

UQAR – Chaire de Recherche EEC

## Ordinary differential equations

Solving them analytically

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① Introduction

② Objectives

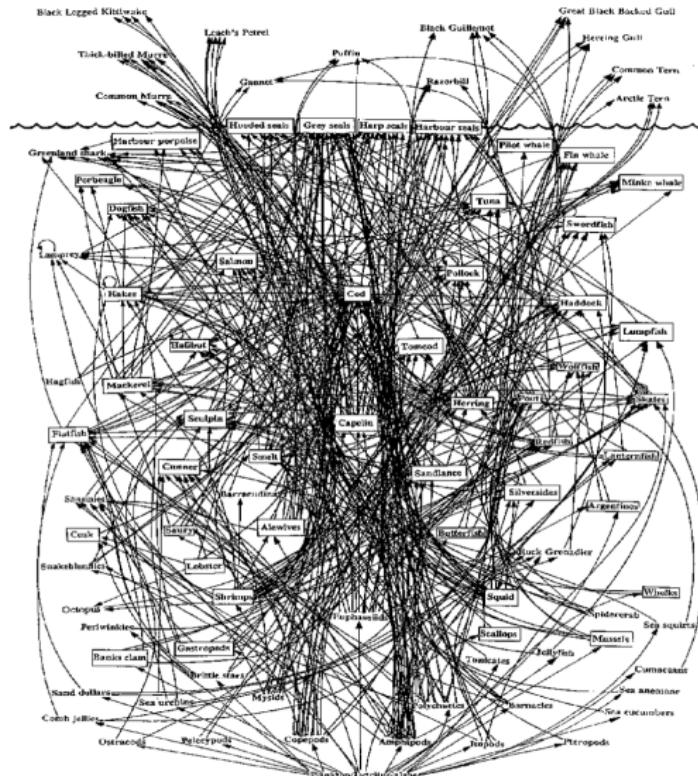
③ Definitions

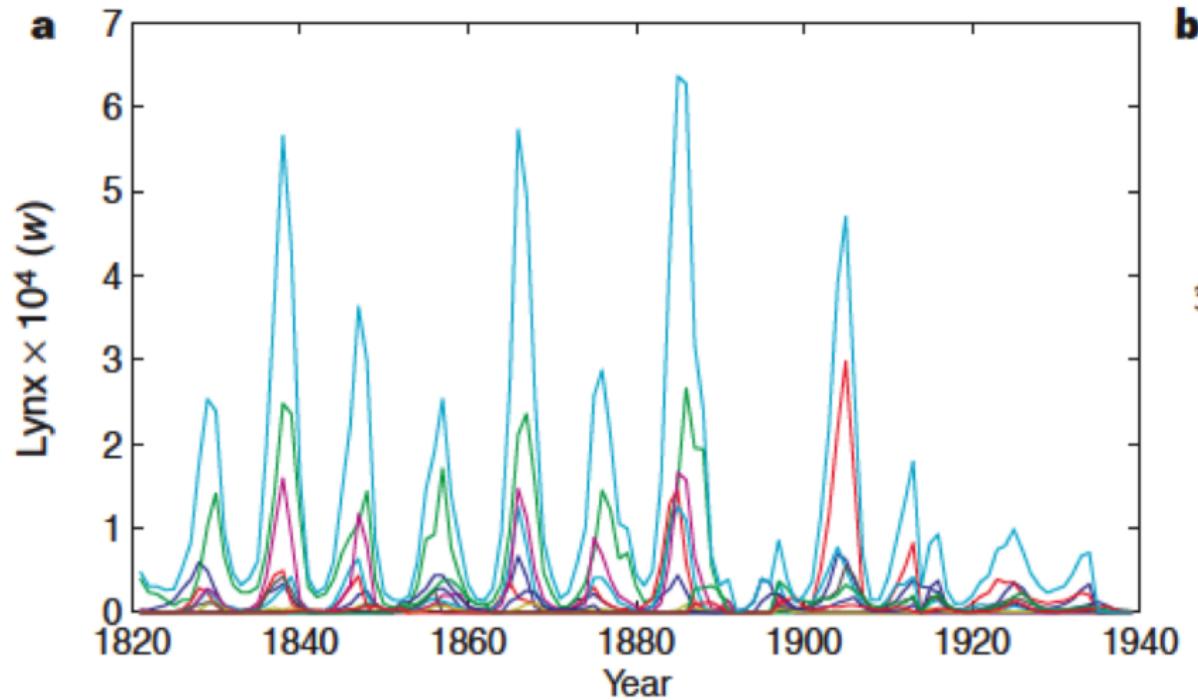
④ Steps

⑤ Equilibrium

⑥ Local stability analysis

## Why do we need models?





Gotelli (1996):

*One answer is that we need models because nature is so complex [...] The mathematical models act as **simplified road maps**, giving us some direction and idea of exactly what **things we should be trying to measure in nature**.*

*The models also generate **testable predictions**.*

*The models highlight the **distinction between the patterns** we see in nature and the different **mechanisms** that might cause those patterns.*

Gotelli (1996):

*The danger is that we build models that are too complex. When this happens, the models may contain many variables that we can never measure in nature.*

*The second danger is that we forget that the models are abstract representations of nature. By carefully focusing on the assumptions of the model, we may be able to pinpoint the places where it departs from reality.*

## Main types of models

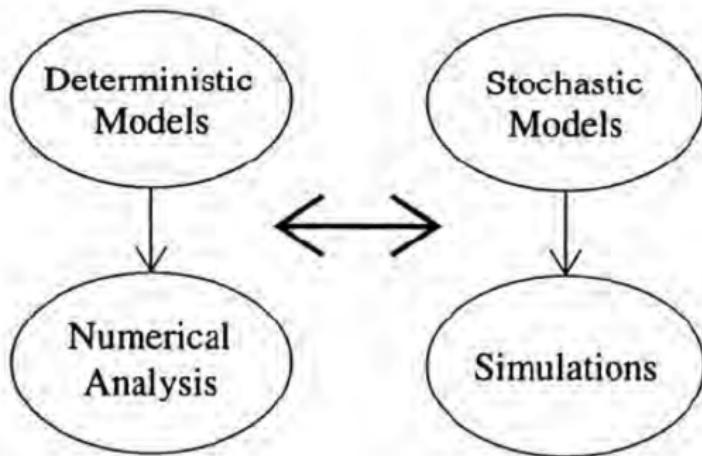
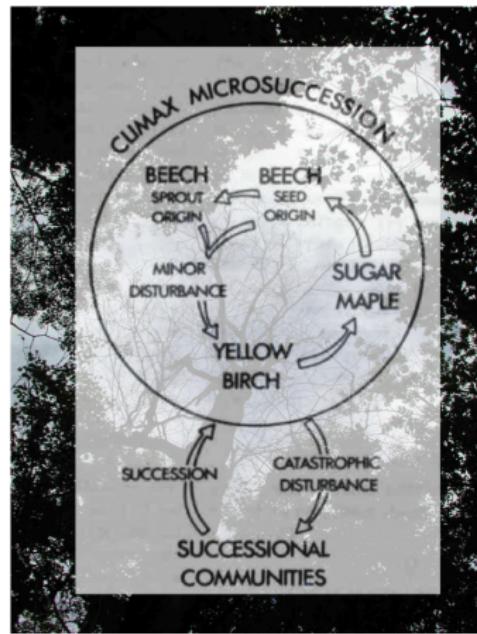
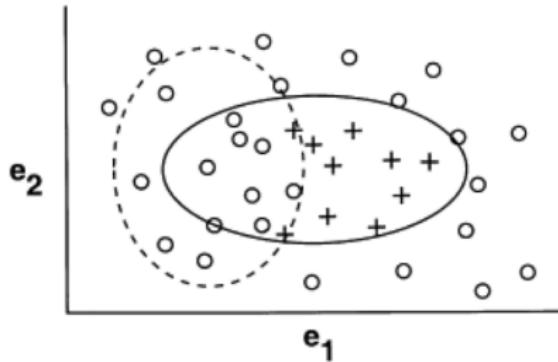


Figure 1.1. Examining deterministic models often requires numerical solutions, whereas stochastic models require computer simulations. Interplay between deterministic and stochastic models can help develop conceptual insight.

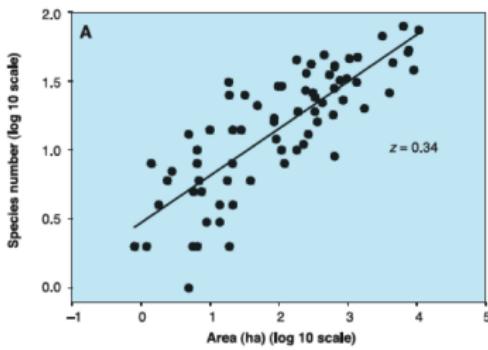
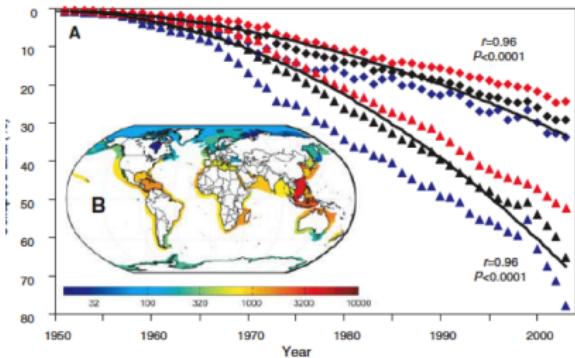
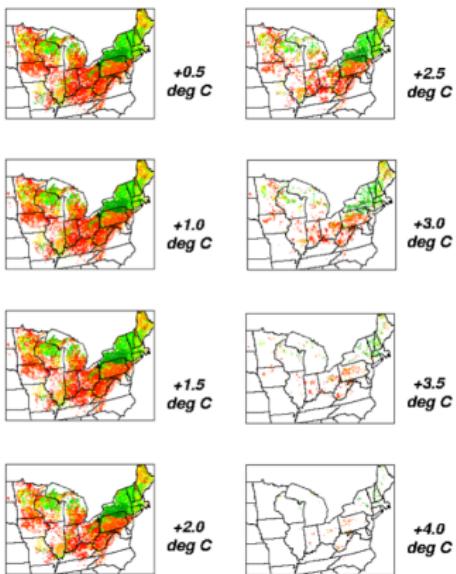
# Main types of models

## Conceptuals



# Main types of models

## Statistical



# Main types of models

## Dynamical

$$N_{t+1} = N_t + B + I - D - E$$

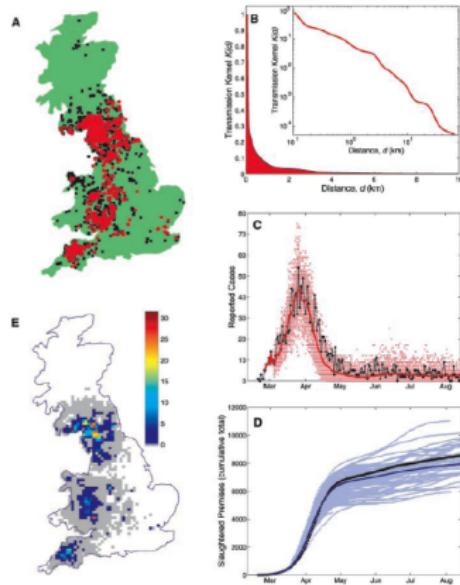
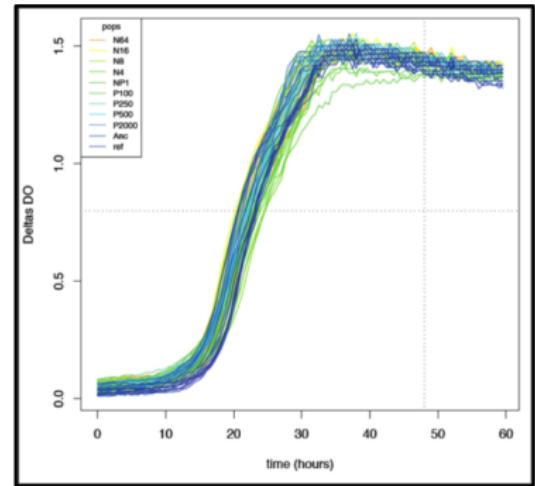
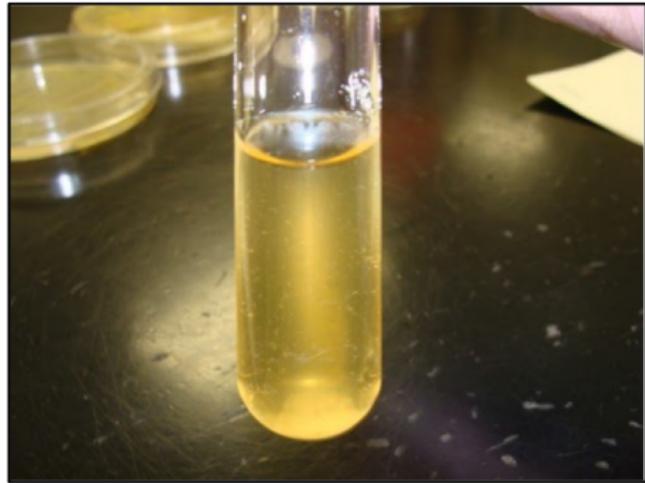


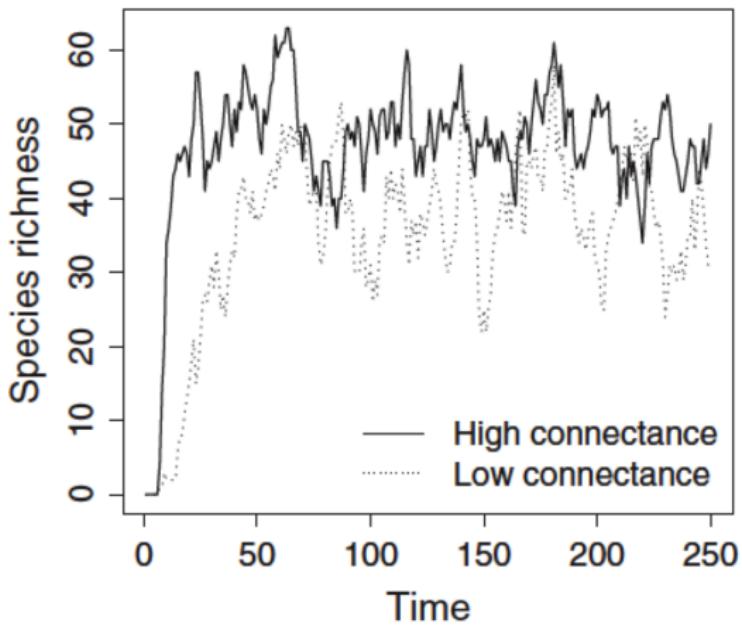
Fig. 1. A comparison between the observed epidemic and 100 replicates of the stochastic model. Simulations start on 23 February 2001 (when movement restrictions were fully in place) and use the reported cases to that date and the position of all susceptible farms as initial conditions. (A) The actual spatial distribution of IPs (red) and culled premises (black). (B) The transmission kernel  $K$  as a function of distance ( $d$ ), calculated from the distance between sources of infection and their secondary infections. (C) Comparison of the number of infected premises. (D) Comparison of the cumulative total of culled or slaughtered premises. Black dots show the observed numbers; pale dots (red or blue) show results from simulations, and solid lines (red or blue) show the average of the results shown are from 100 simulations. (E) The average number of simulated cases in 10-km-by-10-km squares. The model results shown are from 100 simulations.

# Main types of models

## Deterministic

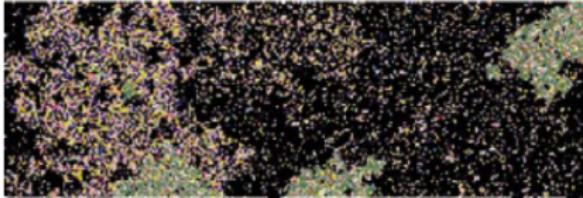
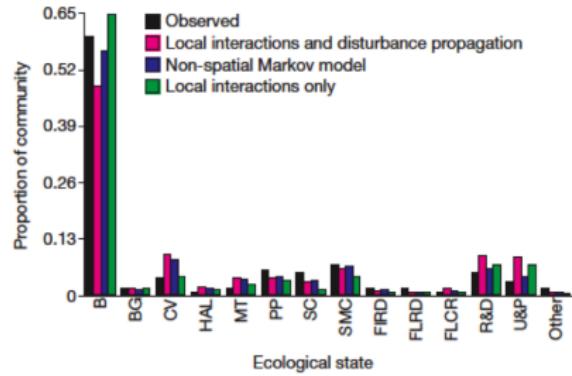


(b)



## Main types of models

### Cellular automaton



## Main types of models

### Individual based models



1. Distinguish between different types of models
2. Understand the concept of equilibrium dynamics and its consequences, including mass balance constraints
3. Understand the R\* principle of consumer-resource interactions

1. Formulate ordinary differential equations describing community dynamics of a given ecological system
2. Analyze the equilibrium states of ordinary differential equations
3. Perform an invasibility analysis
4. Compute the Jacobian matrix
5. Interpret the eigen values of the Jacobian matrix in terms of stability

# Ordinary differential equation

## Technical definition

*An equation containing the derivatives of one or more dependent variables, with respect to one of more independent variables* (Zill - A first Course in Differential Equations)

*A differential equation is a relationship between a function of time & it's derivatives.* (Braun - Differential equations and their applications)

*Let  $f(x)$  define a function of  $x$  on an interval  $I : a < x < b$ . By an ordinary differential equation we mean an equation involving  $x$ , the function  $f(x)$  and one of more of it's derivatives.* (Tenenbaum & Pollard - Ordinary Differential equations)

*The derivative is a measure of how a function changes as its input changes*

*Loosely speaking, a derivative can be thought of as how much one quantity is changing in response to changes in some other quantity; for example, the derivative of the position of a moving object with respect to time is the object's instantaneous velocity.*

## An example with a simple demographic model

Consider the following model:  $N_{t+1} = N_t + B + I - D - E$

Where:

- ▶  $N$  is population size;
- ▶  $B$  is the number of offsprings;
- ▶  $I$  is the number of immigrants;
- ▶  $D$  is the number of deaths;
- ▶  $E$  is the number of emigrants.

Now, calculate after 3 years the population size of a hare population starting with 10 individuals, each giving birth to 5 offsprings per year and with 25% mortality per winter.

## Solution to the geometric growth model

Consider:

$$N_{t+1} = N_t + bN_t + iN_t - dN_t - eN_t = \lambda N_t$$

With the intrinsic rate of increase (omitting spatial exchanges):

$$\lambda = 1 + b - d$$

For a single time step we obtain:

$$N_{t+1} = \lambda N_t$$

For two time steps:

$$N_{t+2} = \lambda N_{t+1} = \lambda(\lambda N_t) = \lambda^2 N_t$$

And for an arbitrary number of time steps:

$$N_{t+n} = \lambda^n N_t$$

Discrete time:

$$N_{t+1} = N_t + B - D$$

$$N_{t+1} - N_t = B - D$$

$$\Delta N = B - D$$

Continuous time: we are interested by the instantaneous change in  $N$  with a small change in  $t$ . **Remember the definition of a derivative!**

$$\frac{dN}{dt} = B - D$$

The continuous time model (exponential growth):

$$\frac{dN}{dt} = \beta N - \delta N = rN$$

Which has for solution (integrating the differential equation over time):

$$N(t) = N_0 e^{rT}$$

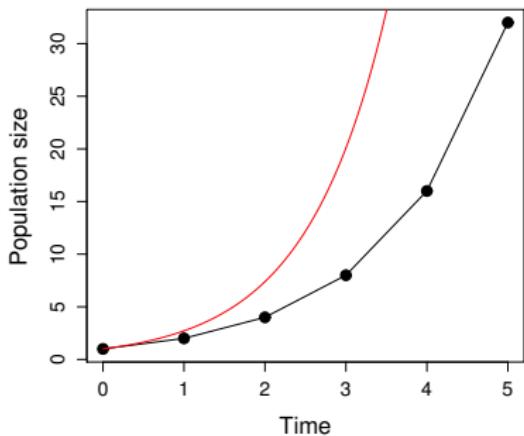
Given that

$$N_{t+n} = \lambda^n N_t$$

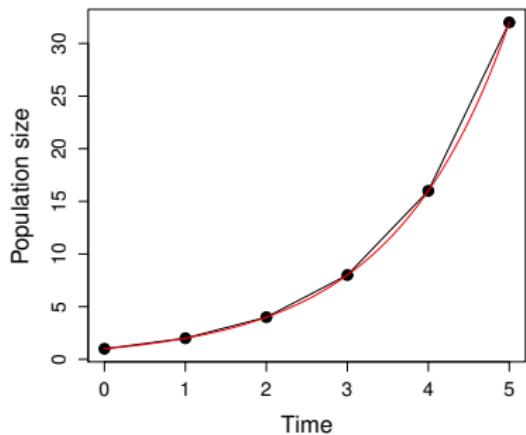
We obtain the equivalence

$$\lambda = e^r$$

With  $r = \lambda - 1$ : WRONG METHOD!



The right method:



Now try to reproduce this figure on R!

# How do we get there?

## Steps of model analysis

A standard approach

1. Conceptualize the system
2. Formulate the differential equation
3. Compute equilibrium states
4. Analyze the different states
5. Analyze the stability of the equilibrium

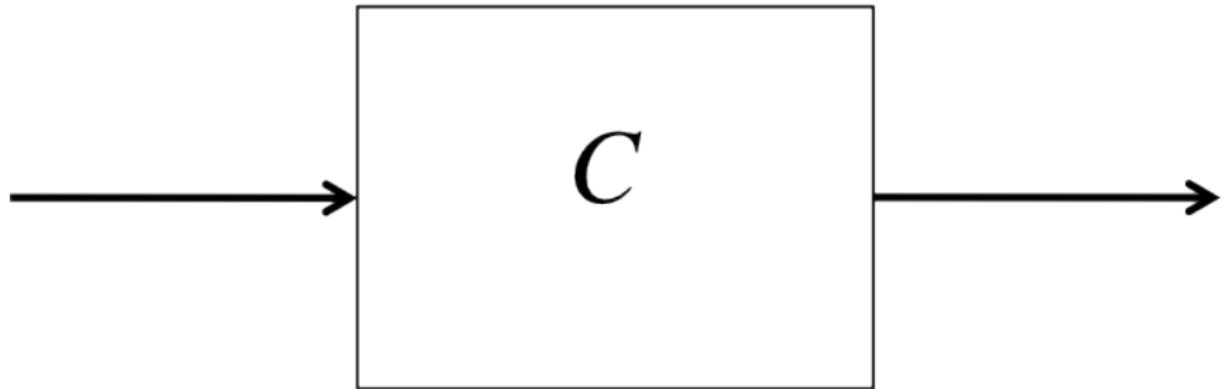
## Step 1

### Conceptualize the ecosystem



## Step 1

Conceptualize the ecosystem



## Step 2

### Formulate equations

We are looking for an equation describing the instantaneous change in concentration of a nutrient. In other words:

$$\frac{dC}{dt} = f(t)$$

Amount of nutrients coming in: rate of inflow X inflow concentration. In other words:

$$qC_I$$

Amount of nutrients going out: rate of outflow X lake concentration. In other words:

$$qC$$

Which leads to the instantaneous change in concentration:

$$\frac{dC}{dt} = qC_I - qC$$



## Step 2

### The law of mass action

**Definition:** *The rate of the reaction is proportional to a power of the concentration of all substances taking part in the reaction*

$$\text{ReactionRate} = k[A]^{\alpha}[B]^{\beta}$$

**Assumption:** the reaction will only occur if the molecules collide.

**Order:** The order of the reaction is the sum of the powers

$$1\text{st order: } R_1 = k_1[A]$$

$$2\text{nd order: } R_2 = k_2[A][B]$$

## Step 2

Remember!

- ▶ Conservation of mass and energy
- ▶ Consistency of units

### Step 3

And now starts the fun part: solving for equilibrium states!

The recipe is pretty easy conceptually: set the time derivative to 0 and isolate the variable of interest:

$$\frac{dC}{dt} = qC_I - qC = 0$$

Which is equivalent to:

$$qC_I = qC$$

And because the  $q$  rates cancel each other, we obtain:

$$\bar{C} = C_I$$

Where the hat (or often a \*) denotes the equilibrium.

The method is standard and conceptually simple. Now we need to practice!

Consider a tri-trophic food chain obeying the dynamics of the general Lotka-Volterra equation, where:

$$\frac{dN_i}{dt} = N_i(b_i + \sum \alpha_{ij} N_j)$$

Where the parameter  $b_i$  is the intrinsic rate of increase (positive for primary producers, negative for consumers) and the  $\alpha_{ij}$  are coefficients giving the per capita effect of species  $j$  on species  $i$ .

## Step 3

### Flipping the problem around

The mass-balance assumption: at equilibrium, everything coming in must cancel what goes out. Consequently, we could infer interaction strength from equilibrium densities.

Consider the following equilibrium densities for the plant  $P$ , the herbivore  $H$  and the carnivore  $C$ :

$$P^* = 100$$

$$H^* = 10$$

$$C^* = 2$$

If the intrinsic growth rates are respectively  $b_P = 10$ ,  $b_H = -0.3$ ,  $b_C = -0.1$ , what are the interaction coefficients (assuming symmetry of interactions for simplicity)?

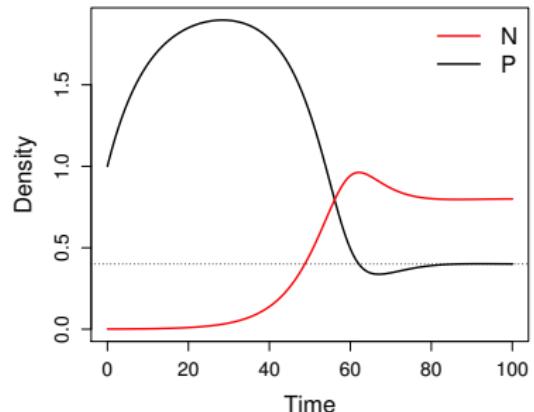
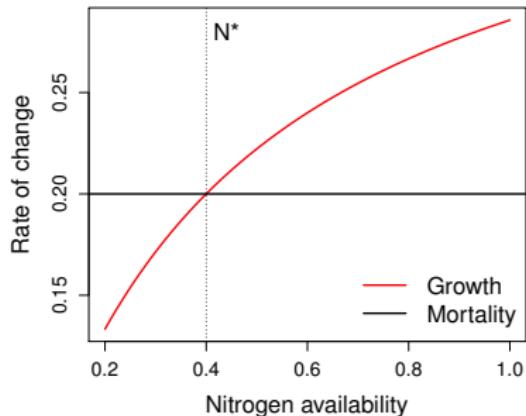
Not all species need to be present at equilibrium (some densities could equal 0). Therefore we need to assess critical conditions allowing a species to invade a community. Consider a standard plant-nutrient model:

$$\begin{aligned}\frac{dN}{dt} &= I - eN - \alpha NP \\ \frac{dP}{dt} &= \alpha NP - bP\end{aligned}$$

1. Compute the equilibrium nutrient availability in absence of the plant
2. Compute the plant growth rate when at low density (i.e. P tends to 0)
3. What is the critical value of  $I$  allowing the plant to establish?

## Step 3

### The $R^*$ principle



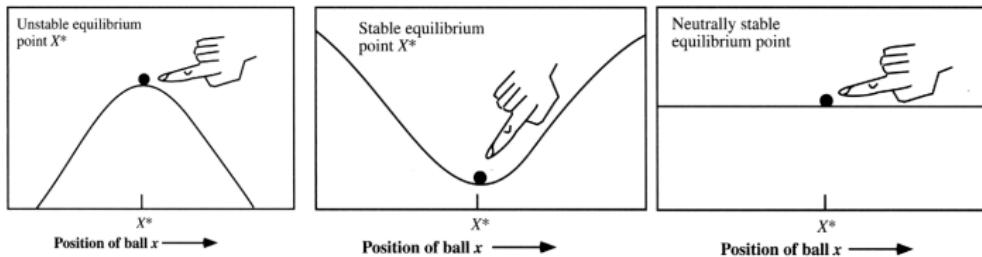
**Definition 1:** The  $R^*$  is the minimal density (or concentration) of resource allowing a species to establish and maintain a population.

**Definition 2:** The  $R^*$  is the equilibrium density of the resource in presence of the consumer.

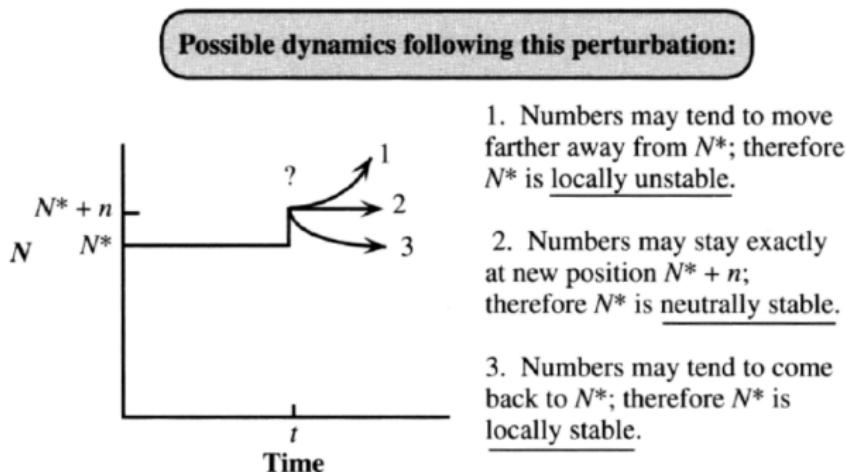
## Step 4

### Local stability analysis: the big deal!

Different types of equilibrium points:



Definition of local stability analysis:



Consider a standard consumer-resource model:

$$\frac{dR}{dt} = R(1 - R) - \alpha RC$$

$$\frac{dC}{dt} = \alpha RC - mC$$

Which has the following equilibrium:

$$R^* = m/\alpha$$

$$C^* = \frac{(1-R^*)}{\alpha}$$

We add small perturbations to this system of equations, defined as:

$$r = R - R^*$$

$$c = C - C^*$$

We now substitute these quantities in the dynamical equations:

$$\begin{aligned}\frac{d(R^*+r)}{dt} &= \frac{dR^*}{dt} + \frac{dr}{dt} \\ \frac{d(C^*+c)}{dt} &= \frac{dC^*}{dt} + \frac{dc}{dt}\end{aligned}$$

Which by definition reduces to:

$$\begin{aligned}0 + \frac{dr}{dt} \\ 0 + \frac{dc}{dt}\end{aligned}$$

We are looking for the dynamics of these perturbations in the neighborhood of the equilibrium. In math, it means we are looking to solve the equations:

$$\begin{aligned}\frac{dr}{dt} &= f(r + R^*, c + C^*) \\ \frac{dc}{dt} &= g(r + R^*, c + C^*)\end{aligned}$$

Because the functions  $f$  and  $g$  are often non-linear, there is usually no solution for the time dynamics  $r(t)$  and  $c(t)$ . There is however a nice and very powerful tool to approximate them. We use a *linearization* around the equilibrium with the Taylor Series. It corresponds to:

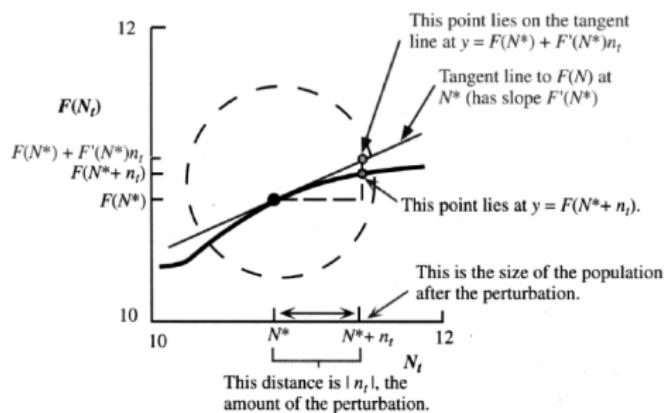
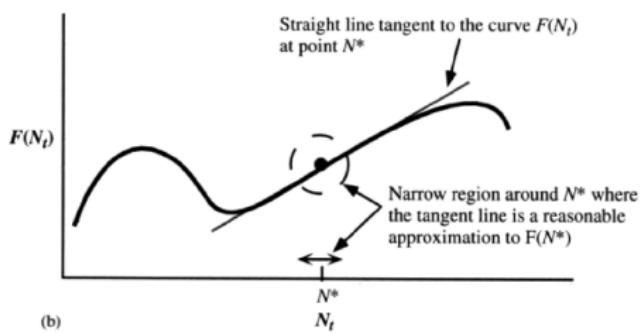
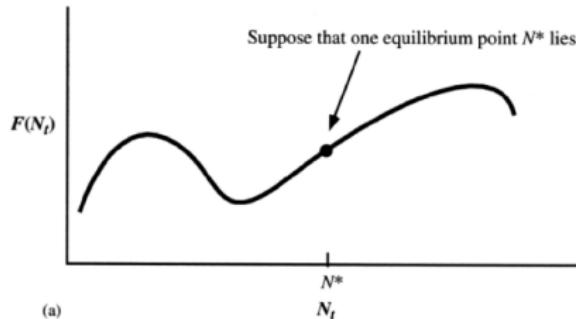
$$f(x) \cong f(x^*) + \frac{f'(x^*)(x-x^*)}{1!} + \frac{f''(x^*)(x-x^*)^2}{2!} + \dots$$

And for the multivariate situation:

$$f(x, y) \cong f(x^*, y^*) + \frac{1}{1!}[(x - x^*) \frac{\partial f(x^*, y^*)}{\partial x} + (y - y^*) \frac{\partial f(x^*, y^*)}{\partial y}] + \dots$$

Where the symbol  $\partial f$  denote partial derivative of function  $f$ . The partial derivative of  $f$  with respect to  $x$  is the derivative of  $f$  considering only the variable  $x$ , with other ones fixed as parameters.

# The Taylor approximation



The set of partial derivatives gives the following system of equations:

$$\begin{aligned}\frac{dr}{dt} &= r \frac{\partial f(R^*, C^*)}{\partial R} + c \frac{\partial f(R^*, C^*)}{\partial C} \\ \frac{dc}{dt} &= r \frac{\partial g(R^*, C^*)}{\partial R} + c \frac{\partial g(R^*, C^*)}{\partial C}\end{aligned}$$

Which written in a matrix format yields:

$$J = \begin{bmatrix} \frac{\partial f(R^*, C^*)}{\partial R} & \frac{\partial f(R^*, C^*)}{\partial C} \\ \frac{\partial g(R^*, C^*)}{\partial R} & \frac{\partial g(R^*, C^*)}{\partial C} \end{bmatrix}$$

Where **J** is the **Jacobian matrix**, also referred as the community matrix. The partial derivatives are computed with equilibrium  $C^*$  and  $R^*$  values. The Jacobian matrix describes the dynamics of all variables around the equilibrium. The local stability is determined from the Jacobian matrix.

Some of you (like me!) might not remember how to derivate complex functions... Here is a trick on R.

```
1 # Define the equation to derivate
2 dCdt = expression(a*R*C - m*C)
3
4 # Use the function deriv to compute the derivate
5 # With respect to C (partial derivate)
6 deriv(dCdt,"C")
7
8 # With respect to R
9 deriv(dCdt,"R")
10
11 # Evaluate the function
12 a = 1
13 m = 0.2
14 R = 10
15 C = 2
16 eval(deriv(dCdt,"R"))
17
18 # Be careful with the output!
```

The system dynamics now reads as:

$$\frac{d\mathbf{n}}{dt} = \mathbf{Jn}$$

Where  $\mathbf{n}$  is the vector of densities.

If we remember that the solution to

$$\frac{dN}{dt} = rN$$

is:

$$N(t) = N_0 e^{rT}$$

Then we could think there is a solution to this simple system of equations. In other words, the linearization with the Taylor series simplifies the dynamics so that it might be possible to have equations for the dynamics of the small perturbations over time.

The problem is that in the solution:

$$N(t) = N_0 e^{\mathbf{J}t}$$

What does it mean to raise  $e$  to the power of matrix  $\mathbf{J}$ ? It would be much easier to do it if  $\mathbf{J}$  would have been a scalar instead of a matrix.

Now the trick is that there is a way to simplify the information contained in a matrix, based on standard linear algebra. It would be much easier if we had a substitution like:

$$\mathbf{J}\mathbf{n} = \lambda\mathbf{n}$$

Where  $\lambda$  would be a set of scalars instead of the matrix  $\mathbf{J}$ . Fortunately, it happens that this equation is exactly the definition of eigen values.  $\mathbf{J}\mathbf{n}$  is the product of a matrix by a vector yielding a vector.

*The eigen values are scalars that when multiplying them by the vector  $\mathbf{n}$ , it yields exactly the same result as the matrix multiplication  $\mathbf{J}\mathbf{n}$ .*

So now we have the situation:

$$\mathbf{J}\mathbf{n} = \lambda\mathbf{n}$$

Which after a simple re-arrangement takes the form:

$$\mathbf{J}\mathbf{n} - \lambda\mathbf{n} = 0$$

And collecting terms we have:

$$(\mathbf{J} - \lambda\mathbf{I})\mathbf{n} = 0$$

Where  $\mathbf{I}$  is the identity matrix. This matrix is a square matrix full of 0s, except for the diagonal where all elements are simply 1. This product yields a matrix full of 0s.

The values of lambda producing a nonzero solution are given by finding values making the determinant of this matrix equal to 0. In other words, we are looking for the solution of  
 $\det(\mathbf{J} - \lambda\mathbf{I}) = 0$

The solution to this problem yields the values of  $\lambda$ s we are looking for. This equation is called the characteristic equation.

As an example (and we'll stay to 2 species for hand calculations!), the determinant of the matrix  $\mathbf{X}$

$$\mathbf{X} = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

Is computed as:

$$ad - bc$$

We solve the problem using the characteristic equation of the matrix  $(J - \lambda I)$ :  
 $\lambda^2 + B_1\lambda + B_2 = 0$

Where

$$B_1 = -(J_{11} + J_{22}) \text{ and } B_2 = J_{11}J_{22} - J_{12}J_{21}$$

This is a quadratic equation, so we know that it has two roots (ie two eigen values). They are:

$$\lambda_1 = \frac{1}{2}(-B_1 + \sqrt{B_1^2 - 4B_2}) \text{ and } \lambda_2 = \frac{1}{2}(-B_1 - \sqrt{B_1^2 - 4B_2})$$

Ouf, that makes a lot of algebra, but we succeeded!

Fortunately, there is also a way to compute eigen values numerically.  
Particularly useful for large matrices.

```
1 # Example of computation of eigen values of a very large matrix.
2 # Draw a random matrix for a community of S species
3 S = 25
4 J = matrix(rnorm(S^2,0,a),nr=S,nc=S)
5
6 # Keep only L links, based on connectance C
7 C = 0.3
8 rand = matrix(runif(S^2,0,1),nr=S,nc=S)
9 J[rand>C] = 0
10
11 # Impose competition along the diagonal
12 diag(J) = -1
13
14 # Compute eigen values
15 res_eigen = eigen(J)$values
16
17 # Keep only the real parts
18 real_eigen = as.real(res_eigen)
```

Now coming back to the dynamics of the small perturbations, we have a solution to our system of equations:

$$r(t) = k_1 e^{\lambda_1 t} + k_2 e^{\lambda_2 t}$$

$$c(t) = k_3 e^{\lambda_1 t} + k_4 e^{\lambda_2 t}$$

Where  $\lambda_1$  and  $\lambda_2$  are the eigen values of the Jacobian matrix. This system of equation tells us that if all eigen values are negative, then the perturbations will shrink and the system will be stable. Otherwise, they will grow to infinity and the system is unstable.

## An example

### Lotka-Volterra predator-prey interactions

Consider the classic Lotka-Volterra predator-prey model:

$$\frac{dR}{dt} = bR - aRC = f(R, C)$$

$$\frac{dC}{dt} = kaRC - dC = g(R, C)$$

Which has the following equilibrium solution:  $C^* = \frac{b}{a}$

$$R^* = \frac{d}{ka}$$

## An example

### Lotka-Volterra predator-prey interactions

The partial derivatives are:

$$\frac{\partial f}{\partial R} = b - aC \text{ and } \frac{\partial f}{\partial C} = bC$$

$$\frac{\partial g}{\partial R} = -aR \text{ and } \frac{\partial g}{\partial C} = -d + bR$$

Which yields the Jacobian matrix:

$$J = \begin{bmatrix} 0 & -d \\ kb & 0 \end{bmatrix}$$

And the characteristic equation:

$$\lambda^2 + db = 0$$

## An example

### Lotka-Volterra predator-prey interactions

This example is a well-known pathologically neutral model. The eigen values are:  $\lambda = 0 + i\sqrt{bd}$  and  $\lambda = 0 - i\sqrt{bd}$

The dynamics could look like:

## A shortcut for 2 species-systems

### Assessing stability without computing eigen values

This technique is pretty heavy, but in some cases it might be simpler using an alternative approach (known as the Routh-Hurwitz criteria) but nonetheless based on the same principle. Remembering the above solution for eigen values

$$\lambda_1 = \frac{1}{2}(-B_1 + \sqrt{B_1^2 - 4B_2})$$

and

$$\lambda_2 = \frac{1}{2}(-B_1 - \sqrt{B_1^2 - 4B_2})$$

The conditions for a stable system to occur are that  $B_1 > 0$  and  $\sqrt{B_1^2 - 4B_2} < B_1$ . Re-arranging the last condition yields that:

$$B_1 = -(J_{11} + J_{22}) > 0$$

and

$$B_2 = J_{11}J_{22} - J_{12}J_{21} > 0$$

These conditions could then be rapidly assessed using only the sign structure of the matrix.

1. Compute the equilibrium
2. Calculate partial derivatives
3. Build the Jacobian matrix
4. Calculate the eigen values
  - ▶  $\lambda < 0$ : stable
  - ▶  $\lambda > 0$ : unstable
  - ▶  $\lambda = 0$ : neutrally stable
  - ▶ No imaginary part: smooth return
  - ▶ Imaginary part: oscillations

Consider the famous M&W model of island biogeography:

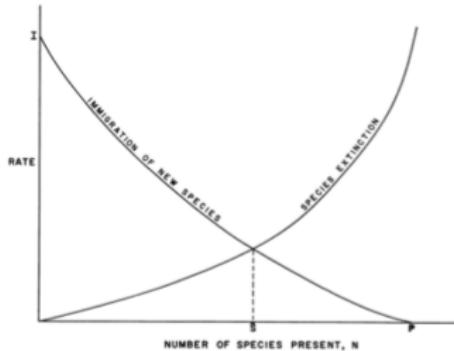


FIG. 4. Equilibrium model of a fauna of a single island. See explanation in the text.

- ▶ Formulate the equation describing the dynamics of species richness on islands
- ▶ Now consider that  $e = \frac{\epsilon}{A^b}$  and solve the model at equilibrium
- ▶ What is the rate of change of equilibrium species richness with habitat destruction? Is 10% habitat destruction affecting more small or large islands?
- ▶ Calculate the stability of equilibrium species richness

Consider another classic model: Lotka-Volterra equations for competition.

$$\frac{dN_i}{dt} = rN_i(1 - \frac{\alpha_{ij} N_j}{K_i} - \frac{N_i}{K_i})$$

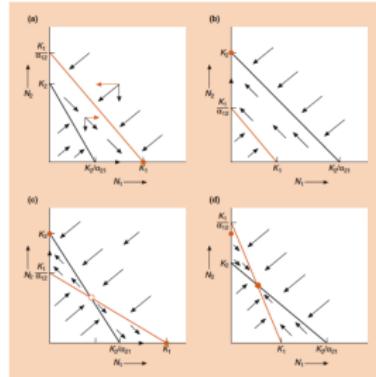


Figure 8.9 The outcomes of competition generated by the Lotka-Volterra competition equations for the four possible arrangements of the  $N_1$  and  $N_2$  zero isoclines. Vectors generally refer to joint populations, and are derived as indicated in (a). The solid circles show stable equilibrium points. The open circle in (c) is an unstable equilibrium point. For further discussion, see the text.

- ▶ Solve the model at equilibrium with two species
- ▶ Compute the stability of the model with one of the two species absent.  
What happens if  $K_1 = K_2 = 1$  and  $\alpha_{ij} = \alpha_{ji} = 0.5$ ?

Consider another classic model: Lotka-Volterra equations for competition.

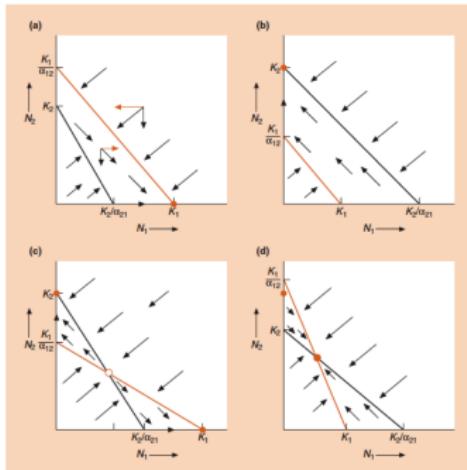


Figure 8.9 The outcomes of competition generated by the Lotka-Volterra competition equations for the four possible arrangements of the  $N_i$  and  $N_j$  zero isoclines. Vectors, generally, refer to joint populations, and are derived as indicated in (a). The solid circles show stable equilibrium points. The open circle in (c) is an unstable equilibrium point. For further discussion, see the text.

$$\frac{dN_i}{dt} = rN_i(1 - \frac{\alpha_{ij} N_j}{K_j} - \frac{N_i}{K_i})$$

- ▶ Solve the model at equilibrium with two species
- ▶ Compute the stability of the model with one of the two species absent.  
What happens if  $K_1 = K_2 = 1$  and  $\alpha_{ij} = \alpha_{ji} = 0.5$ ?