Theory-driven analysis of ecological data

GdR TheoMoDiv - FRB-CESAB

2022-05-16

Program of the week

- **Day 1** theoretical modeling / I Gounand 8h30-17h30
- **Days 2-4** Thematic days: lectures (AM) / practica (PM) 9-17h
  - **Day 2**: time series / E Fronhofer and B Rosenbaum
  - **Day 3**: spatial data / V Calcagno and M Dubart
  - **Day 4**: interaction networks / F Massol, M Barbier and C Jacquet
- **Day 5**: Group projects the morning / present results early afternoon (end 16h)
  - 4-5 groups of 2-3 people
  - Objectives: answer a research question with learnt techniques on a dataset
- Evening seminars at 18h-19h

Evening seminars 18-19h

Monday – KIM CUDDINGTON (Waterloo University, Canada)

What are models for and can we use them more effectively?

Tuesday – FRÉDÉRIC BARRAQUAND (CNRS, Bordeaux)

Title Frédéric's presentation

Wednesday – VIRGINIE RAVIGNÉ (Cirad, Montpellier)

Confronting field and laboratory data to better understand community dynamics: the case of fruit flies in La Réunion

Thursday – SONIA KÉFI (ISEM, Montpellier)

the multiplexity of ecological communities

Program of the first day

Objective: acquire the bases of theoretical modeling in BEE
1-2 adapted from a course of introduction to modeling by Nicolas Loeuille, Professor at Sorbonne Université + Some insights from Elisa Thébault

- Morning 8h30 - 12h30
    - Starter: Theory-driven or Data-driven science?
    1. Scientific approaches and model use
    2. Formalism and structure of models in BEE
- Afternoon 14h - 17h30
    3. Model analysis in BEE
    4. Linking models and data
- Late Afternoon 18h - 19h: Seminar of Kim Cuddington

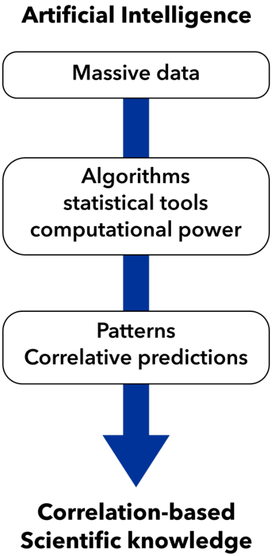
Theory-driven Data science or Data-driven science?

"All models are wrong, but some are useful" 1976, George Box, statistician

"All models are wrong, and increasingly you can succeed without them" 2008, Peter Norvig, Google's research director

"Correlation supersedes causation, and science can advance even without coherent models, unified theories, or really any mechanistic explanation at all"

Theory-driven Data science or Data-driven science?



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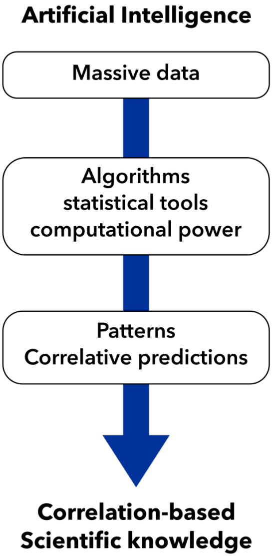
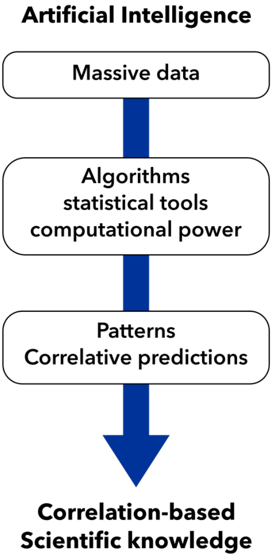
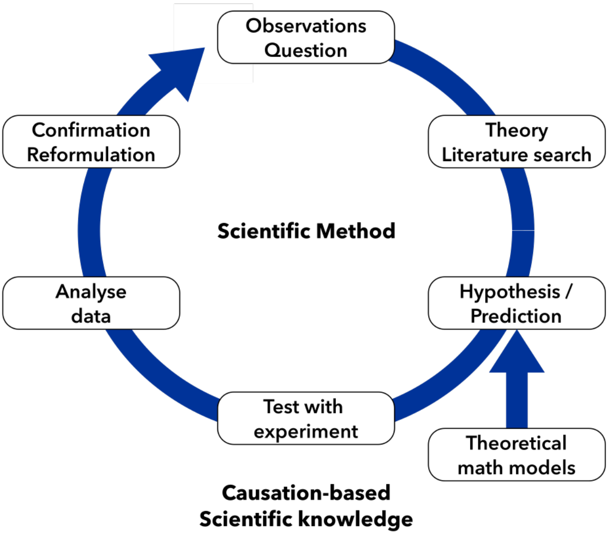


- Data are noisy
- Data are not necessarily representative
- No mechanistic constraint
- Can't predict novel things

Theory-driven Data science or Data-driven science?





Section 1

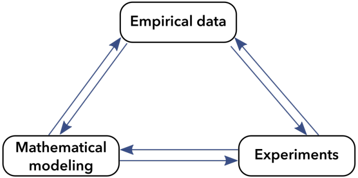
Scientific approaches and model use in Biodiversity Ecology and Evolution

Scientific approaches and model use

Content

1. Introduction to scientific approach in BEE
2. Modeling approach in BEE
    1. Link with the hypothetico deductive approach
    2. An example with Lotka-Volterra model
3. Theoretical modeling and complexity

Scientific approaches and model use (1)



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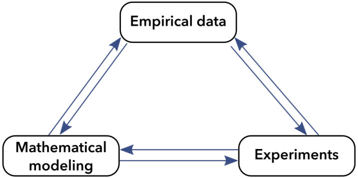
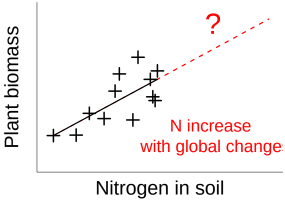
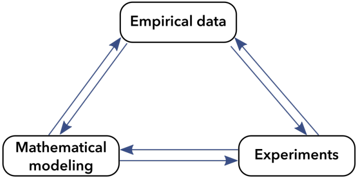
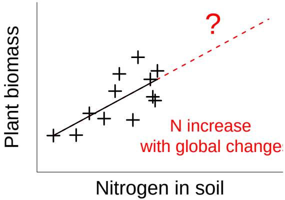




- Empirical data: correlation inducing questions (no causation)

Scientific approaches and model use (1)





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- Experiments: proof of mechanisms, repetition => causation

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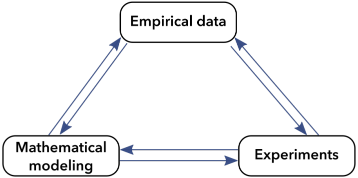
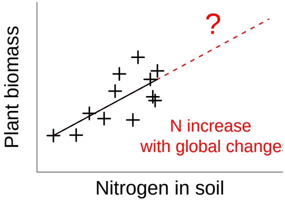
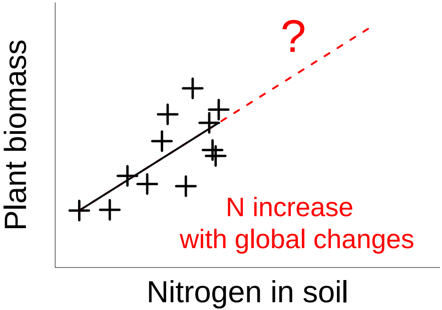




- Empirical data: correlation inducing questions (no causation)
- Experiments: proof of mechanisms, repetition => causation
- Modeling: what implication ? 3 goals of modeling:
  - **understand** (general rules? Lawton 1999)
  - **predict**
  - **upscale** (limited scales of observation and experiment)

Scientific approaches and model use (1)

Extrapolation
from empirical data



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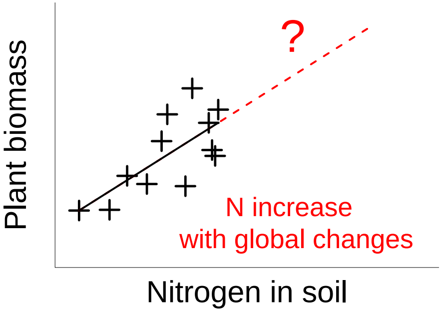
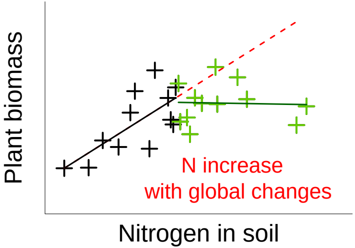


Possible future observations
based on ecological theories



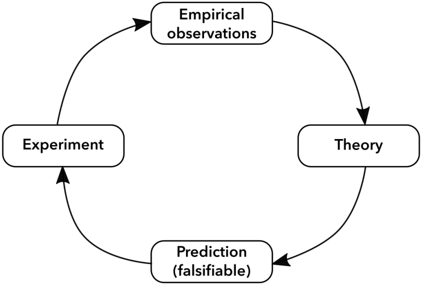
Theoretical frameworks:

- Ecological stoichiometry (Sterner and Elser 2002): change in limitation - Trophic ecology (Oksanen et al 1981): regulation by herbivores

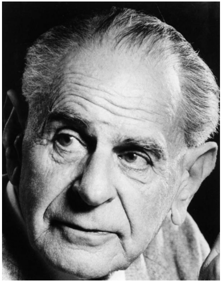
Scientific approaches and model use (2.1)

Link with the hypothetico-deductive approach

Experimental approach

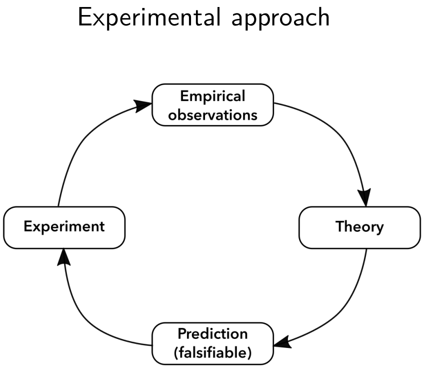


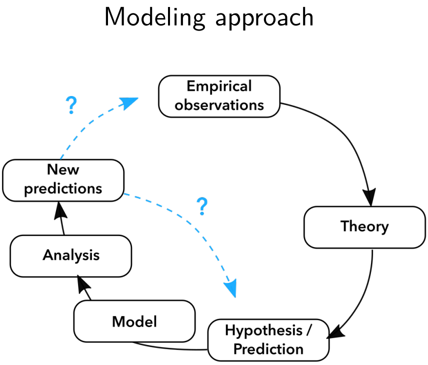
Karl Popper



Scientific approaches and model use (2.1)

Link with the hypothetico-deductive approach





Scientific approaches and model use (2.2)

Application to (Lotka-)Volterra model (1910-1920)

D'Ancona observations

Vito Volterra

```
##            Before war End war 1925
## Predators        12%     40%  15%
## Prey             88%     60%  85%
```

Hypothesis: ecological interaction => trophic transfer with a delay

Scientific approaches and model use (2.2)

Hypothesis: ecological interaction => trophic transfer with a delay

$\frac{dN}{dt} = basalgrowth + interaction$

$\frac{dP}{dt} = basalgrowth + interaction$

- N: density of prey
- P: density of predators

Scientific approaches and model use (2.2)

Hypothesis: ecological interaction => trophic transfer with a delay

$\frac{dN}{dt} = basalgrowth + interaction$

$\frac{dP}{dt} = basalgrowth + interaction$

- N: density of prey
- P: density of predators

Predator-prey model

$\frac{dN}{dt} = r_0 N - aNP$

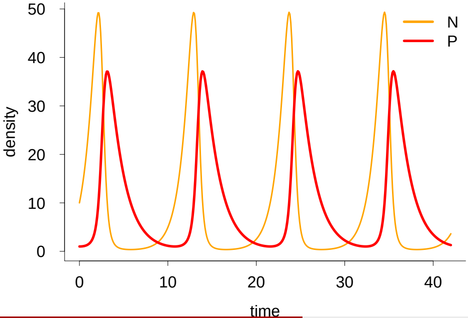
$\frac{dP}{dt} = -mP + eaNP$

Hypotheses:

- Malthusian growth
- Mass action
- e: conversion efficiency

Scientific approaches and model use (2.2)

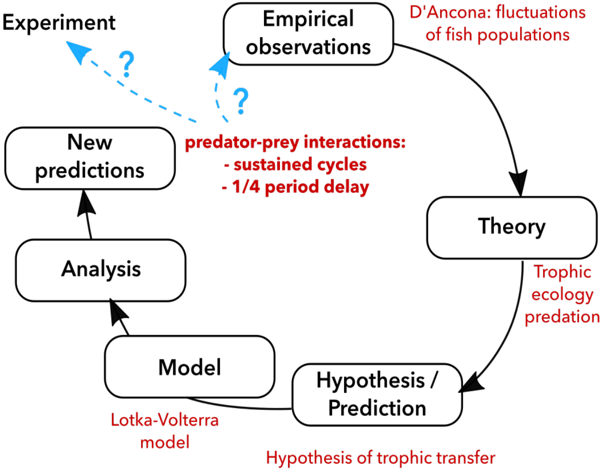
```
library(deSolve)

lv_model <- function(t, state, parms) {
  with(as.list(c(state, parms)), {
    dN = r0*N - a*N*P
    dP = -m*P + e*a*N*P
    return(list(c(dN,dP)))
  })
}

dyn <- data.frame(ode(y = c(N=10,P=1), times = seq(0,42,by=0.1),
      func = lv_model, parms = c(r0=1,a=0.1,m=0.6,e=0.6), method = "rk4"))
```



Predictions

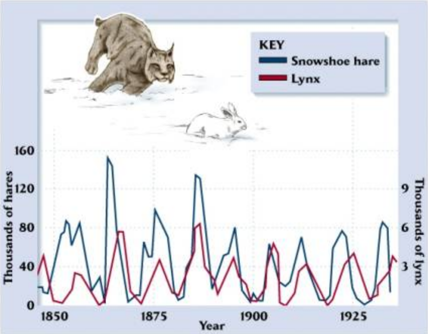
- Sustained cycles
- 1/4 delay between prey and predator pics

Scientific approaches and model use (2.2)



Scientific approaches and model use (2.2)

Test the new predictions with empirical data

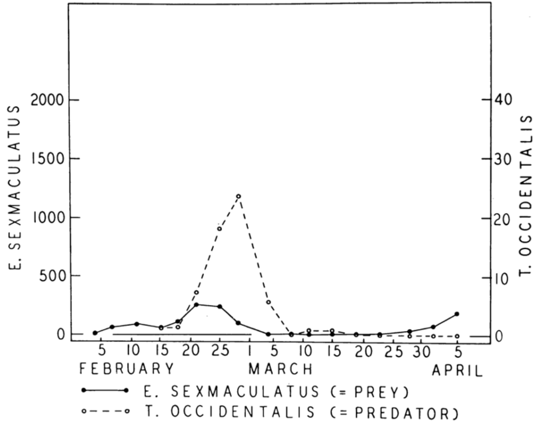


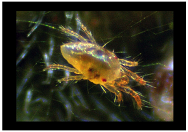
- Does the data match the predictions?
- Density-dependant regulation (Nicholson 1954)
- Role of climatic forcing (Andrewaretha and Birch 1954; Stenseth et al 2003, 2004)? NAO - 10yr oscillations

Scientific approaches and model use (2.2)

Experimental tests of Huffaker (1958)

With no spatial heterogeneity

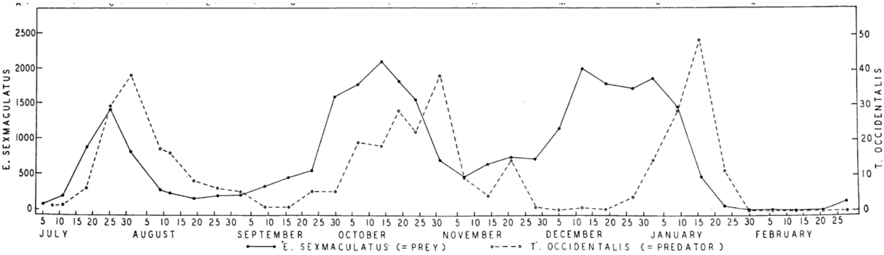




Scientific approaches and model use (2.2)

Experimental tests of Huffaker (1958)

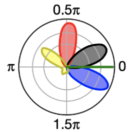
With spatial heterogeneity

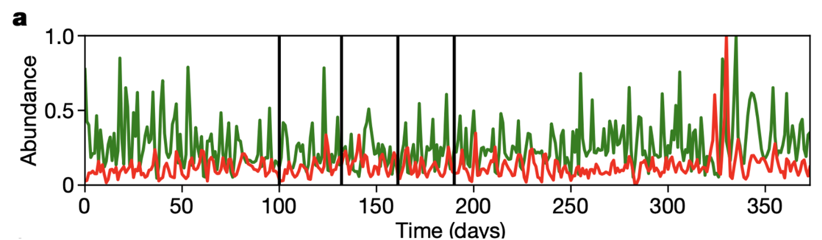


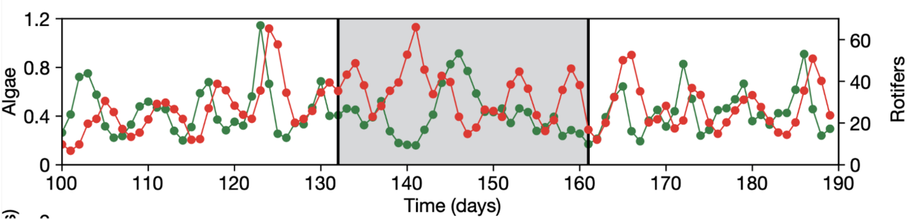
- Are the hypotheses verified?
- What about the global coherence dynamics-model?
-

Scientific approaches and model use (2.2)

Experimental test of Blasius et al (2020)

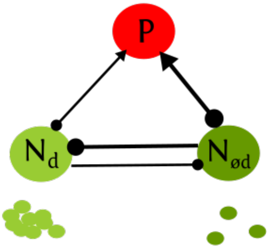


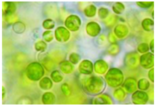




Scientific approaches and model use (2.2)

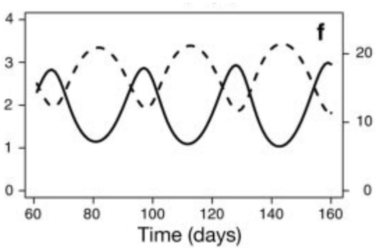
Integration of eco-evolutionary dynamics Yoshida et al. (2003)





Predictions

- longer cycles
- antiphase



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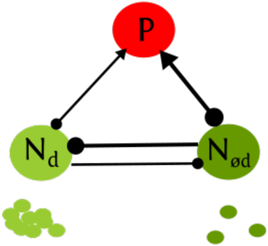

Predictions

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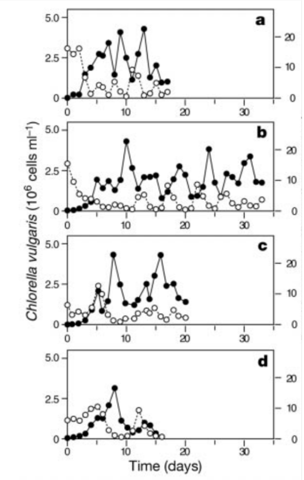
Single clone



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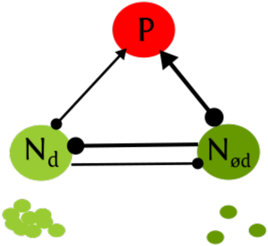

Predictions

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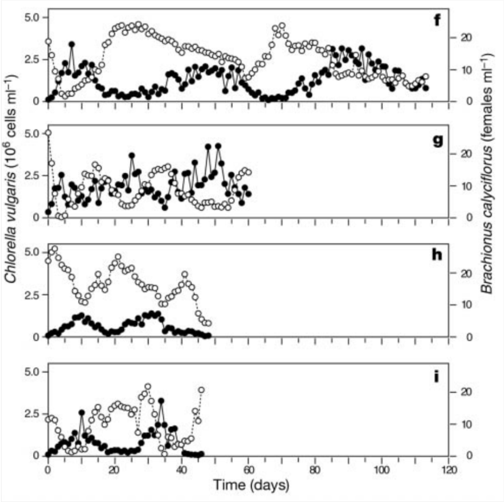
Genetic diversity



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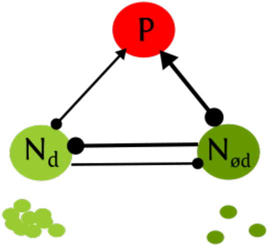

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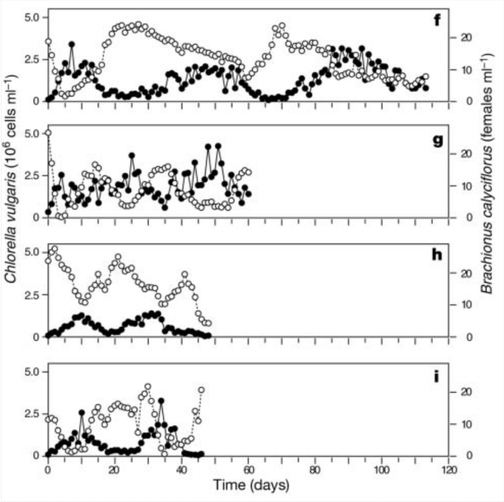

Predictions

- longer cycles
- antiphase
- Hiltunen et al meta-analysis (2014) 12/21 data sets with imprint of eco-evolution

Scientific approaches and model use (3)

Theoretical modeling and complexity

- Complexity = number of variables + parameters
- Simple models can be known at all times and explored with a few values

Scientific approaches and model use (3)

Theoretical modeling and complexity

- Complexity = number of variables + parameters
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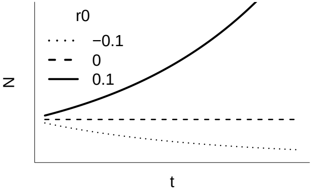
Malthusian growth

$\frac{dN}{dt} = rN$; $N(t) = N_0 e^{rt}$



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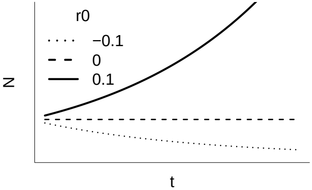
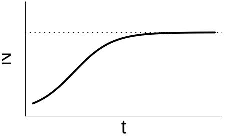


Verhulst's model (logistic)

$\frac{dN}{dt} = rN(1 - \frac{N}{K})$



3 values of r x 3 values of K

Scientific approaches and model use (3)

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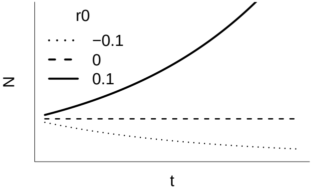

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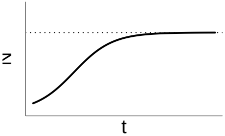

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Theoretical modeling and complexity

- Complexity = number of variables + parameters
- Simple models can be known at all times and explored with a few values
- Relatively simple models can be analyzed through equilibrium: LV (2var ; 4 param) : proof of oscillatory dynamics
- Minimal complete exploration needs 3^n parameters

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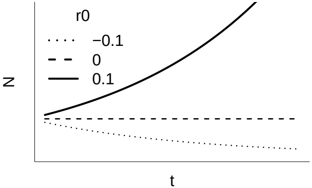

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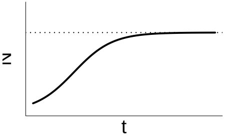


3 values of r x 3 values of K

Scientific approaches and model use (3)

=> resist to complexity!

- Theoretical approach (different from system specific modeling)
- Costly in terms of:
  - understanding
  - simulations

Some thoughts about the degree of complexity

- *"Any darn fool can make something complex; it takes a genius to make something simple."* Pete Seeger
- *"Le simple est toujours faux. Ce qui ne l'est pas est inutilisable."* Paul Valery
- *"Everything should be made as simple as possible, but not simpler"* Albert Einstein

Section 2

Formalism and structure of models in BEE

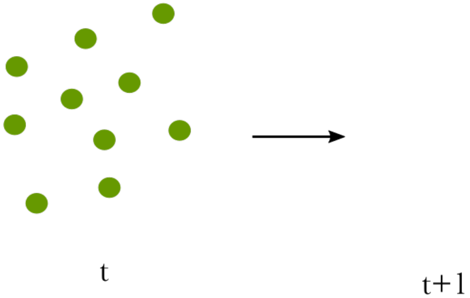
Formalism and structure of models in BEE

Content

1. Panorama of model types (linked to questions)
   - Individual level
   - population level
   - life-history
   - community level
   - space representation
2. Understanding the structure of models
3. Link between structure and hypotheses

Formalism and structure of models in BEE (1)

Individual-based models: Processes at the scale of individuals



Formalism and structure of models in BEE (1)

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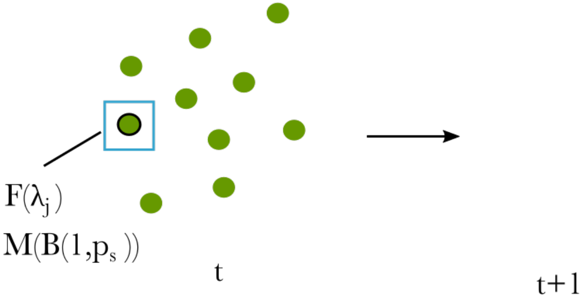

Formalism and structure of models in BEE (1)

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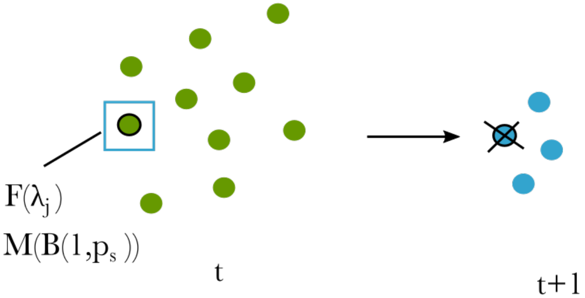

Formalism and structure of models in BEE (1)

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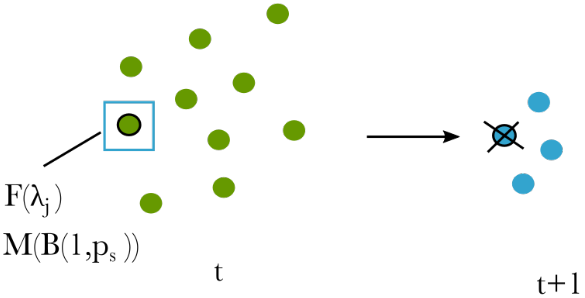

- **advantage**: modeling scale = obs. scale
- **Cost**:
  - mathematical analysis is difficult
  - long simulations (random draws)

Formalism and structure of models in BEE (1)

Example of Hubbel's neutral model of biodiversity (2001)

- Hypotheses: all species have the same biological rates
- Alternative hypothesis to classical niche theory (Hutchinson 1960, Chesson 1997):
  - there is some variation (temporal, spatial) in the environment
  - species reply differently to these varaitions
  - $=>$ this allow maintenance of biodiversity

Formalism and structure of models in BEE (1)

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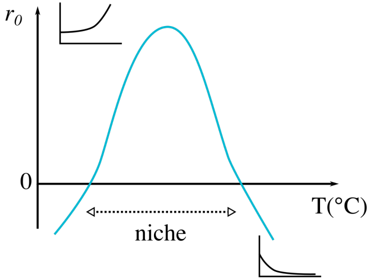

Formalism and structure of models in BEE (1)

Example of Hubbel's neutral model of biodiversity (2001)

- Hypotheses: all species have the same biological rates
- Alternative hypothesis to classical niche theory (Hutchinson 1960, Chesson 1997):
  - there is some variation (temporal, spatial) in the environment
  - species reply differently to these varaitions
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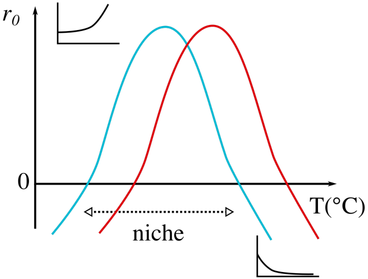

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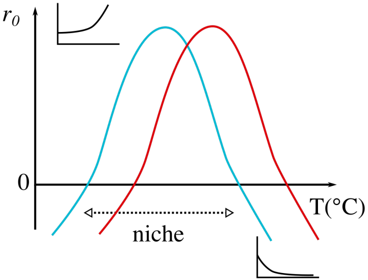

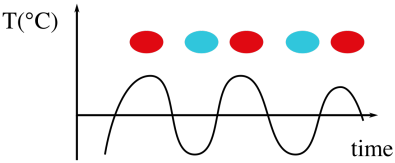

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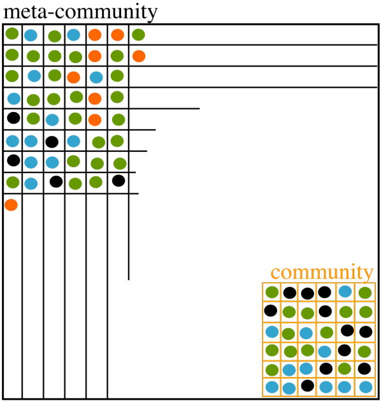

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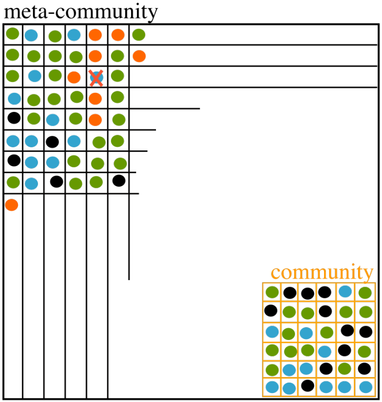

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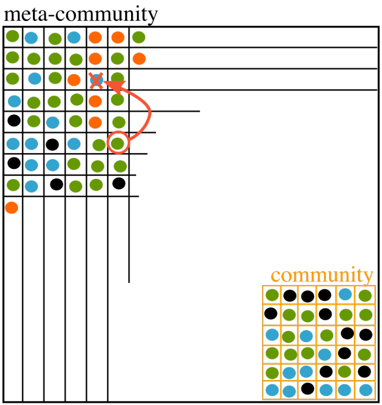

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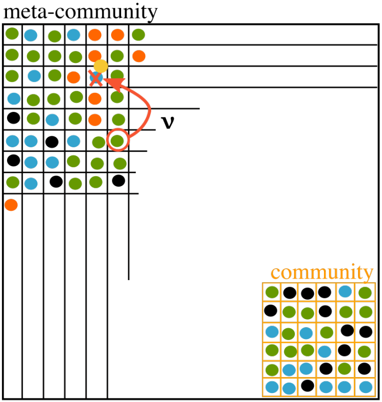

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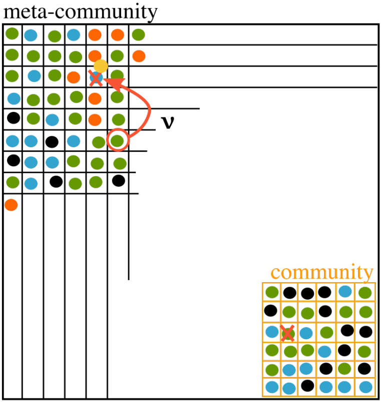

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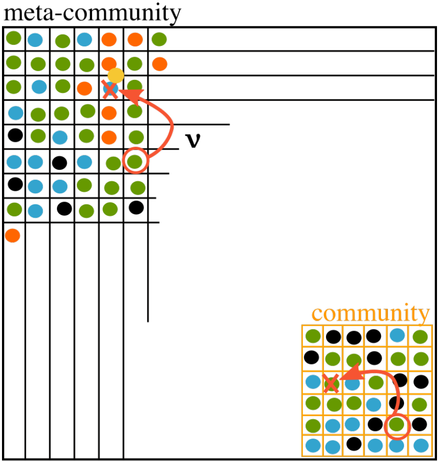

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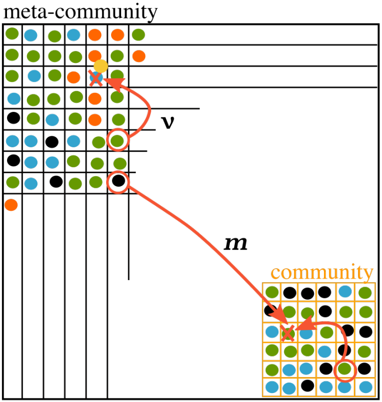

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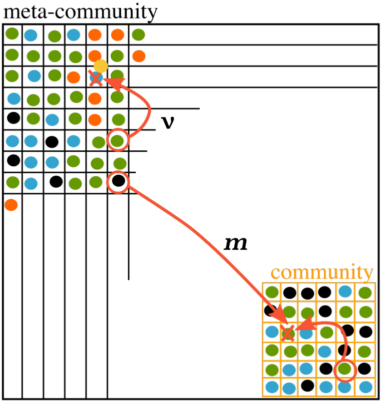

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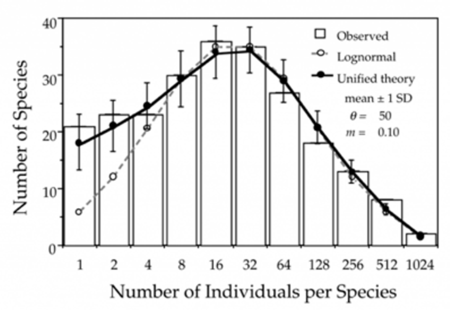
Only 4 parameters:

- J_{meta}: size of the metacommunity
- J_{comm}: size of the community
- ν: speciation rate
- m: dispersal rate

Formalism and structure of models in BEE (1)

Results of Hubbel's neutral model (2001)



tropical forest, Barro Colorado Island, Panama

Prediction: asymmetry of abundances for rare species

Here, a neutral approach is more efficient to reproduce the pattern observed in this forest compared to the expectation under the niche model.

Formalism and structure of models in BEE (1)

Individual-based models: Processes at the scale of individuals

In which case IBM are particularly relevant ?

- **when there not too many parameters**
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=> small populations: questions of **Conservation** / viability of small pops

Formalism and structure of models in BEE (1)

At the scale of populations: ODE or discrete time equations

Continuous time (ODE): $t \in \mathbb{R}$

$$\frac{dN}{dt} = f(N)$$

Discrete time (DE): $t \in \mathbb{N}$

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

Verhulst's model: $\frac{dN}{dt} = rN(1 - \frac{N}{K})$

Discrete time (DE): $t \in \mathbb{N}$

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Equivalent: $N_{t+1} = N_t + RN_t = \lambda N_t$

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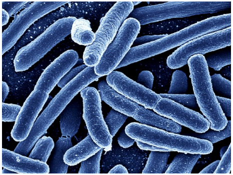

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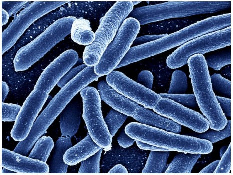

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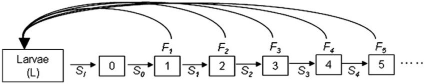
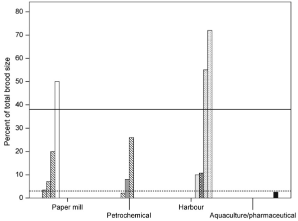
- assumption: variability due to stochastic processes and intraspecific variation is negligible (determinist processes)
- advantage: simple, easier to analyse mathematically
- In which case is ODE or DE relevant: in large populations

Formalism and structure of models in BEE (1)

Models for life cycle questions: Matrix projection model (Leslie matrix)



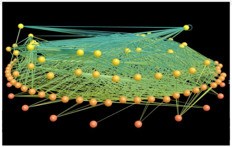
$$M = \begin{pmatrix} 0 & 0 & f_1 & f_2 & \dots & f_i \\ S_l & 0 & 0 & 0 & \dots & 0 \\ 0 & S_0 & & & \dots & 0 \\ 0 & 0 & S_l & 0 & \dots & 0 \\ \dots & \dots & \dots & & & \\ 0 & 0 & 0 & \dots & S_i & 0 \end{pmatrix}$$



(Bergek et al. 2012) on eelpout

- parameters at the scale of individuals (observation / experiment)
- predictions at the scale of population:
  - growth rate predicted by the dominant eigenvalue λ (grows if $\lambda > 1$)
  - elasticity: change in λ with parameter (here S_l and S_O sensitive to toxics)
- relevant for questions where age, stage, or phenotype is at the center

Formalism and structure of models in BEE (1)



Models for communities

Model for n species : $\frac{dN_i}{dt} = F_i(N_1 ... N_n)$;

Generalized Lotka-Volterra model: $\frac{dN_i}{dt} = N_i(r_i + \sum_j a_{ij} N_j)$

with a_{ij} the coefficients of interactions.

Interaction matrix

$$A = \begin{bmatrix} a_{11} & \cdots & a_{1n} \\ \vdots & a_{ij} & \vdots \\ a_{n1} & \cdots & a_{nn} \end{bmatrix} = \begin{bmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & a_{23} & a_{24} \\ a_{31} & a_{32} & a_{33} & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44} \end{bmatrix}$$

Formalism and structure of models in BEE (1)

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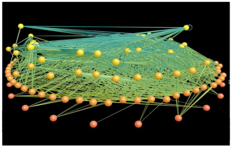

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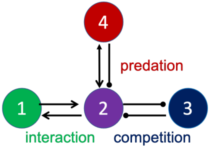

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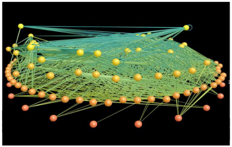

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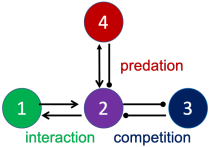

=> structure of communities

=> the more negative the a_{ij}, the more stable the community

Formalism and structure of models in BEE (1)

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Robert May (1972)

Hypotheses:

- non null connectance: there are $a_{ij} \neq 0$
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- Consequences: diversity, increased connectance and stronger interactions destabilize $\neq$ diversity increases stability (Elton 1958, McArthur 1955, Odum 1960)

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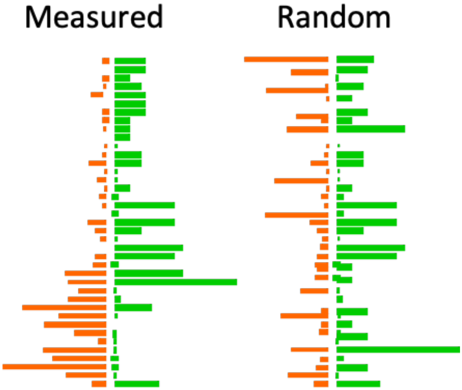

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- **Interactions are not distributed randomly** (De Ruiter et al 1995 *Science*)

Formalism and structure of models in BEE (1)

Questions in relation to space

- **Spatially implicit models**: no exact position
- Spatially explicit models: explicit geographical coordinates

Formalism and structure of models in BEE (1)

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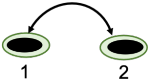
- adding dispersal:

$\frac{dN_1}{dt} = rN_1(1 - \frac{N_1}{K}) - \delta N_1 + \delta N_2$

$\frac{dN_2}{dt} = rN_2(1 - \frac{N_2}{K}) - \delta N_2 + \delta N_1$



δ: dispersal rate (diffusion)

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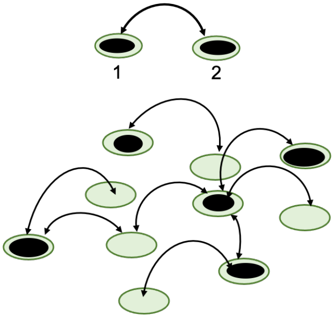
- Levins' model of occupancy (1969)
  $\frac{dp}{dt} = cp(1 - p) - ep$
  - p: proportion of occupied patches
  - c: colonization rate
  - e: extinction rate



metapopulation

prediction of extinction threshold: $p^* = 1 - \frac{e}{c}$

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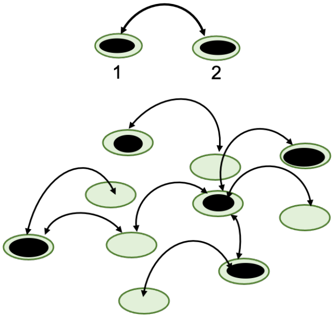

metapopulation ...
metacommunity, metaecosystem

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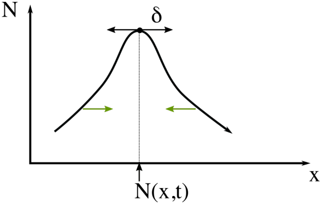
Formalism and structure of models in BEE (1)

Questions in relation to space

- Spatially implicit models: no exact position
- **Spatially explicit models**: explicit geographical coordinates
  - Cellular automata
  - Reaction-diffusion model: partial derivative equations (PDE)

Fisher KPP model (Fisher 1937 /and Kolmogorov-Petrovsky-Piskunov 1937)

$\frac{\partial N}{\partial dt} = \delta \frac{\partial^2 N}{\partial x^2} + rN(1-N)$; x position of individuals; δ dispersal rate.



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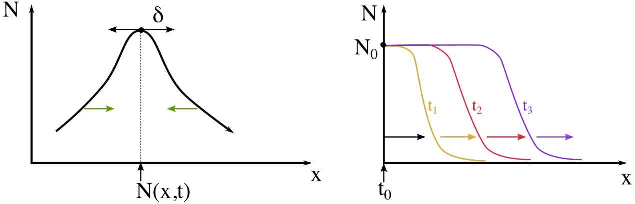

Prediction: $v = 2\sqrt{r\delta}$

in good agreement with some observations (Hastings et al. 2005 EcoLett)

Formalism and structure of models in BEE (2)

Structure of models

Two important points of model structure:

- Distinguish variables (outputs) and parameters (inputs)
- Biological signification of variables and parameters:
  - intervals of definition
  - units: dimension analysis

Models	**Intervals**	**Units**
$\frac{dN}{dt} = r_0 N$	N	N :
$\frac{dN}{dt} = r_0 N(1 - \frac{N}{K})$	t	t :
$\frac{dN}{dt} = r_0 N - aNP$	r	r :
$\frac{dP}{dt} = -mP + aNP$	K	a :

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$\frac{dN}{dt} = r_0 N(1 - \frac{N}{K})$	$t \in \mathbb{R}$	t :
$\frac{dN}{dt} = r_0 N - aNP$	$r \in \mathbb{R}$	r :
$\frac{dP}{dt} = -mP + aNP$	$K \in \mathbb{R}^+$	a :

Formalism and structure of models in BEE (2)

Structure of models

Two important points of model structure:

- Distinguish variables (outputs) and parameters (inputs)
- Biological signification of variables and parameters:
  - intervals of definition
  - units: dimension analysis

Models	Intervals	Units
$\frac{dN}{dt} = r_0 N$	$N \in \mathbb{R}^+$	$N : ind.m^{-2}$
$\frac{dN}{dt} = r_0 N(1 - \frac{N}{K})$	$t \in \mathbb{R}$	$t : yr$
$\frac{dN}{dt} = r_0 N - aNP$	$r \in \mathbb{R}$	$r : yr^{-1}$
$\frac{dP}{dt} = -mP + aNP$	$K \in \mathbb{R}^+$	$a : yr^{-1}.ind^{-1}.m^2$

Formalism and structure of models in BEE (3)

Link between structure and hypothesis

Keep in mind how mathematical choices underlie biological hypotheses

$\frac{dN}{dt} = N(r(N) - f(N,P))$; $\frac{dP}{dt} = P(r(P) + f(N,P))$

Formalism and structure of models in BEE (3)

Link between structure and hypothesis

Keep in mind how mathematical choices underlie biological hypotheses

$\frac{dN}{dt} = N(r(N) - f(N,P))$; $\frac{dP}{dt} = P(r(P) + f(N,P))$

Mathematical choices

$r(N) = r$

$r(N) = r(1 - \frac{N}{K})$

Biological hypotheses

Formalism and structure of models in BEE (3)

Link between structure and hypothesis

Keep in mind how mathematical choices underlie biological hypotheses

$\frac{dN}{dt} = N(r(N) - f(N,P))$; $\frac{dP}{dt} = P(r(P) + f(N,P))$

Mathematical choices	**Biological hypotheses**
$r(N) = r$	No competition
$r(N) = r(1 - \frac{N}{K})$	Intraspecific competition (density dependence)

Formalism and structure of models in BEE (3)

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$f(N,P) = aNP$	

Formalism and structure of models in BEE (3)

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$f(N,P) = \frac{aP}{1+hN}$	

Formalism and structure of models in BEE (3)

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Formalism and structure of models in BEE (3)

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$f(N,P) = aNP$	Type I: mass action law
$f(N,P) = \frac{aP}{1+hN}$	Type II: prey manipulation (h)
$\frac{dN_1}{dt} = rN_1(1 - \frac{N_1}{K}) + \delta(N_2 - N_1)$	
$\frac{dp}{dt} = cp(1-p) - ep$	

Formalism and structure of models in BEE (3)

Link between structure and hypothesis

Keep in mind how mathematical choices underlie biological hypotheses

$\frac{dN}{dt} = N(r(N) - f(N,P))$; $\frac{dP}{dt} = P(r(P) + f(N,P))$

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$\frac{dN_1}{dt} = rN_1(1 - \frac{N_1}{K}) + \delta(N_2 - N_1)$	Patches are the same / diffusion
$\frac{dp}{dt} = cp(1-p) - ep$	

Formalism and structure of models in BEE (3)

Link between structure and hypothesis

Keep in mind how mathematical choices underlie biological hypotheses

$\frac{dN}{dt} = N(r(N) - f(N,P))$; $\frac{dP}{dt} = P(r(P) + f(N,P))$

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$\frac{dN_1}{dt} = rN_1(1 - \frac{N_1}{K}) + \delta(N_2 - N_1)$	Patches are the same / diffusion
$\frac{dp}{dt} = cp(1-p) - ep$	Local demography is faster than e,c

Formalism and structure of models in BEE

Conclusion

- What determine model choices
  - organisation scale of interest
  - importance of stochastic processes
  - how processes happen in time
  - is space important for my question?

Table including the different formalisms

$=>$ Model is a simplified representation of a system / the simpler is the better

Section 3

Model analysis in BEE

Model analysis in BEE

Content

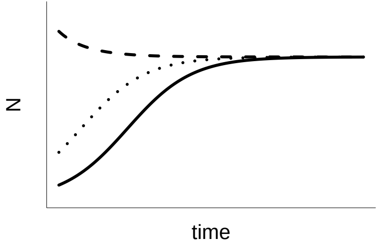
1. Transient versus asymptotic dynamics
2. Equilibrium, stability: caracterisation of asymptotic state
3. Numerical integration

Model analysis in BEE (1)

Transient versus asymptotic dynamics

- sensitivity of transient dynamics to initial conditions
- integration possible only in the simplest cases

Verhulst's model: $N(t) = \frac{K}{1-(\frac{K}{N_0}-1)e^{-r_0 t}}$



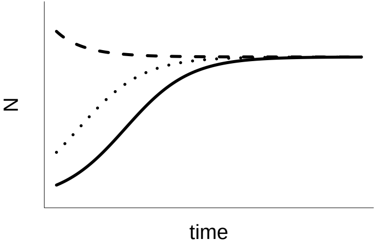
Model analysis in BEE (1)

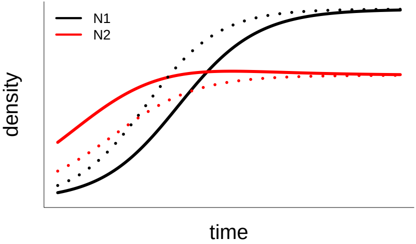
Transient versus asymptotic dynamics

- sensitivity of transient dynamics to initial conditions
- integration possible only in the simplest cases
- otherwise, well-characterized transient dynamics is not possible

Verhulst's model: $N(t) = \frac{K}{1-(\frac{K}{N_0}-1)e^{-r_0 t}}$

2 species competition:



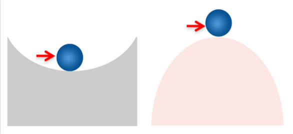


Model analysis in BEE (2)

Equilibrium, stability: characterisation of asymptotic states

Analytical study

1. Derive equilibrium points
2. Local stability analysis (little perturbation)
   - Compute Jacobian matrix J
   - Compute eigenvalues λ
   - Analyse of eigenvalues, $\Re e(\lambda_{max})$



System

$\frac{dN}{dt} = r_0 N - aNP = f(N, P)$

$\frac{dP}{dt} = -mP + aNP = g(N, P)$

Equilibrium points:

(N^*, P^*) such that $f(N^*, P^*) = 0$ and $g(N^*, P^*) = 0$

(pen and paper or software of symbolic calculus)

Model analysis in BEE (2)

1. Derive equilibrium points: the case of LV predator-prey model

$\frac{dN}{dt} = r_0 N - aNP$; $\frac{dP}{dt} = -mP + aNP$

Equilibrium points:

$\frac{dP}{dt} = 0 \iff P^*(aN^* - m) = 0 \iff (P^* = 0 \quad | \quad N^* = \frac{m}{a})$

Case $P^* = 0$

$\frac{dN}{dt} = 0 \iff N^*(r_0 - aP^*) = 0 \iff N^* = 0$

Equilibrium: $(N^*, P^*) = (0, 0)$

Case $N^* = \frac{m}{a}$

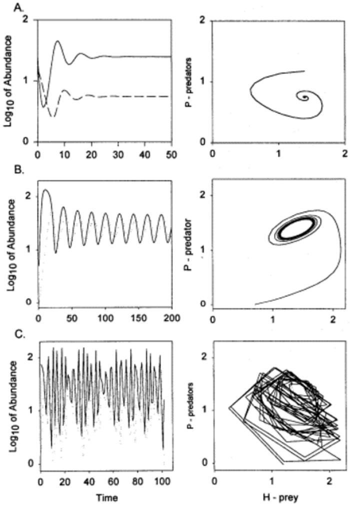
$\frac{dN}{dt} = 0 \iff N^*(r_0 - aP^*) = 0 \iff \frac{mr_0}{a} - mP^* = 0 \iff P* = \frac{r_0}{a}$

Equilibrium: $(N^*, P^*) = (\frac{m}{a}, \frac{r_0}{a})$

Feasibility: when calculate equilibrium, check conditions of intervals

Model analysis in BEE (2)

Type of equilibria (here predator-prey system)



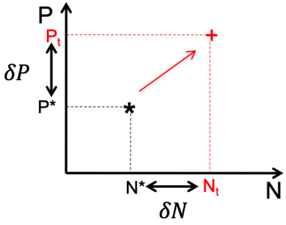
Model analysis in BEE (2)

2. Local stability analysis (little perturbation): the Jacobian matrix

System : $\begin{cases} f(N,P) \\ g(N,P) \end{cases}$

Linear approximation (first order Taylor expansion)

$$\begin{cases} f(N^* + \delta N, P^* + \delta P) = f(N^*, P^*) + \delta N \left.\dfrac{\partial f}{\partial N}\right|_{N^*,P^*} + \delta P \left.\dfrac{\partial f}{\partial P}\right|_{N^*,P^*} \\ g(N^* + \delta N, P^* + \delta P) = g(N^*, P^*) + \delta N \left.\dfrac{\partial g}{\partial N}\right|_{N^*,P^*} + \delta P \left.\dfrac{\partial g}{\partial P}\right|_{N^*,P^*} \end{cases}$$



$$\begin{cases} N_t = N^* + \delta N \\ P_t = P^* + \delta P \end{cases}$$

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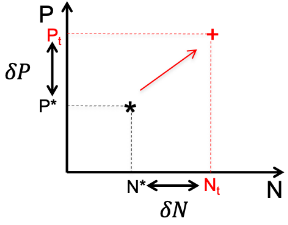

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Matricial formulation

$$\begin{pmatrix} \dfrac{dN_t}{dt} \\ \dfrac{dP_t}{dt} \end{pmatrix} = \begin{pmatrix} \left.\dfrac{\partial f}{\partial N}\right|_{N^*,P^*} & \left.\dfrac{\partial f}{\partial P}\right|_{N^*,P^*} \\ \left.\dfrac{\partial g}{\partial N}\right|_{N^*,P^*} & \left.\dfrac{\partial g}{\partial P}\right|_{N^*,P^*} \end{pmatrix} \times \begin{pmatrix} \delta N \\ \delta P \end{pmatrix}$$

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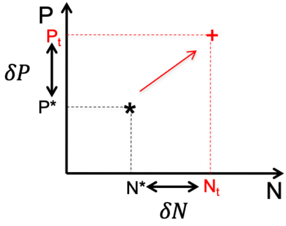

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Model analysis in BEE (2)

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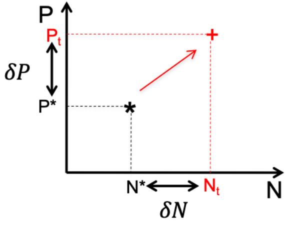

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Model analysis in BEE (2)

2. Local stability analysis (little perturbation): the Jacobian matrix

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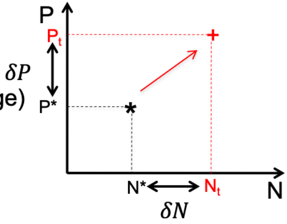

diagonalisation of the J matrix (coordinate system change)

$$\boldsymbol{v_t = C_1 U_1 e^{\lambda_1 t} + C_2 U_2 e^{\lambda_2 t}}$$

J's eigenvalues: $\boldsymbol{\lambda_1}$ and $\boldsymbol{\lambda_2}$
J's eigenvectors: $\boldsymbol{U_1}$ and $\boldsymbol{U_2}$

$$\begin{cases} N_t = N^* + \delta N \\ P_t = P^* + \delta P \end{cases}$$

Matricial formulation

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Model analysis in BEE (2)

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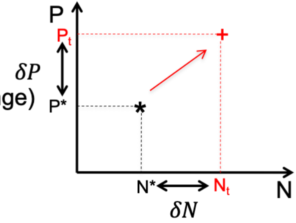

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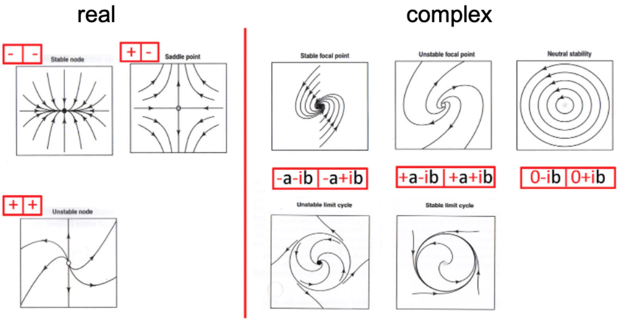
Asymptotical model behaviour

if $\lambda_1$and λ_2 real and negative $\lim_{t\to\infty} v_t = \lim_{t\to\infty} \binom{\delta N}{\delta P} = \vec{0}$ (N^*, P^*) stable

if $\lambda_1$and λ_2 complexe $v_t = e^{\mathcal{R}e(\lambda)t}[a_1 \cos(t\theta) + a_2 \sin(t\theta)]$ oscillations

Model analysis in BEE (2)

2. Local stability analysis (little perturbation): the Jacobian matrix



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Model analysis in BEE (2)

2. Local stability analysis (little perturbation): the eigenvalues

$$J = \begin{pmatrix} \left.\frac{\partial f}{\partial N}\right|_{N^*,P^*} & \left.\frac{\partial f}{\partial P}\right|_{N^*,P^*} \\ \left.\frac{\partial g}{\partial N}\right|_{N^*,P^*} & \left.\frac{\partial g}{\partial P}\right|_{N^*,P^*} \end{pmatrix}$$

Characteristic polynome: $|J - \lambda I| = 0$

Calculate the determinant to find the eigenvalues

Example with Lotka-Volterra model:

$$\begin{cases} \frac{dN}{dt} = r_0 N - aNP \\ \frac{dP}{dt} = -mP + eaNP \end{cases} \qquad \begin{cases} N^* = \frac{m}{a} \\ P^* = \frac{r_0}{a} \end{cases}$$

Model analysis in BEE (2)

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Model analysis in BEE (2)

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$$det \begin{pmatrix} -\lambda & -m \\ er_0 & -\lambda \end{pmatrix} \Leftrightarrow \lambda^2 + mer_0 = 0 \Leftrightarrow \lambda^2 = -mer_0 \Leftrightarrow \lambda = 0 \pm i\sqrt{mer_0}$$

Model analysis in BEE (2)

Same in R (et al.)

1. **Deriving equilibria**:

- software for symbolic calculus Maxima, Scilab, Matlab, Mathematica etc.
- what can be done in R: find the equilibium for a given set of parameters

```
library(rootSolve)
```

```
EvalEq = function(t,y,pars) {
    with(as.list(c(y,pars)), {
    dN1 = N1*(r1+(a_11*N1+a_12*N2))
    dN2 = N2*(r2+(a_22*N2+a_21*N1))
        list(c(dN1,dN2),0)
    })
}
```

```
p = c(r1=0.1,r2=0.2,a_11=-1,a_22=-1,a_12=-0.5,a_21=0.4)
Eq = stode(y = c(N1=2,N2=3),func= EvalEq,parms=p,positive = TRUE)[[1]]
Eq
```

```
##           N1           N2
## 7.244083e-05 2.000290e-01
```

Model analysis in BEE (2)

Same in R (et al.)

2. **Local stability analysis**

- the Jacobian matrix and eigenvalues can be evaluated for a parameter set

```
jac = function(t,y,pars) {
    with(as.list(c(y,pars)), {
    dN1 = N1*(r1+(a_11*N1+a_12*N2))
    dN2 = N2*(r2+(a_22*N2+a_21*N1))
        list(dN1,dN2)
    })
}
```

```
J = jacobian.full(y=Eq,func=jac,parms=p)
eigens = eigen(J)$values
lmax=max(Re(eigens))
lmax
```

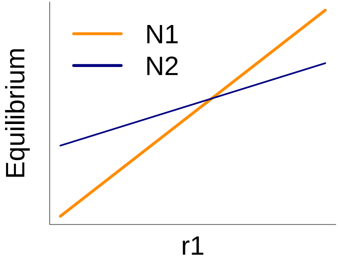
```
## [1] -0.0001738806
```

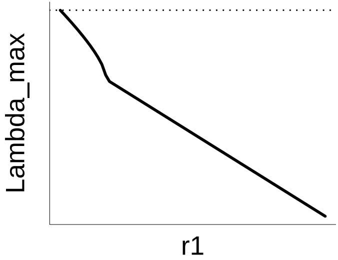
Model analysis in BEE (2)

Same in R (et al.)

2. **Local stability analysis**

```
r1s = seq(0.1,0.8,by=0.01);
tab = matrix(NA,ncol=4,nrow=length(r1s),dimnames=list(NULL,c("r1","N1","N2","lmax")))
i=1
for(i in 1:length(r1s)){
  p["r1"] = r1s[i]
 Eq = stode(y = c(N1=2,N2=3),func= EvalEq,parms=p,positive = TRUE)[[1]]
 J = jacobian.full(y=Eq,func=jac,parms=p)
 tab[i,"r1"] = r1s[i]
 tab[i,"N1"] = Eq[1]
 tab[i,"N2"] = Eq[2]
 tab[i,"lmax"] = max(Re(eigen(J)$values))
}
```





Model analysis in BEE (3)

Numerical integration

Cases where it is not possible to get $N(t) = f(t)$

Principle

- We know the initial state of the system $f(t_0)$: (N_0, P_0)
- We know the derivative relative to time $\frac{df}{dt}$
- Then we can approximate the state of the system at the time $t_0 + \delta t$
- And we can reiterate the operation to trace the dynamics until T_{max}

Model analysis in BEE (3)

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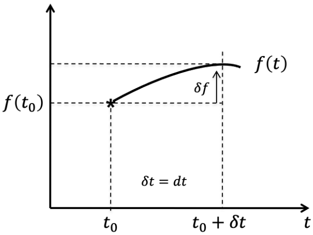
- Euler method



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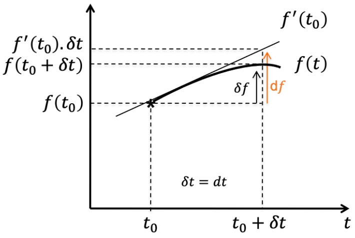
- And we can reiterate the operation to trace the dynamics until T_{max}

- Euler method

Linear approximation (Taylor limited expansion):

$$\tilde{f}(t) = f(t_0 + \delta t) = f(t_0) + f'(t_0).\delta t + \varepsilon$$

if δt is small $\delta f \approx \left(\frac{df}{dt}\right)_{t_0} dt$



Model analysis in BEE (3)

Numerical integration in R

1. **"By hand"**

```
logistic_deriv = function(N,r0,K){c(N=r0*N*(1-N/K))}              #--- Derivative
euler = function(N,r0,K,dt){return(N+dt*logistic_deriv(N,r0,K))} #--- Euler

dyn_euler = function(N0,tmin,tmax,dt,r0,K){                       #--- Iteration
    n=matrix(c(t=tmin,N=N0),1,2)
    for(t in 1:tmax) n=rbind(n,c(t=n[t,1]+dt,euler(N=n[t,2],r0=r0,K=K,dt=dt)))
    return(n)
}
dt = 2; tmax = 80
dyn = dyn_euler(N0=1,tmin=0, tmax=tmax/dt,dt=dt,r0=0.1,K=10)
```

Model analysis in BEE (3)

Numerical integration in R

1. **"By hand"**

```
logistic_deriv = function(N,r0,K){c(N=r0*N*(1-N/K))}              #--- Derivative
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    return(n)
}
dt = 2; tmax = 80
dyn = dyn_euler(N0=1,tmin=0, tmax=tmax/dt,dt=dt,r0=0.1,K=10)
```
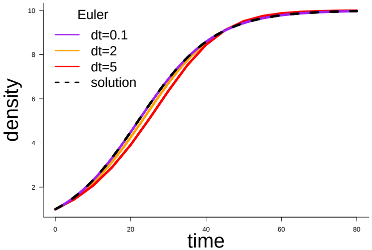
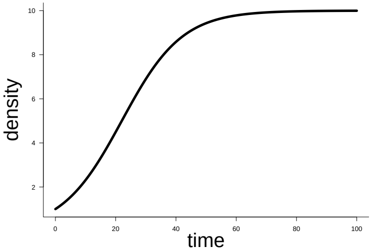



Model analysis in BEE (3)

Numerical integration in R

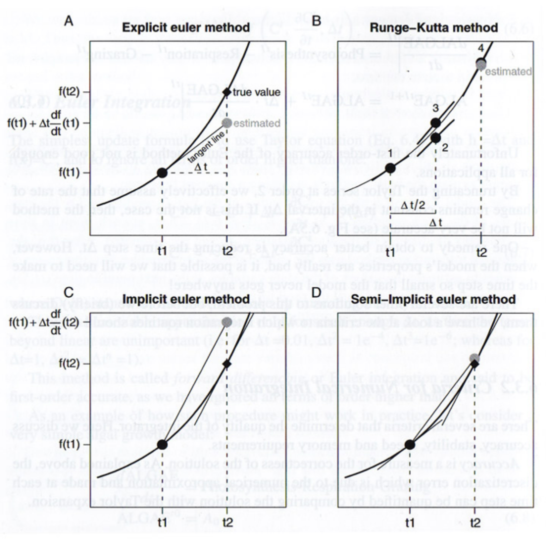
2. **deSolve package**

```
library(deSolve)
logistic_deriv2 = function(t,y,pars) {
    with(as.list(c(y,pars)), {
    dN = r0*N*(1-N/K)
        list(c(dN))
    })}
par(mar=c(7,7,1,2))
dyn=ode(y=c(N=1),times=seq(0,100,0.1),func=logistic_deriv2,parms=c(r0=0.1,K=10),method="euler")
plot(dyn[,"time"],dyn[,"N"],type="l",bty="l",xlab="time",ylab="density",las=1,lwd=6,cex.lab=3)
```



Model analysis in BEE (3)

Other methods than Euler exist

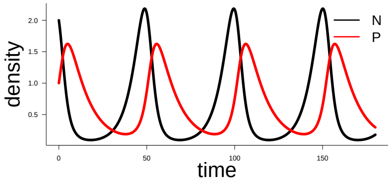


Model analysis in BEE (3)

Numerical integration in R

2. **deSolve package**

```
library(deSolve)
lotka_Volterra_deriv = function(t,y,pars) {
    with(as.list(c(y,pars)), {
    dN = r0*N-a*N*P
    dP = e*a*N*P -m*P
        list(c(dN,dP))
    })}
par(mar=c(7,7,1,2))
dynLV=ode(y=c(N=2,P=1),times=seq(0,180,0.1),func=lotka_Volterra_deriv,
        parms=c(r0=0.2,a=0.3,e=0.5,m=0.1),method="rk4")
plot(dynLV[,"time"],dynLV[,"N"],type="l",bty="l",xlab="time",ylab="density",las=1,lwd=6,cex.lab=
lines(dynLV[,"time"],dynLV[,"P"],lwd=6,col="red")
legend("topright",col = c("black","red"),legend=c("N","P"),cex=2,bty="n",lty=1,lwd=3)
```

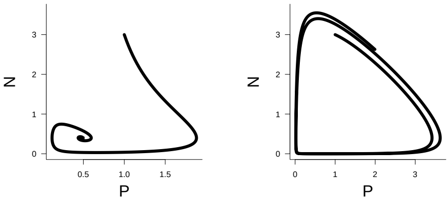


Model analysis in BEE (3)

Numerical analyses Rosenzweig and McArthur model (1963)

Phase plan

```
LVK_deriv = function(t,y,pars) {
    with(as.list(c(y,pars)), {
    dN = r0*N*(1-N/K)-a*N*P/(1+h*N)
    dP = a*N*P/(1+h*N) -m*P
        list(c(dN,dP))
    })}
dynLVk1=ode(y=c(N=3,P=1),times=seq(0,180,0.1),func=LVK_deriv,parms=c(r0=0.2,K=1,a=0.3,e=0.5,m=0.1,h=0.5),method="rk4")
dynLVk5=ode(y=c(N=3,P=1),times=seq(0,180,0.1),func=LVK_deriv,parms=c(r0=0.2,K=5,a=0.3,e=0.5,m=0.1,h=0.5),method="rk4")

layout(matrix(1:2,ncol=2)); par(mar=c(7,7,2,2))
ylims = range(cbind(dynLVk1[,2:3],dynLVk5[,2:3]))

plot(dynLVk1[,"P"],dynLVk1[,"N"],type="l",bty="l",xlab="P",ylab="N",las=1,lwd=6,cex.lab=2,ylim=ylims)
plot(dynLVk5[,"P"],dynLVk5[,"N"],type="l",bty="l",xlab="P",ylab="N",las=1,lwd=6,cex.lab=2,ylim=ylims)
```

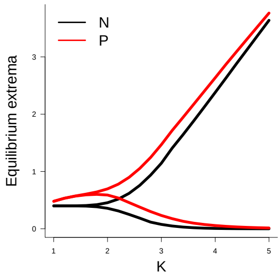


Model analysis in BEE (3)

Numerical analyses Rosenzweig and McArthur model (1963)

Parameter variation

```
ks = seq(1,5,by=0.2); ts = seq(0,500,0.1); tm = length(ts); colos = c("black","black","red","red")
mat = matrix(NA,ncol=5,nrow=length(ks),dimnames=list(NULL,c("K","Nmin","Nmax","Pmin","Pmax")))
for(i in 1:length(ks)){
  dyn=ode(y=c(N=3,P=1),times=ts,func=LVK_deriv,parms=c(r0=0.2,K=ks[i],a=0.3,e=0.5,m=0.1,h=0.5),method="rk4")
  mat[i,] = c(ks[i],range(dyn[(tm-100/0.1):tm,"N"]),range(dyn[(tm-100/0.1):tm,"P"]))
}
layout(1); par(mar=c(7,7,2,2))
plot(mat[,"K"],mat[,"Nmin"],type="l",bty="l",xlab="K",ylab="Equilibrium extrema",las=1,lwd=6,cex.lab=2,ylim=range(mat[,2:5]))
for(i in 3:5)lines(mat[,"K"],mat[,i],lwd=6,col=colos[i-1])
legend("topleft",col = c("black","red"),legend=c("N","P"),cex=2,bty="n",lty=1,lwd=3)
```



Model analysis in BEE

Miscellanous

test asymptotic state

- Compare temporal means on 2 windows
- Fit a linear regression: asymptotic state reached when slope $= 0$

multistability

- Equilibrium sensitive to initial conditions
- Bootstrap initial conditions to find multiple equilibria (if no analytical derivation)

sensitivity analysis

Test the sensitivity of the results to certain parameters by moving each parameter by 10 % and measuring the effect size of the system's response

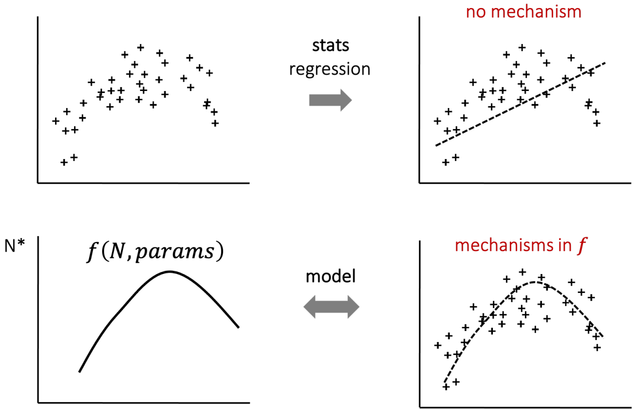
Section 4

Linking models and data

Linking models and data

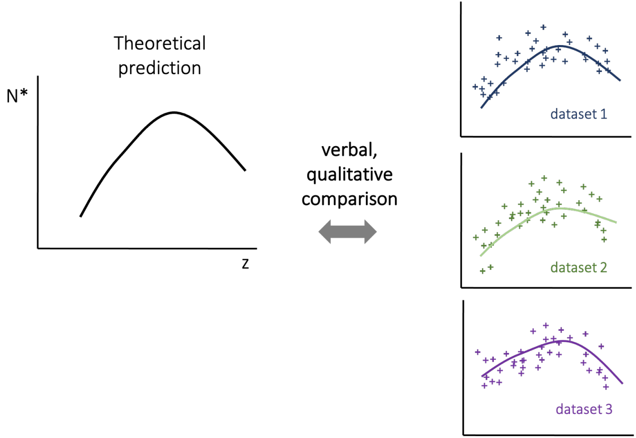
Different approaches for different goals

1. Comparing model predictions with data verbally, qualitatively, to test theory
2. Comparing data to parameterized model predictions qualitatively or quantitatively
3. Model fitting to estimate parameters using data
4. One word on Approximate Bayesian Computing



Linking models and data (1)

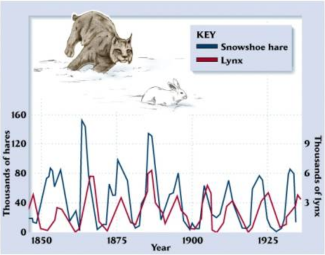
Comparing model predictions with data verbally, qualitatively

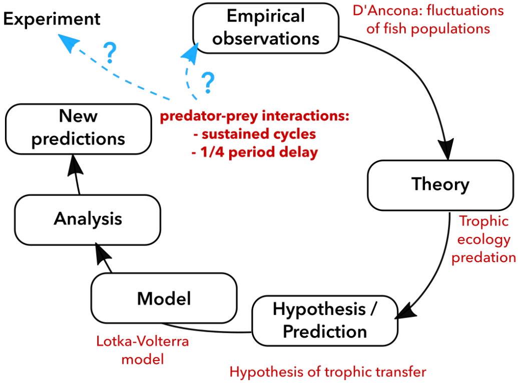


- Statistical analysis / representation of data + qualitative comparison
- Repeated observations on different systems, locations, species, etc. to validate or unvalidate the theory (the easier to falsify, the better)

Linking models and data (1)

Comparing model predictions with data verbally, qualitatively

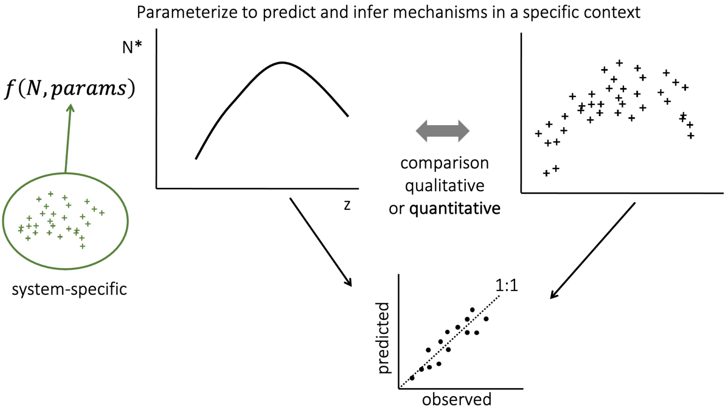




back

Linking models and data (2)

Comparing data to parameterized model qualitatively or quantitatively

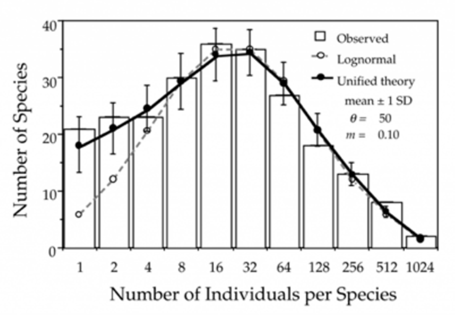


- Aim: determine if a theoretical prediction applies to a specific system
- Parameterization with a subset of the data or other data from the system
- Compare observed data and predictions the models give for this system

Linking models and data (2)

Comparing data to parametrized model qualitatively

Hubbel's neutral model (2001)



Tropical forest, Barro Colorado Island, Panama

back

Linking models and data (2)

Comparing data to parameterized model predictions quantitatively

Parameterization

Problems in community models:

- Number of parameters render models difficult to explore fully
- Need to constrain the parameter space to biologically relevant values
- Measurement of parameters:
  - time consuming (e.g., interaction strength)
  - scale of individuals

Generalized Lotka-Volterra model: $\frac{dN_i}{dt} = N_i(r_i + \sum_j a_{ij} N_j)$

```
- 1 species => 2 parameters
- 2 species => 6 parameters
- 3 species => 12 parameters etc.
```

Using allometric scaling laws

Individual body mass scale with population levels biological parameters.
Yodzis and Innes 1992, Metabolic theory of ecology (Brown et al. 2004)

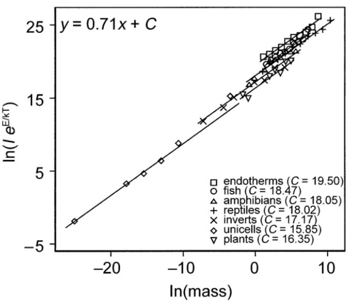
Linking models and data (2)

From Metabolic theory of ecology MTE to Allometric Trophic Model

*Use of body mass M to parameterize **biological rates** and trophic interactions*

Individual Metabolic rate I

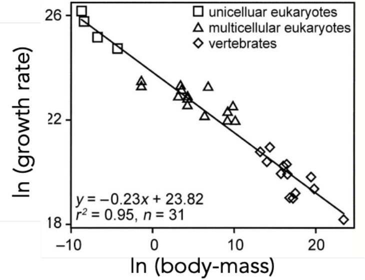
$log(I) = \frac{3}{4} log(M) + log(I_0)$; $I \propto M^{\frac{3}{4}}$



(Brown et al 2004 Ecology)

Population growth rate r

$log(r) = -\frac{1}{4} \times log(M) + c$; $r \propto M^{-\frac{1}{4}}$



(Brown et al 2004 Ecology)

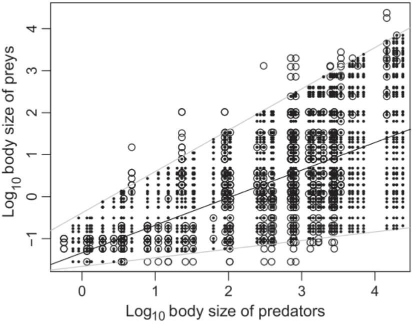
ATM refs: Yodzis & Innes 1992, Brose et al 2006, Berlow et al 2009, Schneider et al 2016, Binzer et al 2016, Delmas et al 2017, Rpackage ATNr (Gauzens & Perti)

Linking models and data (2)

From Metabolic theory of ecology MTE to Allometric Trophic Model

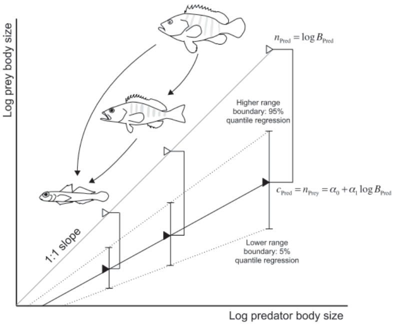
Use of body mass M to parameterize biological rates and ***trophic interactions***

Predator-prey body size relationship



(data from Brose et al. 2005)

Species niche based on body size

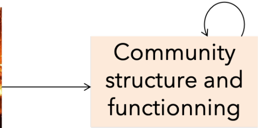


(Gravel et al 2013 MEE)

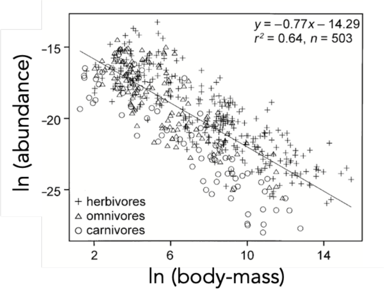
Linking models and data (2)

Comparing data to parameterized model predictions quantitatively

How do disturbance frequency and intensity impact size-abundance relation?



Claire Jacquet



(Brown et al 2004)

Linking models and data (2)

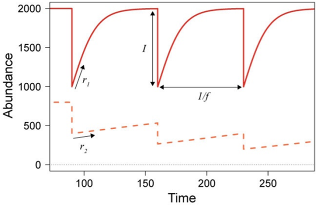
Comparing data to parameterized model predictions quantitatively

How do disturbance frequency and intensity impact size-abundance relation?

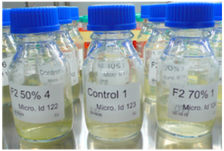
Community structure and functionning

Claire Jacquet

Model



Experiment



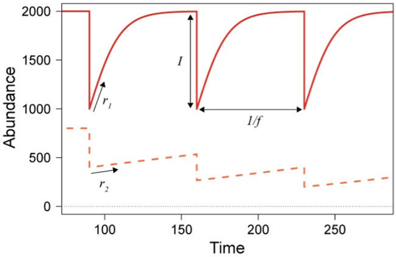
(Jacquet et al 2020 Ecology Letters)

Linking models and data (2)

Comparing data to parameterized model predictions quantitatively

How do disturbance frequency and intensity impact size-abundance relation?

The model: model of multiple populations



$$N_i^* = K_i(\frac{-log(1-I)}{r_i T} + 1)$$

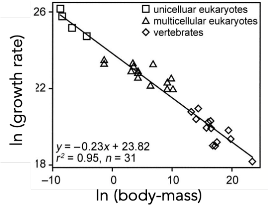
- Logistic growth : $\frac{dN_i}{dt} = r_i N_i(1 - \frac{N_i}{K_i})$
  - r_i growth rate of population i
  - K_i carrying capacity of population i
  - Assumption: dominant effect of intraspecific competition
- Disturbances : $N_{i,D^+} = N_{i,D^-} \times (1 - I)$
  - I disturbance intensity
  - f disturbance frequency
  - T disturbance period

Linking models and data (2)

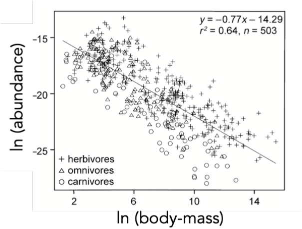
Comparing data to parameterized model predictions quantitatively

How do disturbance frequency and intensity impact size-abundance relation?

The model: model of multiple populations **with allometric scaling**



$$log(r_i) = -0.25 log(M_i) + b_r$$



$$log(K_i) = -0.75 log(M_i) + b_K$$

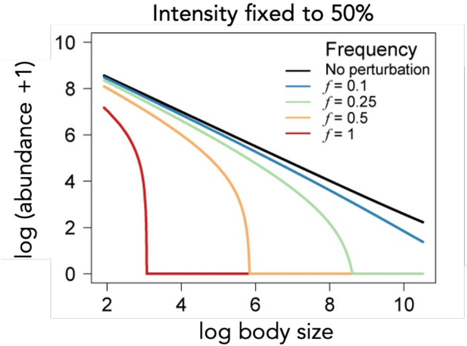
Mean population abundance:

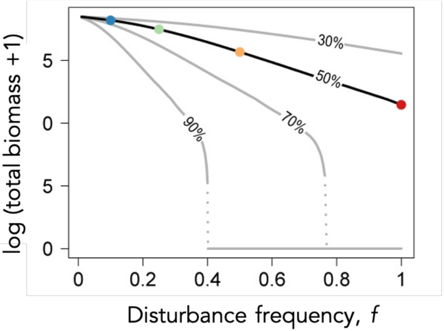
$$N_i^* = K_i(\frac{-log(1-I)}{r_i T} + 1) \Rightarrow log(N_i^*) = -0.75 log(M_i) + b_K + log(\frac{log(1-I)}{Te^{-0.25 log(M_i) + b_r}} + 1)$$

Mean community biomass at equilibrium: $B_i = \sum_i M_i \times N_i^*$

Linking models and data (2)

Model Predictions

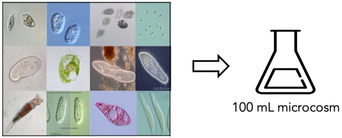




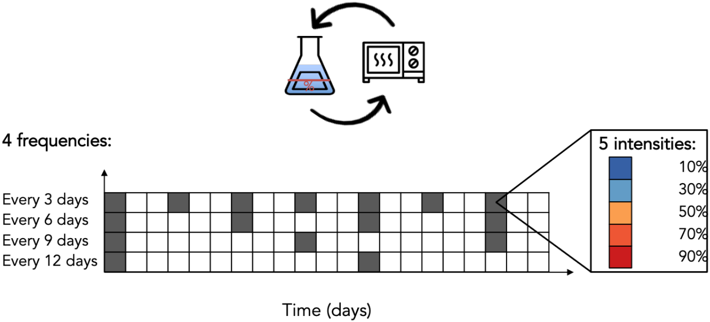
- Large species proportionally more impacted by disturbances
- Community biomass decrease linearly with disturbance frequency

Linking models and data (2)

The experiment

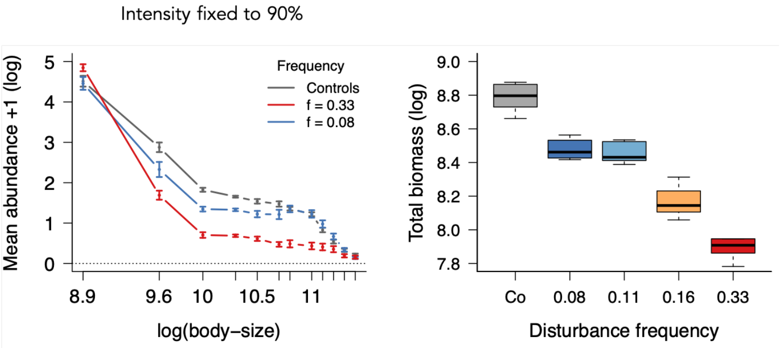


- 13 species with body sizes $\in [10\mu m, 1mm]$
- 6 replicate per treatment + 8 controls
- daily measurements during 21 days (density, size)



Linking models and data (2)

Experimental data - results



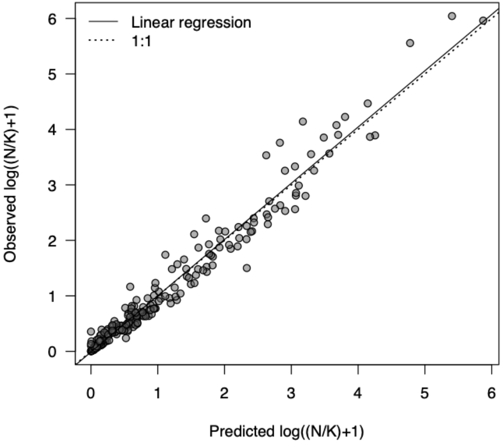
Qualitatively, this looks good: - mean abundances decreases with disturbance frequency, and impact more larger species - Community biomass decrease linearly with disturbance frequency

Linking models and data (2)

How much is the model right?

Parameterization

- K = equilibria in controls
- allometric relationship: $log(r) = -0.37 log(M) + 3.75$ $\{(R^2 = 0.47, P = 0.005)\}$

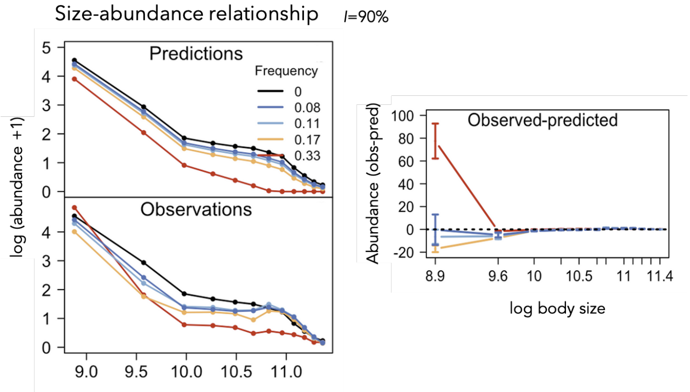


$y = 1.01x - 0.01$
$(R^2 = 0.96, P < 0.001)$

(All size classes and disturbance regimes together ($n = 240$))

Linking models and data (2)

How much is the model wrong?

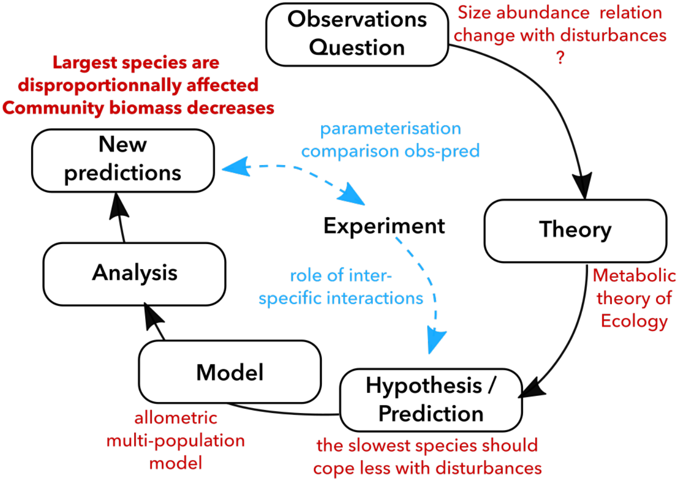


- The model does not predict well the responses of small species
- Interpretation: disturbance-induced interaction release

=> put inter-specific interactions in the model

Linking models and data (2)

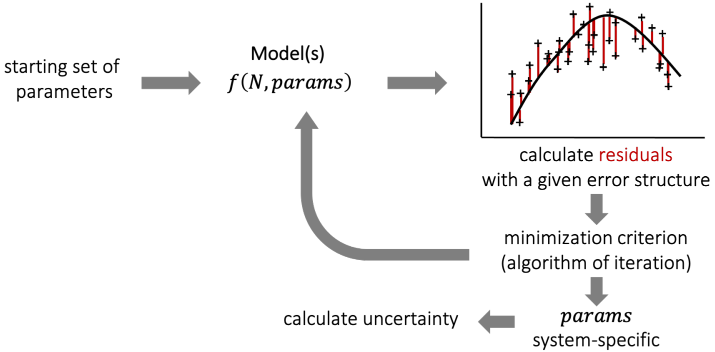
Comparing data to parameterized model predictions quantitatively



back

Linking models and data (3)

Model fitting to estimate parameters using data



- Goal:Estimate parameters in a system assuming a set of mechanisms (models)
- Residuals: choose the error structure
- Minimization criterium for optimization
- Optimization algorithm (e.g., Levenberg-Marquardt routine in minpack.lm)
- Uncertainty:estimate parameter CI (different methods)

Linking models and data (3)

Model fitting to estimate parameters using data in R

Exemple provided by Malcom Haddon's: https://haddonm.github.io/URMQMF/

Classical criteria of best fit to minimize

- Sum of squared residuals ssq()
- Negative log-likelihood or maximizing the product of all likelihoods
- Bayesian method using prior probabilities (most likely parameters)

- Least square residuals:
  $SSQ = \sum_{i=1}^{n} (x_i - \hat{x}_i)^2$
  - x_i the observation
  - $\hat{x}_i$ the prediction

- Product of all Likelihood:
  $L = \prod_{i=1}^{n} L(x_i|\theta)$
  with $L(x_i|\theta)$, the likelihood (probability density) of a data x_i being observed given (1) model, (2) a set of parameters θ, (3) an expected probability distribution of the residuals
- Negative log-likelihood:
  $-negLL = -\sum_{i=1}^{n} log(L(x_i|\theta))$

Linking models and data (3)

Model fitting to estimate parameters using data in R

Exemple provided by Malcom Haddon's: https://haddonm.github.io/URMQMF/

Classical criteria of best fit to minimize

- Sum of squared residuals ssq()
- Negative log-likelihood or maximizing the product of all likelihoods
- Bayesian method using prior probabilities (most likely parameters)

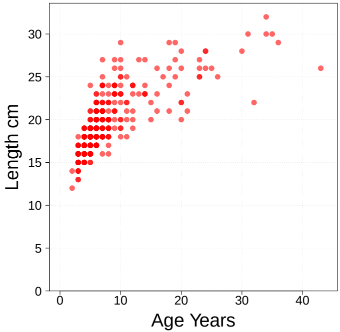
- Posterior probability given data x and parameter set θ: $P(\theta|x) = \frac{L(x|\theta)P(\theta)}{\sum_{i=1}^{n}[L(x_i|\theta)P(\theta)])}$
  - $P(\theta)$ Prior probability of θ, which is updated by the likelihood of the data:
  - $PL(x|\theta)$ Likelihood of x knowing θ
  - $L(x_i|\theta)P(\theta)$ normalizing term so that $\sum(P(\theta|x) = 1)$

- LL: choose the parameters that gives the best likelihood of observing the data we observe for a given model (frequentist approach)
- Bayesian: gives the probability of θ being the parameter set producing the data

Linking models and data (3)

R example: fitting models to length-at-age fish data with SSQ

```
library(MQMF)
data(LatA)
```



Modeling framework of the form: $L_t = \hat{L}_t + \varepsilon$

- L_t the data
- $\hat{L}_t$ the expected or predicted length at age t
- ε normal random deviate ($\in \mathcal{N}(0, \sigma^2)$)

For $\hat{L}_t$, we think of 3 alternative non linear models of growth

- **Bertalanffy model** (1938): $\hat{L}_t = L_{max}(1 - e^{-r(t-t_0)})$
- **Gompertz model**(1925):$ae^{-be^{ct}}$
- **Generalized Michaelis-Menton model**: $\frac{R_0 t}{b+t^c}$

Parameters of Bertalanffy model:

- r: the growth rate coefficient
- L_{max}: the average maximum length
- t_0: the hypothetical age at which $L = 0$

Linking models and data (3)

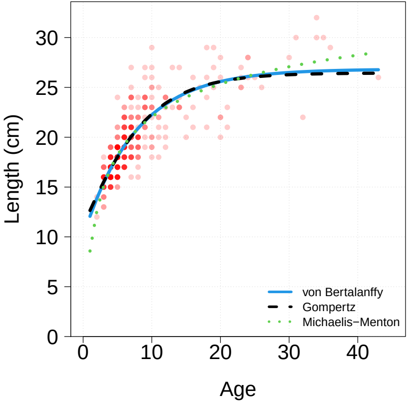
R example: fitting models to length-at-age fish data with SSQ

```r
library(MQMF)
#--- Models
vB = function(p, ages) return(p[1]*(1-exp(-p[2]*(ages-p[3]))))
Gz = function(p, ages) return(p[1]*exp(-p[2]*exp(p[3]*ages)))
MM = function(p, ages) return((p[1]*ages)/(p[2] + ages^p[3]))

#--- Optimiaztion criterium SSQ
ssq <- function(funk,observed,...) {
  predval <- funk(...)
  return(sum((observed - predval)^2,na.rm=TRUE))
}
#--- guess starting values
pars <- c("Linf"=27.0,"K"=0.15,"t0"=-2.0)

#--- run the optimization
bestvB <- nlm(f=ssq,funk=vB,observed=LatA$length,p=pars,ages=LatA$age,typsize=magnitude(pars))

#--- compute the prediction
ages <- 1:max(LatA$age) # used in comparisons
predvB <- vB(bestvB$estimate,ages)

#--- show optimization result
outfit(bestvB,backtran=FALSE,title="vB"); cat("\n")
```

```
## nlm solution:  vB
## minimum     :  1361.421
## iterations  :  24
## code        :  2 >1 iterates in tolerance, probably solution
##          par      gradient
## 1 26.8353971 -1.133576e-04
## 2  0.1301587 -6.192980e-03
## 3 -3.5866989  8.323513e-05
```

Linking models and data (3)

R example: fitting models to length-at-age fish data with SSQ



Model selection

- SSQ => Michaelis Menton
- Gradient (fit quality) => Gompertz
- Aikake's Information criterium (AIC) accounts for the number of parameters: $AIC = Nlog(\hat{s}^2) + 2p$ with:
  - N the number of observations
  - $\hat{s}^2 = \frac{\sum \varepsilon^2}{N} = \frac{SSQ}{N}$ the maxLL of variance
  - p the number of independently adjusted parameters

In our case AIC is not discriminant because the models have the same number of parameters.

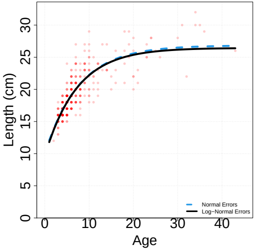
Linking models and data (3)

Influence of the residual error choice on model fit

What about using log-normal deviates instead of normal random deviates?

We simply need to log transform data:
$SSQ = \sum_{i=1}^{n} (log(Obs_i) - log(Pred_i))^2$

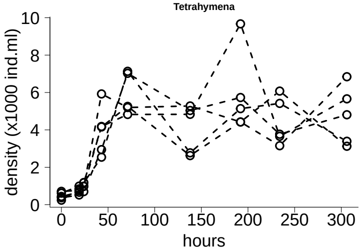
Let's do it for the von Bertalanffy's model; we obtain:




```
## nlm solution:  Normal errors
## minimum      :  1361.421
## iterations   :  22
## code         :  1 gradient close to 0, probably solution
##          par      gradient
## 1 26.8353990 -3.650549e-07
## 2  0.1301587 -1.576574e-05
## 3 -3.5867005  3.210883e-07

## nlm solution:  Log-Normal errors
## minimum      :  3.153052
## iterations   :  25
## code         :  1 gradient close to 0, probably solution
##          par      gradient
## 1 26.4409587  8.903296e-08
```

Linking models and data (3)

R example 2: fitting growth curve with SSQ in minpack.lm



We want to fit the data with the logistic growth model: $\frac{dN}{dt} = N(r_0 - \alpha N)$ in R.

We need:

- the model, to simulate the data
- a function to calculate obs-pred distance
- an algorithm of fit, here in minpack.lm

```
library(deSolve)
library(minpack.lm)

LogGrowth = function(time,y,parms){
  with(as.list(c(y,parms)), {
    dN = (r0 - alpha*N) * N
    list(c(dN))
  })
}

resids_LogG <- function(parms){
  cinit=c(N=sub[1,"Tet"])
  output = ode(y=cinit, times=as.numeric(sub$time_diff), func=LogGrowth, parms=parms)
  return(output[,"N"]-c(sub[,"Tet"]))
}
```

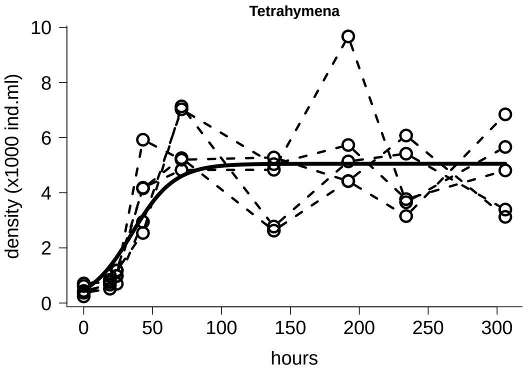
Linking models and data (3)

R example 2: fitting growth curve with SSQ in minpack.lm

```
fitval=nls.lm(par=c(r0=0.08,alpha=0.00001),fn=resids_LogG,
              control=list(maxiter=1000), lower=c(r0=0, alpha=0))
fitval$par
```

```
##           r0        alpha
## 6.463356e-02 1.279623e-05
```

```
fitted_output <- ode(y=yinit, times=c(0:max(xtime)), LogGrowth, fitval$par)
```



Linking models and data (3)

Maximum Likelihood

Aim: search for the model parameter set that maximizes the total likelihood of the observations.

- Specify likelihood of each observation $-negLL = -\sum_{i=1}^{n} log(L(x_i|\theta))$
- The structure of errors need not to be normally distributed
- Model should include an estimate of the spread of parameter probability density (likelihood) σ for normal distribution)
- Using normally distributed residuals gives the same result as minimizing SSQ. NB

```
pars <- c(Linf=27.0,K=0.15,t0=-3.0,sigma=2.5) # starting values
ansvB <- nlm(f=negNLL,p=pars,funk=vB,observed=LatA$length,ages=ages,
             typsize=magnitude(pars))
```

- For some types of data (CPUE, catch, effort) observed data are skewed and it is relevant then to use Log-Normal distribution:

$$L(x_i|m_i, \sigma) = \frac{1}{x_i\sigma\sqrt{2\pi}} e^{\frac{-(log(x_i)-log(m_i))^2}{2\sigma^2}}$$

Linking models and data (3)

Example with Log-normal distribution of residuals

Beverton-Holt stock-recruitment relationship: $R_t = \frac{aB_t}{b+B_t} e^{N(0,\sigma^2)}$

- R_t the recruitment
- B_t the spawning stock biomass
- a asymptotic recruitment level
- b the spawning stock biomass that gives rise to 50% of the maximum recruitment
- σ^2 the variance of the residuals' Log-Normal distribution, which is estimated when fitting the model to the data

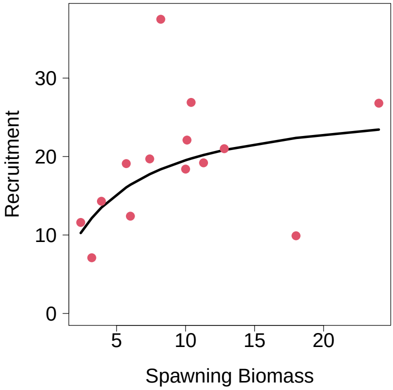
```
data(tigers)
lbh <- function(p,biom) return(log((p[1]*biom)/(p[2] + biom)))
pars <- c("a"=25,"b"=4.5,"sigma"=0.4)   # includes a sigma
best <- nlm(negNLL,pars,funk=lbh,observed=log(tigers$Recruit),biom=tigers$Spawn,typsize=magnituc
outfit(best,backtran=FALSE,title="Beverton-Holt Recruitment")
```

```
## nlm solution:  Beverton-Holt Recruitment
## minimum     :  5.244983
## iterations  :  16
## code        :  1 gradient close to 0, probably solution
##         par      gradient
## 1 27.344523 -5.102771e-08
## 2  4.000166  1.267822e-07
## 3  0.351939  1.781712e-06
```

Linking models and data (3)

Example with Log-normal distribution of residuals

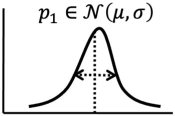
Beverton-Holt stock-recruitment relationship: $R_t = \frac{aB_t}{b+B_t} e^{N(0,\sigma^2)}$

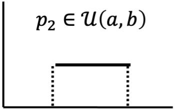


Linking models and data (4)

Bayesian approach: using data knowledge to adjust model (ABC)

Prior distributions

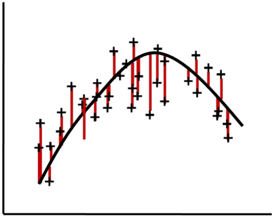




knowledge on parameters

Approximate Bayesian Computation

$f(N, params)$



calculate residuals

ABC

Threshold of rejection

$params$

system-specific