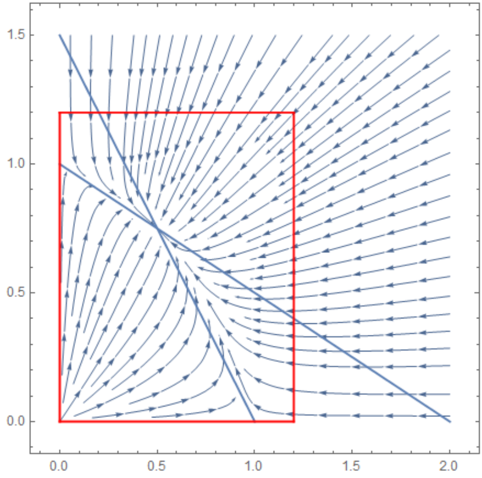


FIGURE – Case (a) : Only case where (u_1^*, u_2^*) is stable.

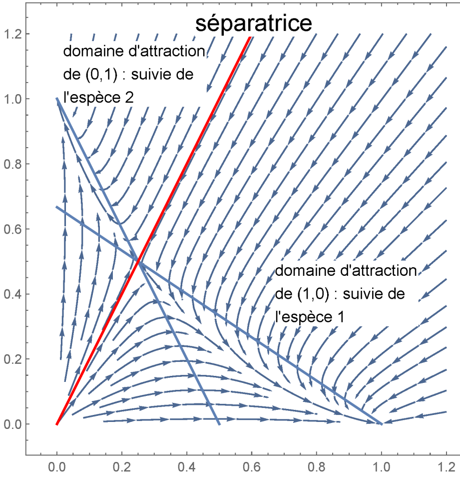


FIGURE – Case (b) : (u_1^*, u_2^*) is a saddle point. Separatrix

Competitive systems

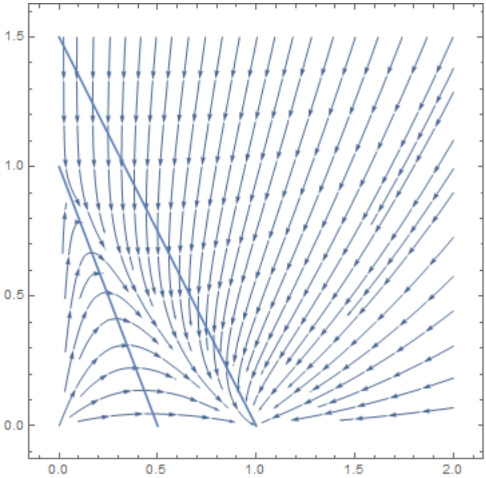


FIGURE – Case (c) : $(1,0)$ only is stable : species 1 survives.

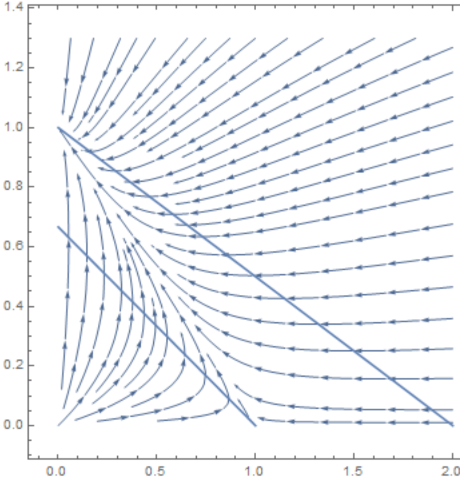


FIGURE – Cas (d) : $(0,1)$ only is stable : species 2 survives.

Monotone systems in $\mathbb{R}^n$: order relations

Consider the open domain $D \subset \mathbb{R}^n$ and let $f : D \to \mathbb{R}^n$ be $C^1(D)$ We consider the system of ODE

$$x' = f(x), \quad f \in C^1(D) \tag{1}$$

Let $\phi_t(x)$ be the solution of (1) passing through point x for $t = 0$.
This defines the flow associated with system (1) $\Phi(t, x) := \phi_t(x)$
The **non-negative cone of $\mathbb{R}^n$** is

$$\mathbb{R}^n_+ = \{(x_1, \cdots, x_n) \in \mathbb{R}^n \ : \ x_i \geq 0 \ \forall i\},$$

and the the partial order associated to it is

$$y \leq x \iff x - y \in \mathbb{R}^n_+ \iff y_i \leq x_i \ \forall i = 1, \cdots, n$$

We say that $x < y$ if $x \leq y$ and $x \neq y$ (i.e. if $x \leq y$ and there is i s.t. $x_i < y_i$) and that $x \ll y$ iif $x_i < y_i$ for all $i = 1, \cdots, n$.

Monotone systems in $\mathbb{R}^n$: Kamke functions

Definition : f is **of type K** in D if

$$f_i(a) \leq f_i(b), \quad \forall a \leq b \text{ and } a_i = b_i.$$

Proposition (Comparison preserving flow) : Let f be of type K in D and $x_0, y_0 \in D$. Let $<_r$ be one of the relations $\leq, <, \ll$. Then, if $x_0 <_r y_0$ and $t > 0$ s.t. $\phi_t(x_0)$ and $\phi_t(y_0)$ are defined, we have

$$\phi_t(x_0) <_r \phi_t(y_0)$$

i.e. if the two points are comparable, the flow preserves the comparison. We remark that the proposition gives a necessary condition for f to be of type K. An analogous proposition is valid for non-autonomous systems.
$x' = f(t, x)$, where f est C^1 in $\mathbb{R}^+ \times D$, and $f(t, \cdot)$ is of type K in D for all $t > 0$.

Monotone systems in $\mathbb{R}^n$: p-convexity

The domain D is **p-convex** if $\forall x, y \in D$, if $x \leq y$, the segment

$$\overline{xy} = \{tx + (1-t)y \ : \ t \in [0,1]\} \subset D$$

D convex $\Longrightarrow$ D p-convex.
If $D \subset \mathbb{R}^n$ p-convex and

$$\frac{\partial f_i}{\partial x_j} \geq 0, \ \forall j \neq i, \ \forall x \in D \tag{2}$$

Then f is of type K in D. (just use the fundamental theorem of calculus)

Monotone systems in $\mathbb{R}^n$: cooperative and competitive systems

Definition :

1. system (1) is **cooperative** in the p-convex domain D if (2) is satisfied.
2. system (1) is **competitive** in the p-convex domain D if

$$\frac{\partial f_i}{\partial x_j} \leq 0, \ \forall i \neq j, \ \forall x \in D$$

Remark : (1) is competitive (with flow $\Phi(t,x) = \phi_t(x)$) iff $x' = -f(x)$ is cooperative, and vice-versa. A cooperative system is a monotone system and it preserves order $<_r$ for $t \geq 0$. A competitive system is such that its flow with time reversed is monotone : i.e. if $x \leq y$ and $t < 0$, then $\phi_t(x) \leq \phi_t(y)$.
Exercise : Show that a competitive system's flow preserves the property of non-comparability of two points (for $t \geq 0$).

Tumor Growth : Proliferative and quiescent cells

It has been observed that not all cells proliferate. Observations show that a big part of cells stay in a quiescent state. To take into account this effect, we should consider at least two states of cells : proliferative cells with density P, quiescent cells with density Q. A simple model is

$$\begin{cases} \dfrac{dP}{dt} = F(P) - bP + cQ, \\ \dfrac{dQ}{dt} = bP - cQ - dQ, \end{cases}$$

with the parameters :

- F growth function (e.g. $F(P) = rP(1 - (\frac{P}{K})^a)$ with $r, a, K > 0$) ;
- $b, c > 0$ transition coefficients ;
- d death rate.

This system is complemented with initial data P_0, Q_0. The density of tumor cells is given by $N(t) = P(t) + Q(t)$.

Tumor Growth : Proliferative and quiescent cells

Proposition

We have

1. *Preservation of positivity and monotonicity* :

$$P_0, Q_0 \geq 0 \;\Rightarrow\; P(t), Q(t) \geq 0, \forall\, t \geq 0.$$

$$\begin{cases} u_0 := F(P_0) - bP_0 + cQ_0 \geq 0, \\ v_0 := bP_0 - (c+d)Q_0 \geq 0 \end{cases} \;\Rightarrow\; \frac{dP}{dt} \geq 0, \frac{dQ}{dt} \geq 0.$$

2. *Equilibria :* There are two steady states : $(0,0)$ and $(\overline{P}, \overline{Q})$ with $\overline{P} = K(1 - \frac{bd}{r(c+d)})^{1/a}$, $\overline{Q} = \frac{b}{c+d}\overline{P}$. And we have
   - For $d \ll 1$, the steady state $(\overline{P}, \overline{Q})$ is asymptotically stable.
   - If $r > b + c + d$, the steady state $(0,0)$ is linearly unstable.

Tumor Growth : Proliferative and quiescent cells

Proof : The system is monotone - this yields *positivity and monotonicity.* *Equilibria.* We solve the system

$$F(\overline{P}) - b\overline{P} + C\overline{Q} = 0 \;, \qquad b\overline{P} - (c+d)\overline{Q} = 0.$$

It gives

$$\overline{Q} = \frac{b}{c+d}\overline{P} \;, \qquad \overline{P}\left(r(1 - (\frac{\overline{P}}{K})^a) - \frac{bd}{c+d} \right) = 0.$$

Thus, we have two equilibria $\overline{P} = \overline{Q} = 0$ or $\overline{P} = K(1 - \frac{bd}{r(c+d)})^{1/a}$, $\overline{Q} = \frac{b}{c+d}\overline{P}$. *Stability.* The Jacobian is given by

$$J = \begin{pmatrix} F'(\overline{P}) - b & c \\ b & -(c+d) \end{pmatrix} = \begin{pmatrix} r(1-(1+a)(\frac{\overline{P}}{K})^a) - b & c \\ b & -(c+d) \end{pmatrix}.$$

At the equilibrium $(\overline{P}, \overline{Q})$, we have

$$J = \begin{pmatrix} -ra - b + (1+a)\frac{bd}{c+d} & c \\ b & -(c+d) \end{pmatrix}.$$

When $d = 0$, we have $\mathrm{Tr}\, J = -ra - b - c < 0$ and $\mathrm{Det}\, J = rac > 0$. Hence, the real part of eigenvalues is negative. By continuity it is also true for d small.

Tumor Growth : Proliferative and quiescent cells

At the equilibrium $(0,0)$, then the Jacobian is

$$J_0 = \begin{pmatrix} r-b & c \\ b & -(c+d) \end{pmatrix}$$

Then Tr $J_0 = r - b - c - d$. Then, if $r > b + c + d$, we deduce that one eigenvalue (at least) has a positive real part. Thus, it is linearly unstable.

Proliferative and quiescent cells : action of a therapy

Action of a therapy.
We usually consider that there are two different drugs : cytotoxic drugs kills proliferative cells, cytostatic drugs block the proliferation. We can add these effects in the simple model above :

$$\begin{cases} \dfrac{dP}{dt} = F(P) - (b + c_{\text{stat}})P + cQ - c_{\text{tox}}P, \\ \dfrac{dQ}{dt} = (b + c_{\text{stat}})P - cQ - dQ, \end{cases}$$

where c_{stat} and c_{tox} represent the concentration of cytostatic and cytotoxic drugs, respectively.

- Effect of c_{stat}

We replace b by $b + c_{\text{stat}}$ in the previous equilibrium. Then they are given by $(0, 0)$ and

$$\overline{P} = K\Big(1 - \frac{d(b + c_{\text{stat}})}{r(c + d)}\Big)^{1/a}, \quad \overline{Q} = \frac{b + c_{\text{stat}}}{c + d}\overline{P}.$$

Proliferative and quiescent cells : action of a therapy

In the latter case, we have then,

$$\overline{N} = \overline{P} + \overline{Q} = K\Big(1 + \frac{b + c_{\mathsf{stat}}}{c+d}\Big)\Big(1 - \frac{d(b + c_{\mathsf{stat}})}{r(c+d)}\Big)^{1/a}.$$

Thus $\overline{P}$ diminishes, but $\overline{Q}$ increases. We notice that in the particular case $\frac{d}{r} \ll 1$, $\overline{N}$ increases, i.e. the size of the tumor increases !

- Effect of c_{tox}

The non-zero equilibrium is given by

$$\overline{P} = K\Big(1 - \frac{c_{\mathsf{tox}}}{r} - \frac{bd}{r(c+d)}\Big)^{1/a}, \quad \overline{Q} = \frac{b}{c+d}\overline{P}.$$

and

$$\overline{N} = \overline{P} + \overline{Q} = K\Big(1 + \frac{b}{c+d}\Big)\Big(1 - \frac{c_{\mathsf{tox}}}{r} - \frac{bd}{r(c+d)}\Big)^{1/a}.$$

This is always efficient since $\overline{N}$ decreases.

Reaction-Diffusion Models

Reaction-diffusion equation

Metapopulations are interesting when we want to model the dynamics of interconnected metapopulation. However, if we are interested in the diffusion process of individuals, we have to consider the spatial variable and then we have to deal with partial differential equations. Here, we only consider reaction and diffusion.

Reaction-diffusion equation

If we denote by $n(t,x)$ the density of a population, we have

$$\partial_t n - \underbrace{\mathrm{div}(D\nabla n)}_{\text{diffusion}} = \underbrace{f(x,n)}_{\text{reaction}}.$$

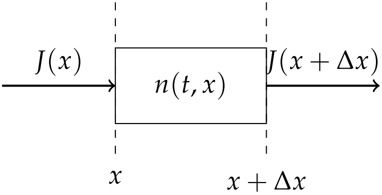
D is the diffusion matrix ; when it is constant the diffusion is homogeneous (no preferential direction to diffuse). The reaction term may model the birth, death, interaction between population, chemical reactions, ...
This equation may be derived thanks to a conservation law of the form

$$\text{temporal variation} \;=\; \text{flux} \;+\; \text{local source} \;.$$

In order to illustrate this derivation, let us first consider the one-dimensional case.

Reaction-diffusion equation

Let $\vec{J} = J\vec{e}_x$ be the flux along the x axis. We write the balance law in the cell $(x, x+\Delta x)$ during the time interval $(t, t+\Delta t)$:



- Variation of number of individuals : $(n(t+dt,x) - n(t,x))\Delta x$;
- Flux entering the domain during time Δt : $J(t,x)\Delta t$;
- Flux out of the domain : $J(t,x+\Delta x)\Delta t$;
- Birth and death in the domain during the time Δt : $f(x,n(t,x))\Delta x \Delta t$.

Thus in one dimension, the balance law implies

$$(n(t+dt,x) - n(t,x))\Delta x = (J(t,x) - J(t,x+\Delta x))\Delta t + f(x,n(t,x))\Delta x \Delta t.$$

Reaction-diffusion equation

To avoid congestion, individuals have a natural tendency to move apart from each other towards less crowded areas. To model this phenomenon, we consider that the flux is inversely proportional to the gradient of the concentration :

$$J(t,x) = -D\frac{\partial}{\partial x}n(t,x). \qquad \text{(Fick's law)}$$

We arrive at, after dividing by $\Delta t \Delta x$,

$$\frac{n(t+dt,x)-n(t,x)}{\Delta t} = -D\frac{\frac{\partial}{\partial x}n(t,x)-\frac{\partial}{\partial x}n(t,x+\Delta x)}{\Delta x} + f(x,n(t,x)).$$

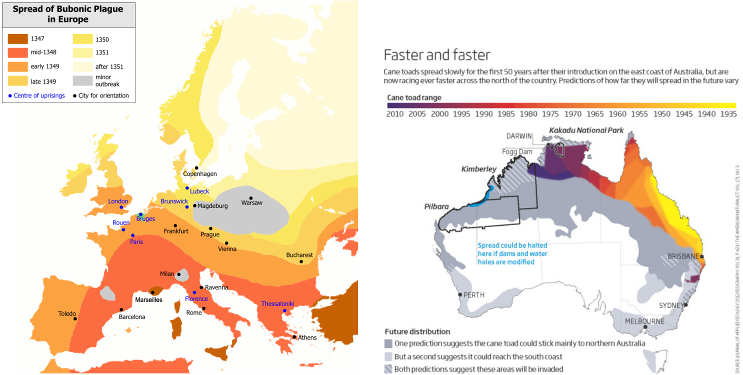
Letting $\Delta t, \Delta x \to 0$, we recover the one dimensional reaction-diffusion equation

$$\partial_t n = D\partial_{xx}n + f(x,n).$$

Obviously, this derivation may be extended to higher dimensions.

Introduction

Interesting phenomena modeled by reaction-diffusion equation in full space is propagation phenomena, mathematically described thanks to traveling waves. In biology, traveling waves have been used in many situations to explain invasiveness of a species, spread of a genetic trait, propagation of epidemy, ...



Spread of Bubonic Plague in Europe

Faster and faster

Cane toads spread slowly for the first 50 years after their introduction on the east coast of Australia, but are now racing ever faster across the north of the country. Predictions of how far they will spread in the future vary

Spread could be halted here if dams and water holes are modified

Future distribution

- One prediction suggests the cane toad could stick mainly to northern Australia
- But a second suggests it could reach the south coast
- Both predictions suggest these areas will be invaded

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FIGURE – Two examples of invasion phenomena : Left : bubonic plague in Europe during the middle age ; Right : cane toads in Australia nowadays.

Examples

Consider a population with density N we assume that

- the population growths with a rate r and is limited with an environmental capacity K ;
- individuals are allowed to move randomly in space with diffusion coefficient ν.

Then the dynamics of the density is given by

$$\partial_t N - \nu \Delta_x N = rN(1 - \frac{N}{K}).$$

This is the monostable Fisher/KPP equation.

Without spatial diffusion, we know that the density converges towards the environmental capacity K.

Question Can we observe a phenomenon of spatial invasion of the population ? How fast ?

Examples

Consider now a population with density N such that

- there is an environmental capacity K ;
- for low density the growth is nonpositive ;
- individuals are allowed to move randomly in the space with diffusion coefficient ν.

Then the dynamics of the density is given by

$$\partial_t N - \nu \Delta_x N = rN(N-\theta)(1-\frac{N}{K}).$$

This is the bistable Allen-Cahn equation.

Without spatial diffusion, the density may converge towards extinction or the environmental capacity K.

Question Adding spatial diffusion, is it possible to observe the extinction of the population or its fixation ?

Traveling waves : setting of the problem

To simplify, we work in one space dimension and consider one species whose dynamics is governed by the reaction-diffusion equation :

$$\partial_t u - \partial_{xx} u = f(u), \quad t > 0, x \in \mathbb{R}.$$

Definition

A traveling wave solution is a solution of the form $u(t,x) = v(x - ct)$ with $c \in \mathbb{R}$ a constant called traveling speed.

We usually consider the case where the function f admits two stationary states $f(0) = f(1) = 0$:

- Fisher/KPP (monostable) equation : $f(u) = u(1-u)$.
- Allen-Cahn (bistable) equation : $f(u) = u(1-u)(u-\theta)$.

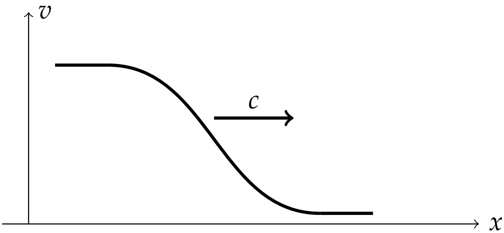
We complete the definition by the conditions $v(-\infty) = 1$, and $v(+\infty) = 0$.
When $c > 0$, this expresses the fact that the state $v = 1$ invades the state $v = 0$.
When $c < 0$, the state $v = 0$ invades the state $v = 1$.
Injecting the expression $u(t,x) = v(x-ct)$ into the equation, we arrive at the system :

Traveling waves : setting of the problem

Problem

We look for a real-valued function v and a real c such that

$$\begin{aligned} &v'' + cv' + f(v) = 0, \quad \text{on } \mathbb{R}, \\ &v(-\infty) = 1, \quad v(+\infty) = 0. \end{aligned}$$



When $c = 0$, we say that we have a stationary state or a standing wave.

Traveling waves : setting of the problem

Observations :

- The problem is invariant by translation :
  If $v(x)$ is a solution, then $v(x+a)$ is a solution for any $a \in \mathbb{R}$. Then, we normalize by setting for instance $v(0) = \frac{1}{2}$.
- Multiplying by v', we get

$$\frac{1}{2}((v')^2)' + c(v')^2 + (F(v))' = 0, \quad \text{where } F(v) = \int_0^v f(s)\,ds.$$

Integrating (using the fact that $v'(\pm\infty) = 0$), we find

$$c\int_{\mathbb{R}} (v'(x))^2\,dx = F(1) = \int_0^1 f(s)\,ds.$$

An important consequence is that

c has the same sign as $\int_0^1 f(s)\,ds$.

For instance, in the Fisher/KPP case, $f(u) = u(1-u) \geq 0$ for $u \in [0,1]$, thus $F(1) > 0$, it means that $v = 1$ is invading.

The monostable equation with ignition temperature

For $\theta \in (0,1)$, $\mu > 0$, we take $f(u) = \begin{cases} 0 & \text{for } 0 \le u < \theta, \\ \mu(1-u) & \text{for } \theta < u \le 1. \end{cases}$

Lemma

For f as above, there is a unique traveling wave solution (c^*, v) with v decreasing and normalized with $v(0) = \theta$.

Proof. We have seen above that $c > 0$. Thanks to the normalization $v(0) = \theta$ and the fact that v is decreasing, we look for a solution with $v > \theta$ for $x < 0$. Then $f(v) = \mu(1-v)$ for $x < 0$,

$$cv' + v'' + \mu(1-v) = 0.$$

The solution is given by $v = 1 - (1-\theta)e^{\lambda_+ x}$, $x \le 0$ with $\lambda_+ = \frac{1}{2}(-c + \sqrt{c^2 + 4\mu}) > 0$.
For $x > 0$, we look for $v < \theta$, then $f(v) = 0$. The solution is $v(x) = \theta e^{-cx}$ for $x \ge 0$.
It remains to check that v is differentiable at $x = 0$, that is

$$-c\theta = -(1-\theta)\lambda_+.$$

This equation admits an unique solution $c^* > 0$ (since $c \mapsto \lambda_+$ is decreasing). ☐

Bistable equation

We can extend the argument above to the bistable case. We take for $\theta \in (0,1), \mu > 0, \nu > 0$, $f(u) = \begin{cases} -\nu u & \text{for } 0 \leq u < \theta, \\ \mu(1-u) & \text{for } \theta < u \leq 1. \end{cases}$

Lemma

For f as above, there is a unique solution (c^*, v) with v decreasing and normalized with $v(0) = \theta$.

Proof. For $x < 0$, the equation is $v'' + cv' + \mu(1-v) = 0$. Then, $v(x) = 1 - (1-\theta)e^{\lambda_1 x}$, $\lambda_1 = \frac{1}{2}(-c + \sqrt{c^2 + 4\mu})$.
For $x > 0$, the equation is $v'' + cv' - \nu v = 0$. Then, $v(x) = \theta e^{-\lambda_2 x}$, $\lambda_2 = \frac{1}{2}(c + \sqrt{c^2 + 4\nu})$.
To match the derivatives at $x = 0$, we have to impose $\lambda_2 \theta = (1-\theta)\lambda_1$. The function $c \mapsto \lambda_1$ is decreasing, whereas $c \mapsto \lambda_2$ is increasing, and the limits at $\pm\infty$ are opposite infinity. Thus this latter equation admits a unique solution c^*. $\square$

Analytical example

We take for $\theta \in (0,1), \mu > 0$, $f(u) = \begin{cases} \mu(1-\theta)u & \text{for } 0 \leq u < \theta, \\ \mu\theta(1-u) & \text{for } \theta < u \leq 1. \end{cases}$

Lemma

For f given as above. There exists a minimal speed $c^* = 2\sqrt{(1-\theta)\mu}$ and for all $c \geq c^*$ a unique solution (c, v) with v decaying and normalized by $v(0) = \theta$.

Proof. For $x < 0$, we want $v > \theta$, then the equation is

$$v'' + cv' + \mu\theta(1-v) = 0.$$

The unique solution that tends to 1 at $-\infty$ is

$$v(x) = 1 - (1-\theta)e^{\lambda_+ x}, \quad x \leq 0, \qquad \lambda_+ = \frac{1}{2}(-c + \sqrt{c^2 + 4\mu\theta})$$

For $x > 0$, we look for $v < \theta$, then $v'' + cv' + \mu(1-\theta)v = 0$. The characteristic polynomial for this ODE is $\lambda^2 + c\lambda + \mu(1-\theta)$. If $c < c^*$, then the roots of this polynomial are complex conjugate, then there no solutions decaying and nonnegative to the ODE. For $c \geq c^*$, both roots of the polynomial are negative and are given by $\mu_\pm = \frac{1}{2}(-c \pm \sqrt{c^2 - 4\mu(1-\theta)})$.

Analytical example

Then, for $x \geq 0$,

$$v(x) = \theta e^{\mu_- x} + a(e^{\mu_+ x} - e^{\mu_- x}), \qquad \mu_\pm = \frac{1}{2}(-c \pm \sqrt{c^2 - 4\mu(1-\theta)}).$$

This function is positive iff $a \geq 0$. It remains to check that the derivatives match at $x = 0$, that is $-(1-\theta)\lambda_+ = \theta a \mu_- + a(\mu_+ - \mu_-)$. This requires that

$$c - (1-\theta)\sqrt{c^2 + 4\mu\theta} + \theta\sqrt{c^2 - 4\mu(1-\theta)} = 2a\sqrt{c^2 - 4\mu(1-\theta)}.$$

For $c > c^*$, the left hand side is positive. Therefore, we can compute a unique $a > 0$ satisfying this equality for any $c \geq c^*$. This allows to contruct a positive and decaying function v. ☐

The monostable equation with ignition temperature

θ=*ignition temperature* : minimal temperature required to burn a gas and start the reaction.

$$\partial_t u - \partial_{xx} u = f_\theta(u), \qquad f_\theta(u) = \begin{cases} 0 & 0 \leq u \leq \theta \\ > 0 & \theta < u < 1 \\ 0 & u = 1 \end{cases}$$

Traveling wave problem

Find c and v such that

$$-v'' - cv' = f_\theta(v), \quad x \in \mathbb{R},$$
$$v(-\infty) = 1, \qquad v(+\infty) = 0.$$

Theorem

There is a unique decreasing traveling wave solution (c^*, v) normalized with $v(0) = \frac{1}{2}$ and it holds that $c^* > 0$.

The Fisher/KPP equation

We consider the Fisher/KPP case :

$$\partial_t u - \partial_{xx} u = u(1-u).$$

The situation is quite different than the case with ignition temperature. A famous result is

Theorem

For any $c \geq c^* = 2$, there is a unique traveling wave solution v with $0 \leq v \leq 1$ and v monotically decreasing.

- The quantity c^* is called the minimal propagation speed.
- This result can be extended to general equation

$$\partial_t u - \nu \partial_{xx} u = f(u), \text{ with } f(0) = f(1) = 0, \ f(u) > 0 \text{ for } 0 < u < 1.$$

In this case, the minimal propagation speed is $c^* = 2\sqrt{f'(0)\nu}$.

The Fisher/KPP equation

Formally, we may use a simple analysis to deduce the behavior. Since u is expected to be small at $+\infty$, we consider the linear equation (by neglecting u^2)

$$\partial_t u - \nu \partial_{xx} u = f'(0)u.$$

Looking now for a solution $u(t,x) \sim Ae^{-a(x-ct)}$ as $x \to +\infty$, with $a > 0$, and $A > 0$, c being the wavespeed. Injecting this expression into the linearized equation, we obtain

$$ca = f'(0) + \nu a^2.$$

This is the *dispersion relation*. This equation admits a solution $a > 0$ if and only if $c \geq c_{\text{min}} = 2\sqrt{f'(0)\nu}$.
Notice that when $f'(0) < 0$, there always exists a real root to this second order polynomial.

Allen-Cahn (bistable) equation

We consider the *bistable* case, i.e. 0 and 1 are both stable steady states.

Traveling wave solution

We look for $c \in \mathbb{R}$ and a real-valued function v such that

$$v'' + cv' + f(v) = 0$$

$$v(-\infty) = 1, \quad v(+\infty) = 0, \quad v(0) = \frac{1}{2}.$$

We will make use of the notation $F(u) = \int_0^u f(v)\,dv$. We assume that

$$f(0) = 0, \quad f'(0) < 0, \quad f(\theta) = 0, \quad f(1) = 0, \quad f'(1) < 0,$$
$$f(u) < 0 \text{ on } (0,\theta), \qquad f(u) > 0 \text{ on } (\theta,1).$$

Adapting the phase space method, we may prove :

Theorem

Under these assumptions, there exists a unique traveling wave solution (c^*, v) with v decreasing.
We have $c^* > 0$ for $F(1) > 0$, $c^* = 0$ for $F(1) = 0$, $c^* < 0$ for $F(1) < 0$.

Allen-Cahn (bistable) equation

A simple choice of bistable function satisfying the assumptions is

$$f(u) = u(1-u)(u-\theta).$$

In this case, we have the explicit expression of the traveling wave solution

$$v(x) = \frac{e^{-x/\sqrt{2}}}{1+e^{-x/\sqrt{2}}}, \qquad c^* = \sqrt{2}(\frac{1}{2}-\theta).$$

Indeed, we may compute with this expression,

$$v' = \frac{1}{\sqrt{2}}v(v-1), \qquad v'' = \frac{v'}{\sqrt{2}}(2v+1) = v(v-1)(v+\frac{1}{2}).$$

Thus, $-c^*v' - v'' = v(1-v)(v+\frac{c^*}{\sqrt{2}}+\frac{1}{2}) = f(v)$.

Example of field application : Mosquito population control with the Sterile Insect Technique (SIT)

Epidemic control with SIT

$$
\begin{aligned}
S_H' &= b_H H - \frac{\beta_M}{H} I_M S_H - b_H S_H \\
E_H' &= \frac{\beta_M}{H} I_M S_H - \gamma_H E_H - b_H E_H \\
I_H' &= \gamma_H E_H - \sigma_H I_H - b_H I_H
\end{aligned}
$$

$$
\begin{aligned}
S_M' &= b_M M \left(1 - \frac{M}{K}\right) \frac{\alpha M}{1 + \alpha(M + \gamma M_s)} - \frac{\beta_M}{H} S_M I_H - d_M S_M \\
E_M' &= \frac{\beta_M}{H} S_M I_H - \gamma_M E_M - d_M E_M \\
I_M' &= \gamma_M E_M - d_M I_M
\end{aligned}
$$

$$
M_S' = u - d_S M_S
$$

Instant Releases

Considering again instant releases the equation for the sterile mosquitoes becomes :

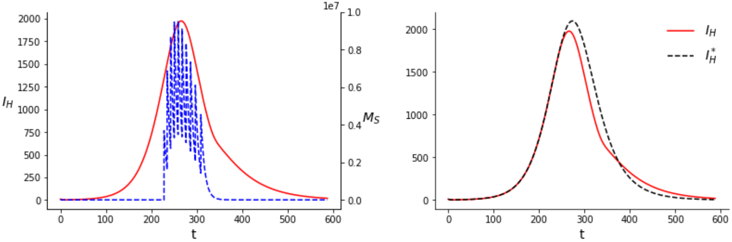
$$\begin{cases} M_S' & = & -d_S M_S, \quad t \in [t_i, t_{i+1}], \quad i = 0, \dots, n \\ M_S(t_i^+) & = & M_S(t_i^-) + c_i, \quad i = 1, \dots, n \end{cases}$$

We can solve this equation explicitly, finding

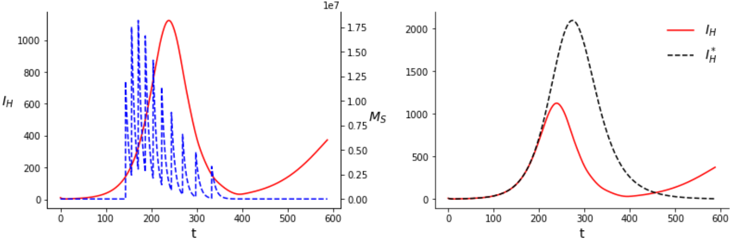
$$M_S(t) = \sum_{j=1}^{i} c_j e^{-d_S(t-t_j)}, \quad t \in [t_i, t_{i+1}], \quad i = 0, \dots, n$$

Results : 10 instant releases

$\mathbf{C = 7.5 \cdot 10^7}$
Reduction :
12.3%

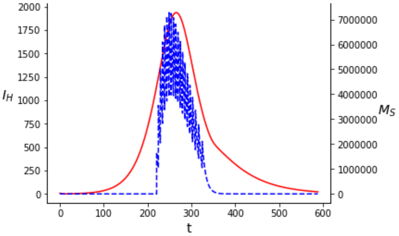


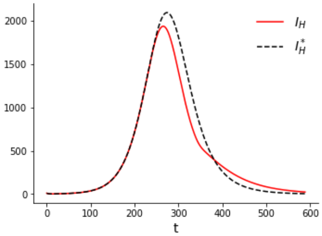
$\mathbf{C = 1.5 \cdot 10^8}$
Reduction :
49.1%



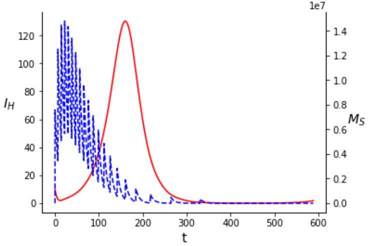
Results : 20 instant releases

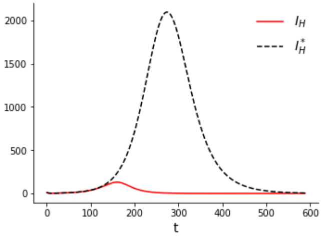
$\mathbf{C = 7.5 \cdot 10^7}$
Reduction :
13.9%





$\mathbf{C = 1.5 \cdot 10^8}$
Reduction :
99.9%





Sterile Mosquito Technique

- Strategy and results depend highly on the number of releases considered (when low).
- After ~ 20 releases almost no improvement.
- With few mosquitoes : spaced releases around the peak.
- With a lot of mosquitoes : spaced releases from the beginning.

Spatial problem - invasive wave propagation

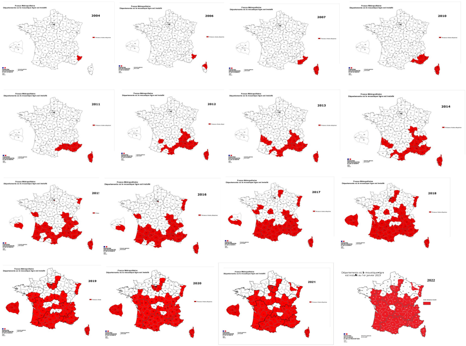


FIGURE – Expansion of Aedes albopictus in mainland France, 2004-2022

Global warming and trade help Aedes mosquitoes to settle in many temperate regions including Europe. They are not only an invasive species but also vectors for many diseases including dengue, Zika and chikungunya.

Traveling Waves : Monostable VS Bistable Dynamics

$$u(t;x) \equiv \text{Proportion of mosquitoes at time } t \text{ and position } x$$

$$\underbrace{\partial_t u - \Delta u}_{\text{Diffusion}} = \underbrace{g(u)}_{\text{Growth}}$$

Two possibilities depending on **Allee effect** : Fisher KPP (without) or Allen-Cahn (with)

Monostable dynamics (Fisher-KPP)

$$g(u) = u(1-u)$$

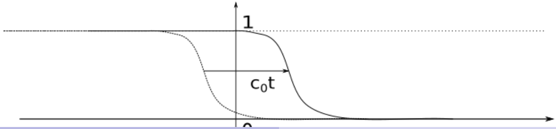
- 2 steady states : $\{\ 0\ ;\ 1\ \}$
- 1 stable : 1
- 1 unstable : 0

Bistable dynamics (Allen-Kahn)

$$g(u) = u(1-u)(u-\theta)$$

- 3 steady states : $\{\ 0\ ;\ \theta\ ;\ 1\ \}$
- 2 stable : 0 and 1
- 1 unstable : θ

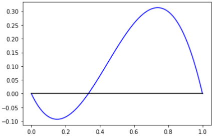
When invasion occurs, it is like a **traveling wave solutions** :



Bistable Dynamics and Traveling Wave solutions

Assumption : Bistable dynamics

$$\underbrace{\partial_t u - \Delta u}_{\text{Diffusion}} = \underbrace{g(u)}_{\text{Growth}}$$



Natural set of solutions : the traveling wave solutions $u(x,t) = \phi(x - c_0 t)$.

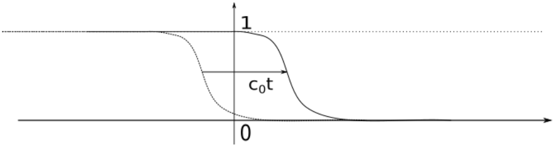
$$\partial_t u - \Delta u = g(u) \quad \longrightarrow \quad -c_0\phi' - \phi'' = g(\phi).$$

ϕ connects the two stable steady states :

$$\phi(-\infty) = 1 \quad \text{and} \quad \phi(+\infty) = 0.$$

The sense of propagation depends on $\text{sign}(c_0) = \text{sign}\left(\int_0^1 g(v)dv\right)$

Assumption : $\text{sign}(c_0) > 0$: naturally, the mosquitoes invade the territory



Barrier construction

We want to study the possibility to construct a barrier to block invasion by releasing sterile males on a domain of width L. Numerical simulations taking $u = \overline{U}\mathbf{1}_{[0,L]}$.

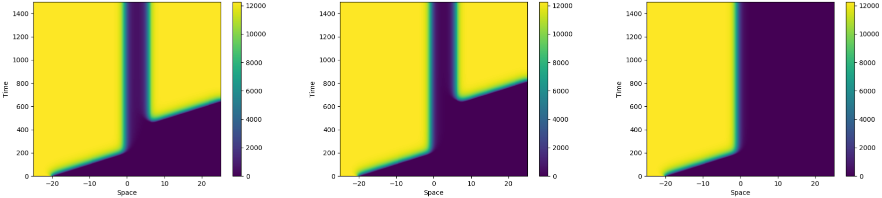


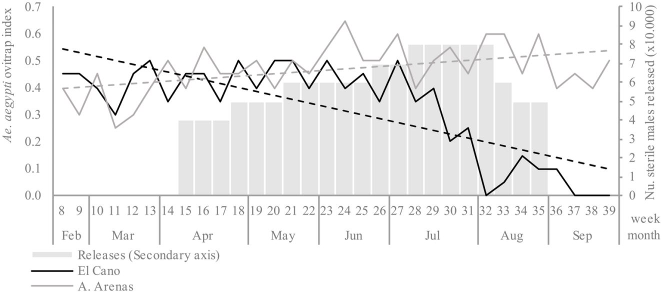
FIGURE – Numerical simulations for $u = \overline{U}\mathbf{1}_{[0,L]}$ with $L = 5$ km and $\overline{U} = 10\,000$ km^{-1} day^{-1} (left), $\overline{U} = 20\,000$ km^{-1} day^{-1} (center), and $\overline{U} = 30\,000$ km^{-1} day^{-1} (right).

Theorem (A, Estrada, Vauchelet), Math. Model. Nat. Phenom. 2022

For any $L > 0$, there exists $\overline{U}$ large enough, such that there exists a barrier for the SIT system.

Pilot study and scale-up

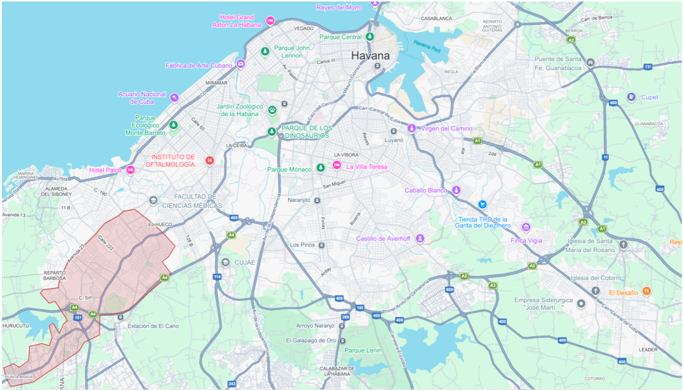
The WHO and IAEA have been financing many pilot studies in many countries like, for instance, in Cuba in 2020 and the results have been very encouraging



Pilot study done in areas of 20 to 25 ha in Cuba in 2020.

Scale-up

However, scaling-up to region or country-wide interventions raises many new problems including interesting mathematics



Planned intervention over a 1000 ha area starting in 2026

The rolling carpet strategy

The idea is to *act* on a finite interval $(0, L)$ and move this *action* like a rolling carpet in the opposite sense to that of the natural invasion traveling wave.

$$\begin{cases} \partial_t u - \Delta u = g(u) + Act(u) 1_{\{ct<x<L+ct\}}, \\ u(-\infty) = 1, \\ u(+\infty) = 0 \end{cases}$$

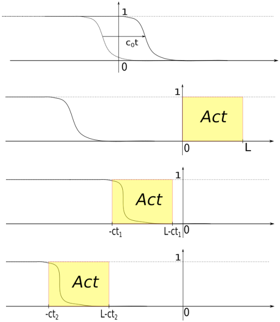


FIGURE – The free system and with action at $t = 0,\ t = t_1 > 0,\ t = t_2 >= t_1$

The rolling carpet strategy

The idea is to *act* on a finite interval $(0, L)$ and move this *action* like a rolling carpet in the opposite sense to that of the natural invasion traveling wave.

Aim of the work : generate a traveling wave with a negative speed solution of

$$\begin{cases} -c\phi_L' - \phi_L'' = g(\phi_L) + Act(\phi_L)1_{\{0<x<L\}}, \\ \phi_L(-\infty) = 1 \qquad \phi_L(+\infty) = 0 \end{cases}$$

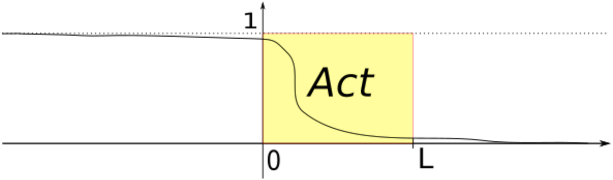


FIGURE – The traveling wave solution ϕ_L

The main result for SIT

Aim : Obtain a traveling wave solution $\phi_{L,M}$

$$\begin{cases} -c\phi'_{L,M} - \phi''_{L,M} = g(\phi_{L,M}, m_S), \\ -cm'_S - m''_S = \mathrm{M}1_{\{0<x<L\}} - \mu_M m_S \\ \phi_{L,M}(-\infty) = 1, \quad \phi_{L,M}(\infty) = 0. \end{cases}$$

Theorem (A - LÃ©culier - Vauchelet, SIAM J. Math. Anal. 2023)

For every speed $c \leq 0$ and size $L > 0$, there exists a critical number of mosquitoes $\Pi(c, L)$ such that

1. If $M < \Pi(c, L)$ then the system does **not** admit a solution $\phi_{L,M}$.
2. If $M > \Pi(c, L)$ then the system admits a traveling wave $\phi_{L,M}$.

Moreover, we have

$$\lim_{L\to 0}\Pi(c, L) = +\infty, \quad \liminf_{L\to +\infty} \Pi(c, L) > 0 \quad \text{and} \quad \lim_{c\to -\infty} \Pi(c, L) = +\infty.$$

Numerical results

We perform numerical simulations of

$$\partial_t f - \partial_{xx} f = g(f, m_S),$$

for $c = -0.1$, $L = 20$ and two sizes of releases M.

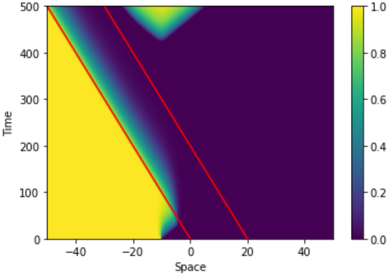


FIGURE – $\mathrm{M} = 3.3$

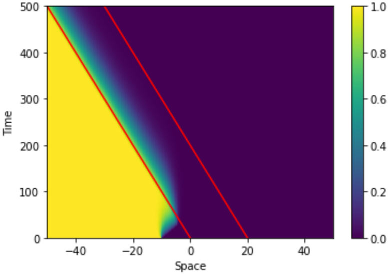


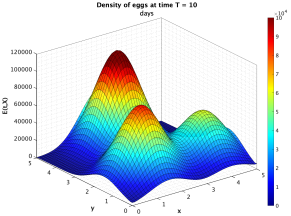
FIGURE – $\mathrm{M} = 3.6$

Inhomogeneous setting : PDE model

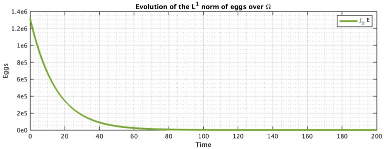
$$\begin{cases}
\dfrac{\partial E}{\partial t} = \beta_E F(1 - \dfrac{E}{K(x)})\dfrac{\eta M}{1+\eta(M+\gamma M_s)} - (\nu_E + \delta_E)E,\ t \geq 0,\ x \in \Omega, \\
\dfrac{\partial F}{\partial t} - d_1 \Delta F = \nu \nu_E E - \delta_F F, t \geq 0,\ x \in \Omega, \\
\dfrac{\partial M}{\partial t} - d_2 \Delta M = \nu \nu_E E - \delta_M M,\ t \geq 0,\ x \in \Omega, \\
\dfrac{\partial M_s}{\partial t} - d_3 \Delta M_s = u((E,F,M,M_s)^T) - \delta_s M_s,\ t \geq 0,\ x \in \Omega, \\
\dfrac{\partial F}{\partial n} = \dfrac{\partial M}{\partial n} = \dfrac{\partial M_s}{\partial n} = 0,\ t \geq 0,\ x \in \partial\Omega, \\
(E(0,x), F(0,x), M(0,x), M_s(0,x))^T = (E^0(x), F^0(x), M^0(x), M_s^0(x))^T,\ x \in \Omega
\end{cases} \tag{3}$$

Inhomogeneous setting : PDE model

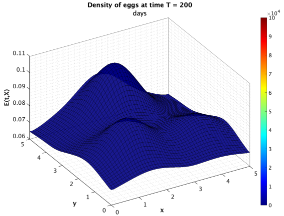
Feedback control of pest populations in heterogeneous settings using SIT



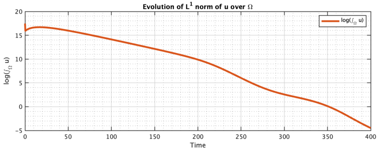
Density of eggs at time T = 10 days



Evolution of the L^1 norm of eggs over Ω



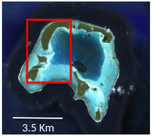
Density of eggs at time T = 200 days

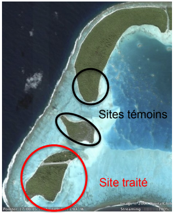


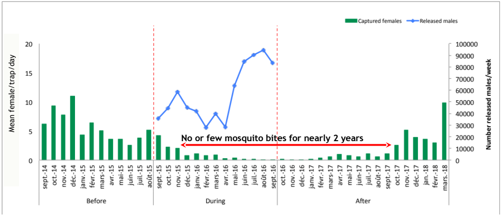
Evolution of L^1 norm of u over Ω

To help improve field interventions in a robust way

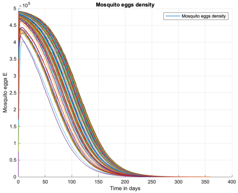
Field work with Incompatible Insect Technique (IIT) in Tetiaroa by HervéBossin and Françoise Mathieu-Daudé (ILM, IRD, Univ. Polynésie Française)

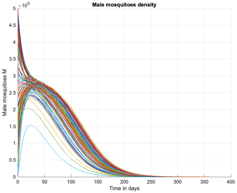


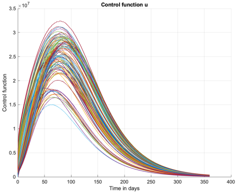




Robustness of Backstepping stabilization control







Backstepping feedback stabilization result

We define for $\theta > 0$ and $\alpha > 0$

$$u((x^T, M_s)^T) := \max\left(0, G((x^T, M_s)^T)\right). \tag{4}$$

$$\begin{aligned} G((x^T, M_s)^T) :&= \frac{\gamma_s \psi E (\theta M + M_s)^2}{\alpha (M + \gamma_s M_s)(3\theta M + M_s)} + \frac{1}{\alpha}(\theta M - M_s) \\ &+ \frac{((1-\nu)\nu_E \theta E - \theta \delta_M M)(\theta M + 3M_s)}{3\theta M + M_s} + \delta_s M_s, \end{aligned} \tag{5}$$

$$\mathcal{R}(\theta) := \frac{\beta_E \nu \nu_E}{\delta_F (1 + \gamma_s \theta)(\nu_E + \delta_E)}. \tag{6}$$

Theorem (Kala Agbo bidi,, L.A., Jean-Michel Coron 2023)

Assume that $R_\theta < 1$, then $\mathbf{0}$ is globally asymptotically stable in $\mathcal{D} = \mathbb{R}_+^4$ for the SIT system with the feedback law (4).

Projects

- PEPR project Maths-ArboV (dengue outbreaks in mainland France, 2025-2030)
- WHO TDR/IAEA project PAC-SIT (Ae. aegypti in Tahiti, Cook Islands [Aitutaki atoll] and Easter Island, 2025-2026)

TE MARAE ORA COOK ISLANDS Ministry of Health

COMMUNE DE PAEA

ilm

IRD Institut de Recherche pour le Développement FRANCE

DIRECTION DE LA SANTÉ

CSIRO

QIMR Berghofer Medical Research Institute

Consortium régional d'évaluation de l'efficacité de la Technique de l'Insecte Stérile contre les moustiques vecteurs de maladies

TDR For research on diseases of poverty UNICEF • UNDP • World Bank • WHO

IAEA Joint FAO/IAEA Division of Nuclear Techniques in Food and Agriculture

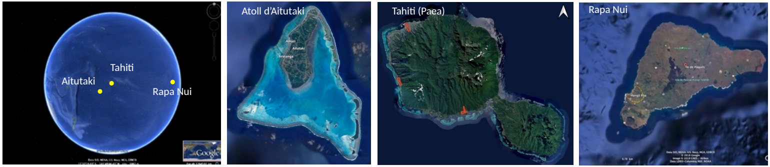
World Health Organization

CDC CENTERS FOR DISEASE CONTROL AND PREVENTION

Liberté • Égalité • Fraternité RÉPUBLIQUE FRANÇAISE

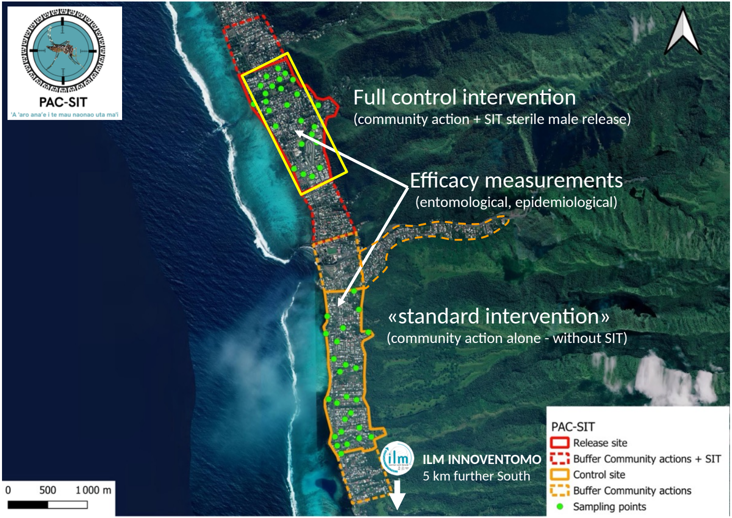
FONDS PACIFIQUE

Îles Cook Polynésie française Chili



PACSIT WHO pilot study : intervention and monitoring

Evaluation PAC-SIT
Pilote Paea



Full control intervention
(community action + SIT sterile male release)

Efficacy measurements
(entomological, epidemiological)

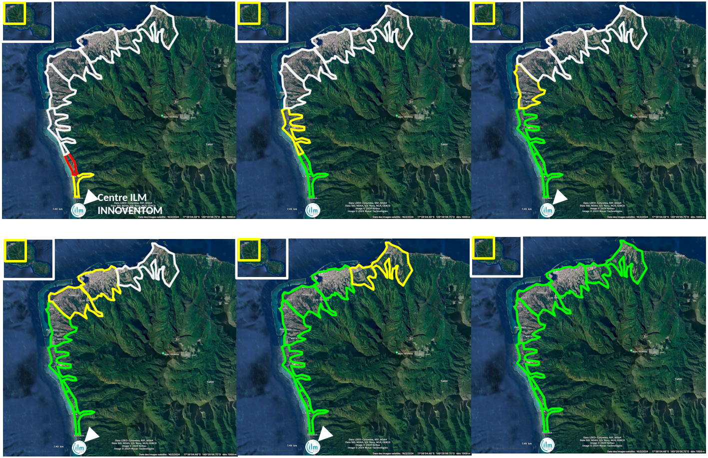
«standard intervention»
(community action alone - without SIT)

ILM INNOVENTOMO
5 km further South

Beyond PACSIT - area-wide rolling carpet SIT intervention in Tahiti

Rolling Carpet Strategy from Paea to Greater Papeete urban area

Protect 50% of the Tahiti Population



SIT Treated Area Monitoring and Feedback Control Area