Theory-driven analysis of Ecological data

GDR-TheoMoDiv   FRB-CESAB

https://theodatasci.github.io/

Montpellier, 2023 – 04 – 03/07

Theory-driven analysis of Ecological data

Day 1: **intro to theoretical modeling** / S Kéfi, I Gounand, C Jacquet 8h30-17h30

Days 2-4: Thematic days: lectures (AM) / practica (PM) 9-17h

- Day 2: **Temporal series** and dynamics in ecology/ E Fronhofer and Jhelam Deshpande
- Day 3: **Spatial data**, macro-ecology and co-occurrences / V Calcagno and M Dubart
- Day 4: **Interaction networks**, trophic networks, and complexity in ecology / F Massol, M Barbier and C Jacquet

Day 5: **Group projects** the morning / present results early afternoon (end 16h)

Evening seminars at 18h-19h

Theory-driven analysis of Ecological data

Day 1: **Kim Cuddington** (Waterloo University, Canada): What are models for and can we use them more effectively?

Day 2: **Frédéric Barraquand** (CNRS, Bordeaux): Overcompensating models for common voles

Day 3: **Davide Martinetti** (INRAe Avignon) About opportunistic and citizen data, machine learning, and spatial models

Day 4: **Sonia Kéfi** (CNRS, Montpellier): The multiplexity of ecological communities

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TheoMoDive

Theory-driven analysis of Ecological data

8:30 – 8:45 General intro

8:45 – 10:00: Why theoretical models? Sonia Kéfi

10:00 – 10:15 Coffee break

10:15 – 12:30: What types of theoretical models? Isabelle Gounand

12:30 – 14:00 Lunch break

14: 00 - 15:00: speed dating

15:00 - 16:15: How to compare models and data? Claire Jacquet

16:15 - 16:30: Coffee break

16:30 - 17:30: Math reminder

17:30 – 18:00: break

18:00 – 19:00 : Seminar Kim Cuddington

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TheoMoDive

Types of dynamical models used in ecology and evolution

Content

1. Historical tips in ecological theory and modeling → different ways of seeing the world
2. Levels of biological organization and related questions
3. Different model formalisms
    - IBM versus differential equations models
    - Analytical versus simulation models
    - Discrete versus continuous and deterministic versus stochastic models
    - Spatial heterogeneity
    - Quantitative versus qualitative models

Isabelle Gounand

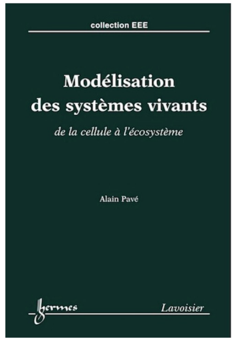
CESAB, Montpellier,
March 3, 2023

Acknowledgements

Content inspired from 2 courses on introduction to modeling by:

- Pr Nicolas Loeuille https://sites.google.com/site/nicolasloeuille/home?authuser=0
- Pr Jean-Christophe Poggiale https://people.mio.osupytheas.fr/~poggiale/

And a book by Pr Alain Pavé (2012)

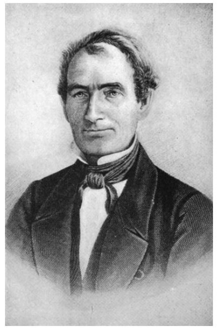


1. Historical tips in ecological theory and modeling

Medieval History

1202 Leonardo of Pisa (Fibonnaci): *Liber abaci* ("The book of calculation")

Modern History

1792 Malthus: exponential model (human demography)
1828 Gompertz model (model of mortality rate)
1844 Verhulst: logistic model

1853 1st International conference of statistics
1865-66 Mendel's work: "Experiments on Plant hybridization"
1880-1900 Linear regression, correlations, Markov and ramification processes (Galton-Watson)

"The half-century of enlightenment"

1910 Principle of Hardy-Weinberg → Population genetics
1917 D'Arcy Thompson: Allometric relationships (shape and growth rate)
1920's Fisher: "The Correlation between relatives on the supposition of Mendelian Inheritance" (1918), "The Genetical theory of natural selection" (1930). Statistics, experimental design, Fisher KPP reaction-diffusion model

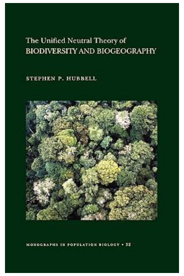
1930's Lotka, Volterra, Kostitzin, Teissier: The golden age of theoretical ecology – Non linearity of biological phenomena.
Population genetics and evolution: Fisher, Haldane, Wright, Teissier, L'Héritier
1941 Monod model: bacterial population growth
1947 Weiner: Cybernetics

from Pavé 2012

1. Historical tips in ecological theory and modeling

Contemporary History

1950-60	Compartment models
1960	Hutchinson: niche theory
1969	Levin's metapopulation model
1960-70	***First use of computers in biology: numerical calculus***
1970's	Kimura: Neutralist theory of evolution (1964 → Synthesis: 1983)
1972	May: unstability in population dynamics and communities
1975 ...	Multivariate analysis of data
1980 ...	Large data bases and associated algorithms
1980-2000	***Second age of informatic applications: databases, graphical application, bioinformatics***
1981	Oksanen: trophic chain models
1997	Chesson: theory of coexistence
2000	Williams and Martinez: Niche food web model
2001	Hubbel: Neutral theory of biodiversity



Integration of complexity

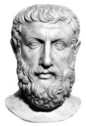
~2000 ...	Eco-evolutionary feedbacks (Henry and Kinnison 1999, Hairston et al. 2005, after Pimentel 1961)
2002	Sterner and Elser: Ecological stoichiometry
2003-4	Metacommunity (Leibold et al.) and Meta-ecosystem (Loreau et al.) models
2004	Metabolic Theory of Ecology (Brown et al. ; after Yodzis & Innes 1992)
2005	Brose et al.: Allometric trophic network model (then Berlow et al. 2009)
2008-Now	***Artificial Intelligence ... do we still need theory ?***
2016	Vellend: Theory of ecological communities

adated from Pavé 2012

1. Different ways of seeing the world

Unchanging cosmos

~VI-V th BC Parmenide



Heaven garden

1755 Carl Von Linne
Taxonomy

Thermodynamics of systems at equilibrium

Ecosystem ecology

1916 F. Clements
Climax super organism

1935 A. Tansley
Ecosystem

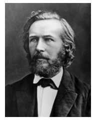
1953 E. Odum
Ecosystem: energy and material fluxes; equilibrium; homeostasy

1967 R. MacArthur & E. O. Wilson
Island biogeography; r-K strategy => ecosystem at equilibrium

1979 J. Lovelock
Gaïa hypothesis

1988 E. O. Wilson
Biodiversity

Ecosystem view
deterministic architecture, "cathedral"



1866 Ernst Haeckel
Ecology

Naturalists
Zoologists
Botanists
Biogeochemists

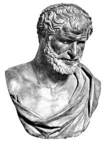
1920-1940: Lotka, Volterra, R. Fisher ...

Theoretical ecological

... 1970 ...
population biology and genetics

Quantitative biology
Biometry
Modeling

Synthesis ?

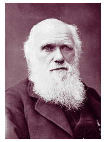


~ VI-V th BC Héraclite

changing and messy world

1802 J-B Lamarck: Transformism

1859 C Darwin: Evolution



Evolution

Thermodynamics of systems far from equilibrium

Evolutive ecology

1926 H A Gleason
Community: disordered set of individuals

1973 W. Drury & I. Nisbet
Succession: random mix of individuals

1977-8 J Connell et al
No cooperation no determinism no equilibrium

1985 S T A Pickett & P S White
The ecology of natural disturbances

1993 Allen et al. Chaos reduces specie extinctions

2001 S. Hubbel Neutral theory of biodiversity

Random ecological network view
flexible and changing architecture, "bazaar"

adapted from Pavé

1. Different ways of seeing the world

Ecology

Ecosystem and Landscape ecology

Biogeochemical cycles

flux of energy

transfers of matter and energy
among abiotic and biotic entities

Population and community ecology

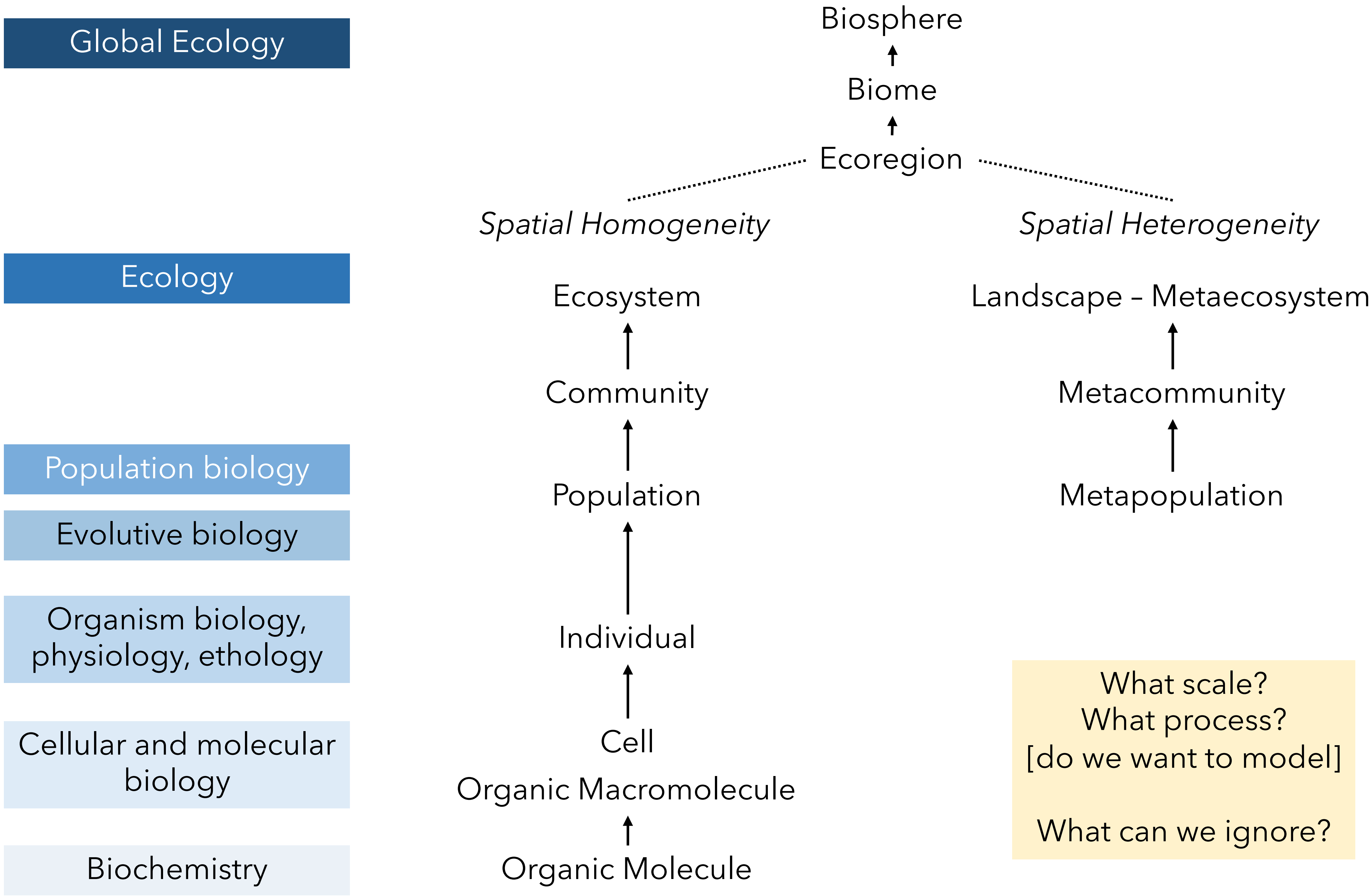
demographic processes

environmental forcing

Abiotic climatic conditions
physio-chemical properties
space
nutrients

Biotic prey
predators
competitors

from Poggiale's lecture 2012



Global Ecology
Ecology
Population biology
Evolutive biology
Organism biology, physiology, ethology
Cellular and molecular biology
Biochemistry
Biosphere
Biome
Ecoregion
Spatial Homogeneity
Spatial Heterogeneity
Ecosystem
Community
Population
Individual
Cell
Organic Macromolecule
Organic Molecule
Landscape – Metaecosystem
Metacommunity
Metapopulation
What scale?
What process?
[do we want to model]
What can we ignore?

2. Characterization of levels of organization and related questions

Individuals growth, fertility, mobility, behaviour, adaptation to the environment, genetics

• What are the factors that determine the rates of growth, development and reproduction of organisms?
• What are the causes of mortality? • How does behavior contribute to organism's adaptation to the environment?

Population density, age structure, body size distribution, genetic distribution

• What determines whether a population is growing or decreasing? • Why some populations are stable during several generation while others are exploding and crashing regularly? • What are the drivers of population extinction?

Community specific composition, richness, functional composition, community structure, niche overlap

• What determines if populations of different species can coexist? • Are the details of predator–prey relationships important? Who eats whom and how does it impact community dynamics?

Ecosystem biotope, communities, physical and chemical processes, biogeochemical cycles

• How chemical energy and elements are stored and flow in an ecosystem? • What is controling these flux? • How do energy and material flows affect the dynamics of the different populations that make up the ecosystem?

Metapopulation, metacommunity, metaecosystem landscape

landscape structure, species / individual spatial distribution, spatial heterogeneity of the environment

• How does spatial heterogeneity drive species coexistence, biodiversity and population synchrony? • How do spatial flow affect ecological dynamics and drive ecosystem response to disturbances? What are the drivers of spatial flows?

2. Characterization of levels of organization and related questions

This is neither the aim nor relevant to model all details

The upper level is slower than those below and impose constraints
Depending on the system and study question, the dynamics of other levels can be ignored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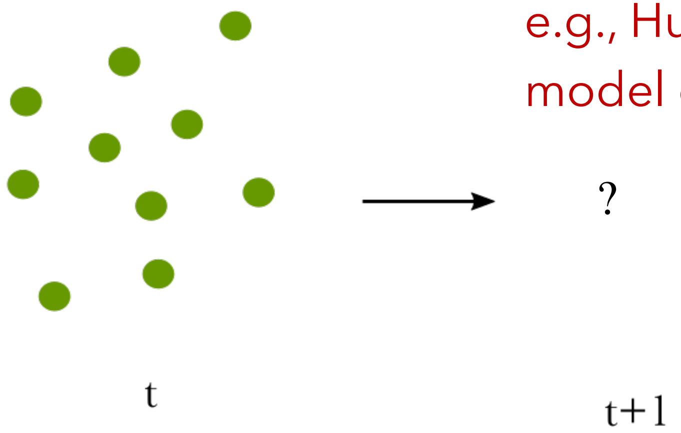
Some integrative views provide bridges between levels

- Ecological stœchiometry (Sterner and Elser 2002)
- Metabolic theory of ecology (Brown et al. 2004)

3. Different model formalisms

IBM
Individual-based Modeling



e.g., Hubbel's neutral model of biodiversity

- Variables are individuals
- Easier to represent processes with a series of rules
- the relations between variables emerge from elemental processes
- Computational comsuming
- Rarely tractable

Note that IBM's are a particular example of ABM : Agent base modeling, that can represent any level of organization. The specificity of ABM is that there is no math , only an algorithm (series of rules / events using probabilities)

DEs
DE Difference equations
ODE Ordinary Differential Equations
SDE Stochastic Differential Equations
PDE Partial Differential Equations...

$$\boxed{N_t} \xrightarrow[\frac{dN}{dt} = rN]{} \boxed{N_{t+dt}}$$

e.g., Verhulst's model

- Variables are population densities / biomasses
- Use of math for simplification => approximations
- Have large analysis power for extreme cases
- Fast computation
- Easier to fit to data
- The relations between variables are imposed: processes synthetized

3. Different model formalisms

Analytical versus simulation models → Parcimony provides analytical power

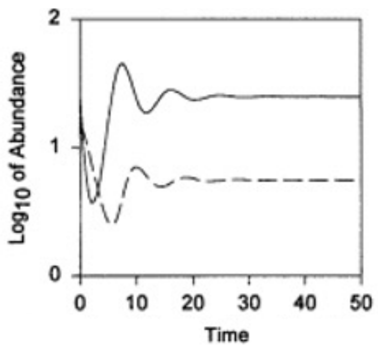
When the model has a solution:

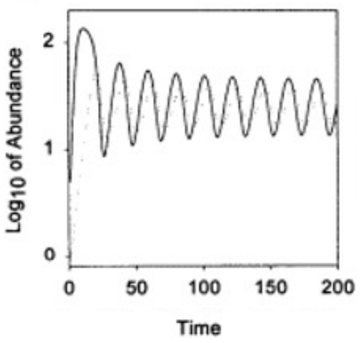
$$\frac{dN}{dt} = f(N) \rightarrow N = f(t)$$

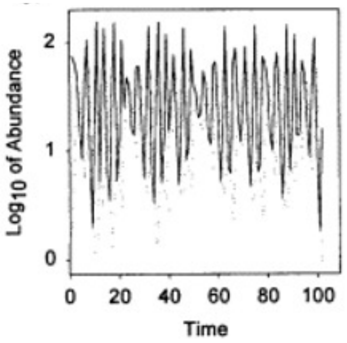
We know fully the behavior of the model

When the model is tractable:

You can describe model behaviour at equilibrium







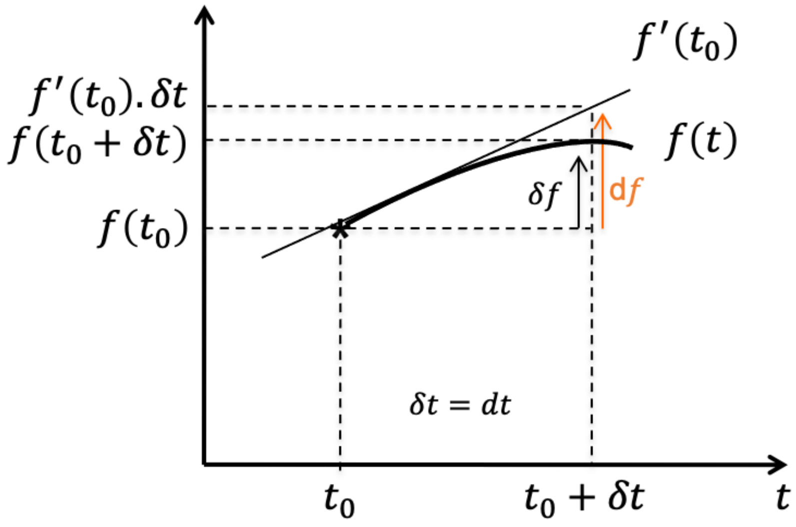
You can get read of the sensitivity to initial conditions and predict long term dynamics

When the model is untractable:

You need to run simulations;

→ numerical algorithm (IBM)

→ numerical integration (approximation)



Results are specific to your set of parameters and possibly initial conditions → run a lot of simulations

3. Different model formalisms

IBM
Individual-based Modeling

In which cases IBMs are particularly relevant?

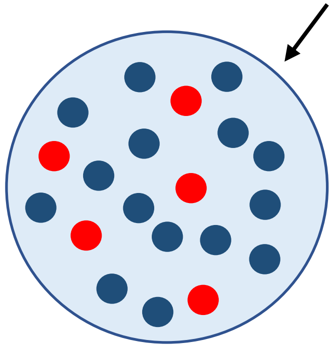
- when there are not too many parameters
- when stochastic processes are dominant
  - Neutrality: ecological drift
  - Genetic drift (small populations)
  - Allee effect
  - Demographic stochasticity

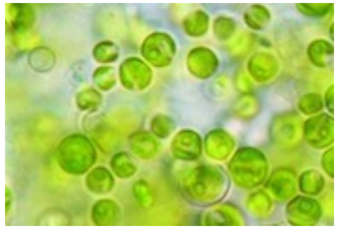
→ Questions of conservation
Viability of small populations

DEs
DE Difference equations
ODE Ordinary Differential Equations
SDE Stochastic Differential Equations
PDE Partial Differential Equations...

In which case DE's are particularly relevant?

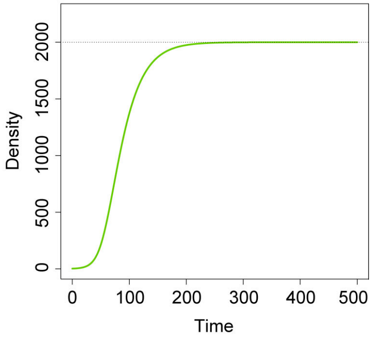
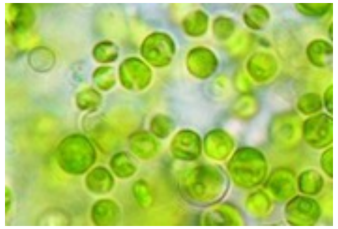
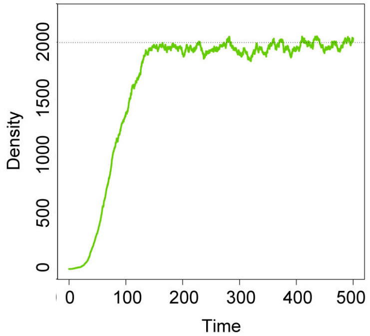
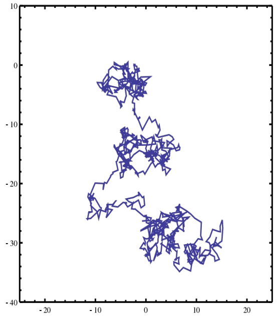
- when processes can be summarized with average parameters: mean growth rate, mass action
- For large populations





3. Different model formalisms

Discrete versus continuous time and stochastic versus determinitic models

	Deterministic processes can be summarized with average parameters	**Stochastic** random processes / inter individual variability are important
Continuous time processes happen continuously generations overlap	ODE: Verhulst's model $\frac{dN}{dt} = \mathrm{rN}(1-\frac{N}{K})$  	SDE: demographic noise, brownian motion  

+ State-transition model SIR (Kendrick and McCormick 1927)
Can be used in continuous or discrete time

Deterministic

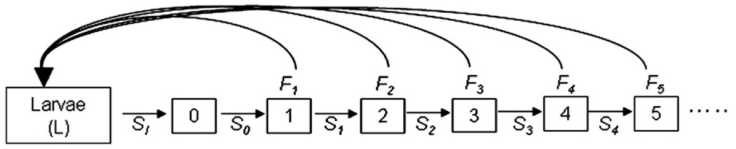
Discrete time

processes happen at specific times (e.g., seasons)
generations are synchronized

DE: Ricker's model

$$N_{t+1} = N_{t+1} e^{r_0(1-\frac{N_t}{K})}$$

Leslie Matrix projection model



(eelpout: Bergek et al. 2012)

- parameters at the scale of individuals
- predictions at the scale of population on growth (matrix analysis)
- relevant for questions where age, stage, or phenotype is at the center

Original model is deterministic (large populations) but stochastic versions exist

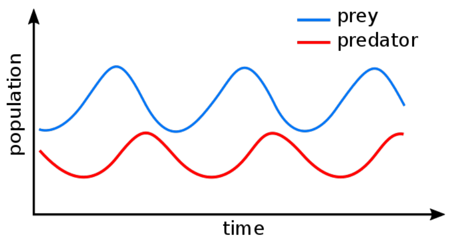
3. Different model formalisms

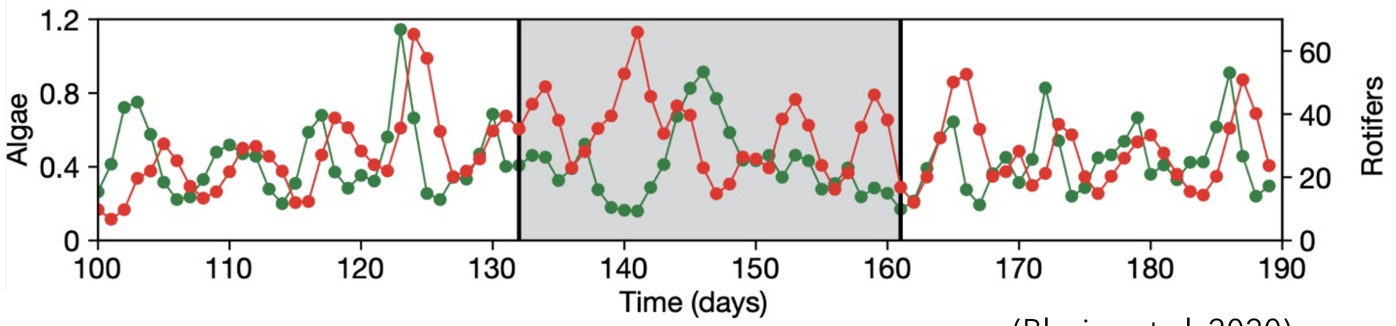
From populations to communities and ecosystems (here: deterministic continuous ODE)

- **Populations** Malthus', Verhult's, Monod's models
- **2 species in interaction** Lotka-Volterra predator-prey model

  Rosenzweig-MacArthur model

Predictions
- sustained cycle
- ¼ delay between prey and predator peaks





(Blasius et al. 2020)

- **Communities**

- **Ecosystems**:

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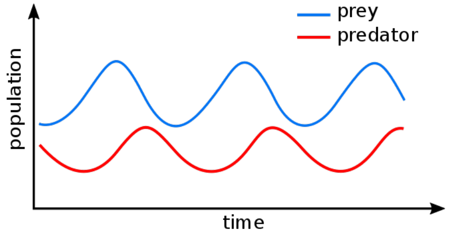
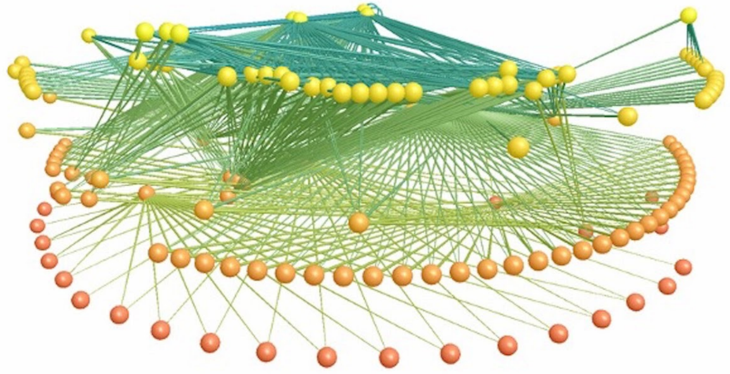
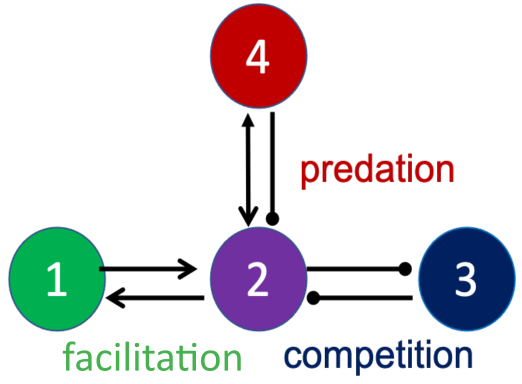
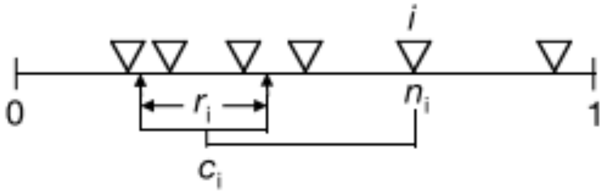


- **Communities**
  - General Lotka- Volterra model
  - Niche model (Williams & Martinez 2000)
  - Allometric trophic network models





- **Ecosystems**



$$\begin{bmatrix} -0.5 & 0.1 & 0 & 0 \\ 0.2 & -0.6 & -0.1 & -0.2 \\ 0 & -0.1 & -0.5 & 0 \\ 0 & 0.2 & 0 & -0.5 \end{bmatrix}$$

3. Different model formalisms

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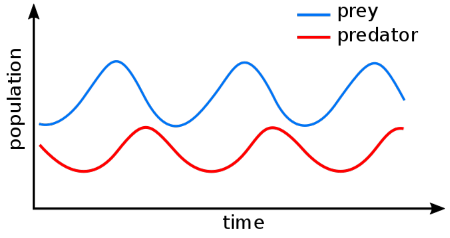

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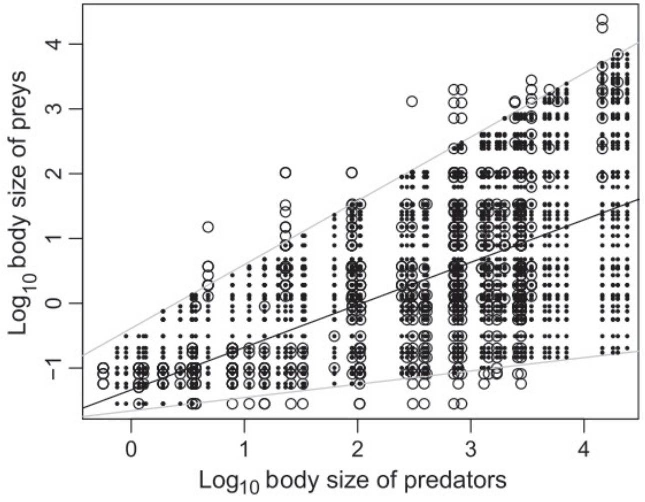
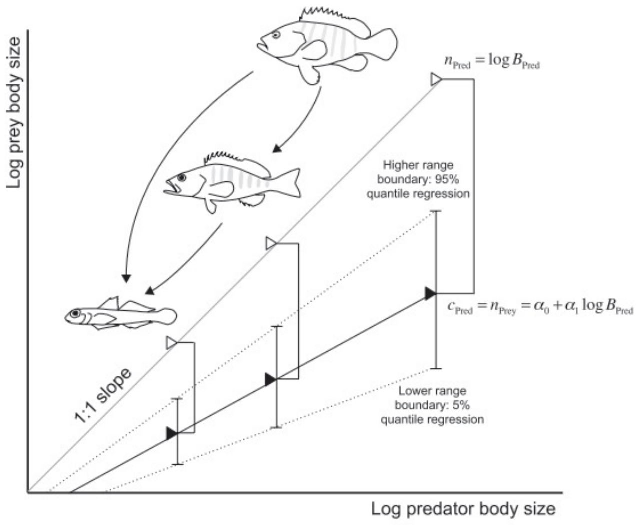
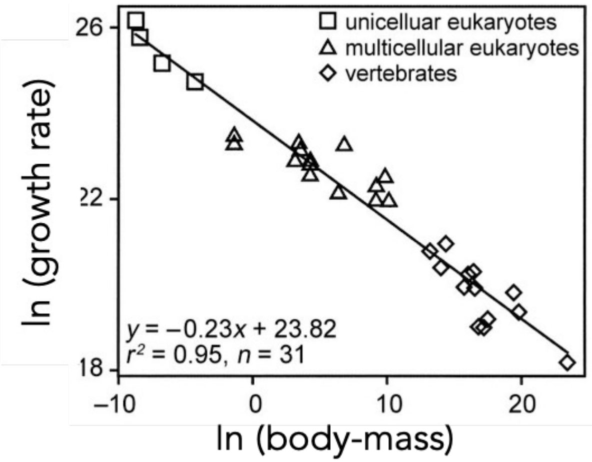


(Brose et al. 2005)



(Gravel et al. 2013)

- **Ecosystems**



(Brown et al. 2004)

3. Different model formalisms

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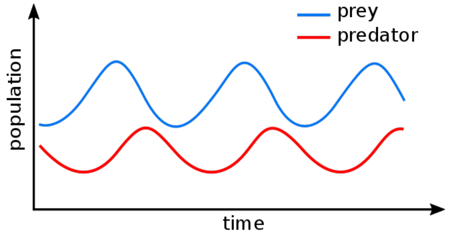

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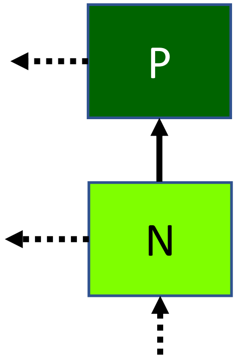
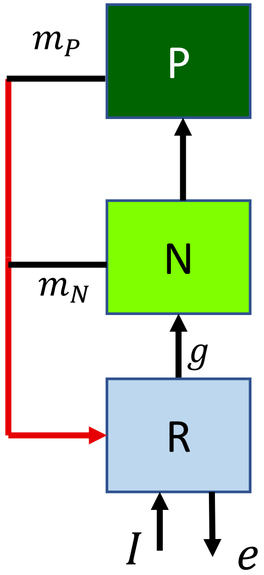




Assumption

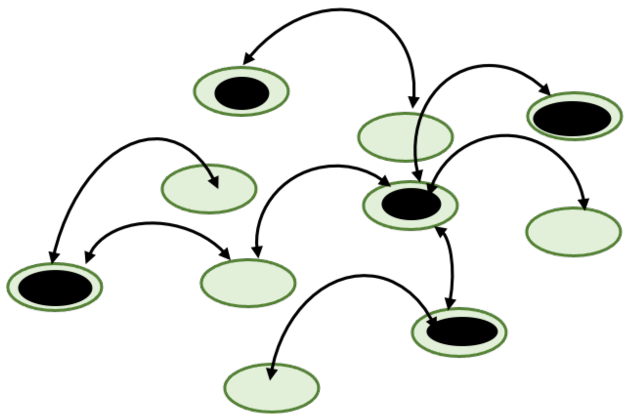
Feedback between demography and resource availability: nutrients are taken-up quickly

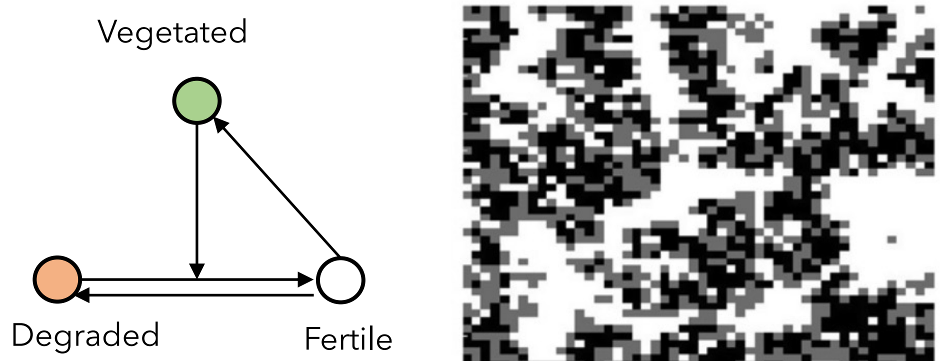
- **Ecosystems**
  - Compartment models (e.g., De Angelis 1980)

3. Different model formalisms

Integrating spatial heterogeneity

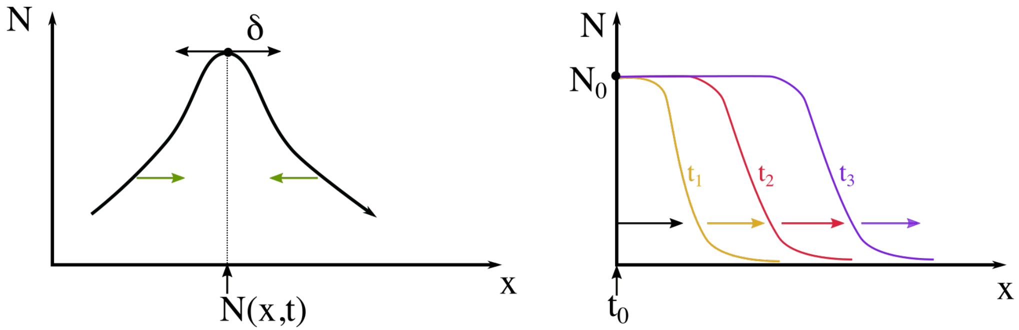
	Deterministic	Stochastic
Discrete space (implicit)	Metapop model (ODE)	vegetation models in arid systems
Continuous space (explicit)	FKPP reaction-diffusion model (PDE)	stochastic reaction-diffusion model (PDE)

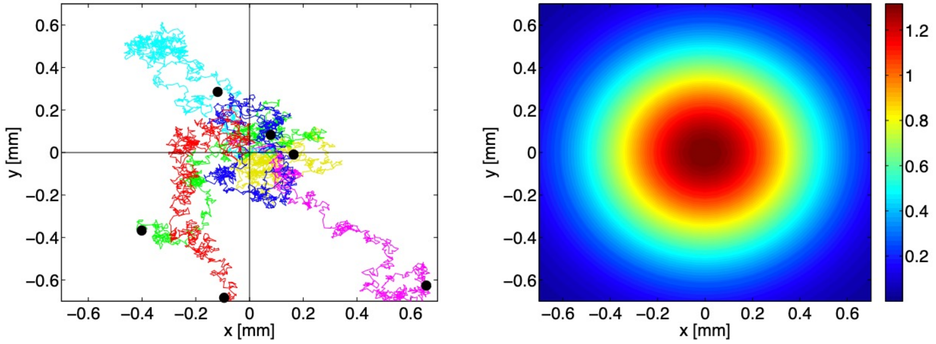




cellular automata
Mean field and pair approximations

(Kéfi et al 2007)





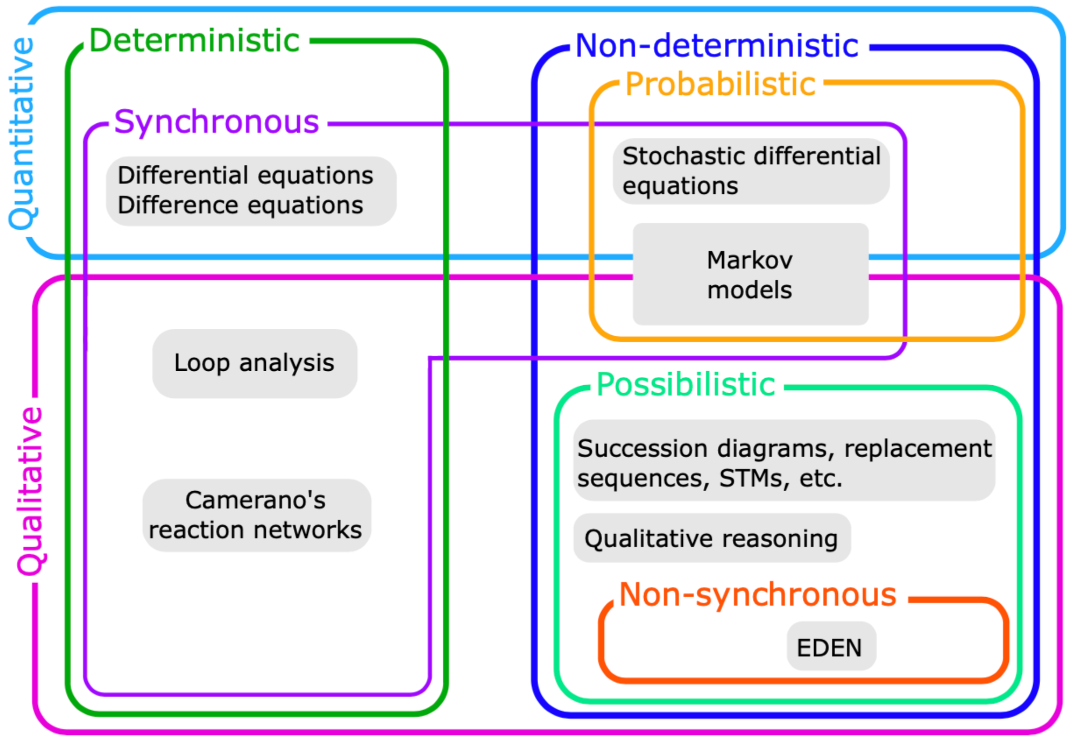
(Erban et al 2007)

3. Different model formalisms

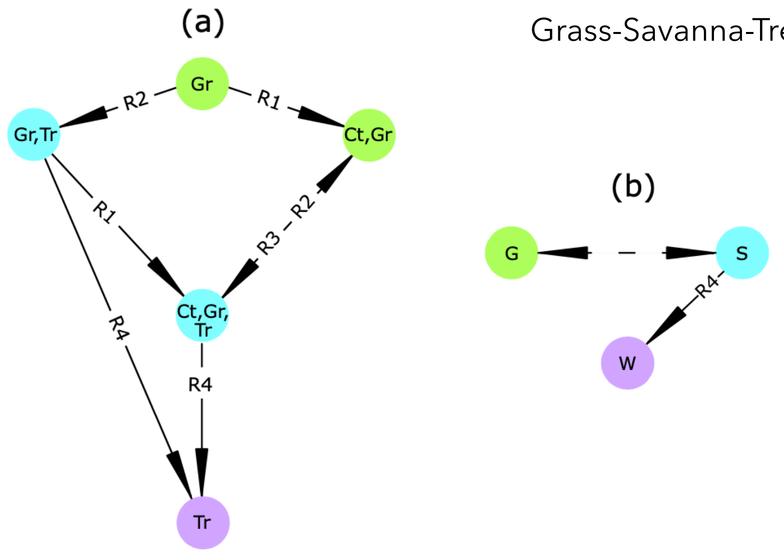
Quantitative versus qualitative models

What are qualitative models? Abstractions of quantitative phenomena focusing on qualitative states of the system

Why qualitative models? to allow integrate non numerical expert knowledge, or if quantitative data is scarce



R1		Gr+	→	Ct+	Grasses attract cattle.
R2		Gr+	→	Tr+	Grasses promote tree growth.
R3	Ct+,	Gr+	→	Tr−	Cattle control trees if there is enough grass.
R4		Tr+	→	Gr−, Ct−	Trees outcompete grasses and thus exclude cattle.
R5		Tr−	→	Gr+	Grasses reestablish if trees are cut.



Grass-Savanna-Tree toy model

(Cosme 2022)