Theory-driven analysis of Ecological data – Day 1

10:30-12:00 **What types of theoretical models in ecology?**

13:45-14:45 **How to build a model?**

14:45-15:45 **How to analyze a model?**

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CESAB, Montpellier,
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What types of theoretical models in ecology?

Content

1. What system? What question? What hypotheses? What model type?
2. What model formalism?
   - Deterministic – stochastic processes
   - Time: discrete – continuous
   - Accounting for space?
3. What technical choices?
   - Analytical vs Numerical
   - Agent Based Models vs Equations

1. What system? What question? What hypotheses?

Global Ecology

Ecology

Population biology

Evolutive biology

Organism biology, physiology, ethology

Cellular and molecular biology

Biochemistry

Biosphere
↑
Biome
↑
Ecoregion

Spatial Homogeneity

Ecosystem
↑
Community
↑
Population
↑
Individual
↑
Cell
Organic Macromolecule
↑
Organic Molecule

Spatial Heterogeneity

Landscape – Metaecosystem
↑
Metacommunity
↑
Metapopulation

What scale?
What process?
[do we want to model]

What can we ignore?

1. What system? What question? What hypotheses?

System + Question → **Scale** → What can we ignore? → What assumptions do we make?
→ **Variable + Processes**

Example: landscape with plants and herbivores

Individuals
Which factors determine individuals development?
Physiology, morphology, behavior, life-cycle etc

Population
How do resources regulate population growth?
Intra-specific competition, pop level rates, etc.

Community
How does grazing impact plant diversity?
Herbivore preferences, plants relative growth, etc.

Ecosystem
Can grazing increase primary production?
Ecosystem fluxes, recycling, etc.

Landscape
Can spatial heterogeneity promote plant diversity?
Spatial connectivity, dispersal rates, etc.

1. What system? What question? What hypotheses?

System + Question → Scale → Variable + Processes **→ What can we ignore?** → What assumptions do we make?

This is neither the aim nor relevant to model all details.
Some processes are much faster or much slower than focal ones and can be considered constant.
Example: the upper level is often slower than those below and impose constraints

Physiology question
=> ignore tree dynamics

Long term population dynamics
=> include tree mortality dynamics

Year-scale fish population dynamics
=> ignore human demography

Century-scale fish population dynamics
⇒ include human demography (variation in catch effort)

1. What system? What question? What hypotheses?

System + Question → Scale → What can we ignore? → **What assumptions do we make?**
→ Variable + Processes

Assumptions → Model → Analysis → Prediction

(simplification of the system) | (= mathematical formulation of assumptions or series of rules) | (mathematical method) | (truth according to assumptions)

overinterpretation

Types of assumptions

- critical: crucial to test the verbal hypothesis
- exploratory: important to vary and test but not core to the verbal hypothesis
- logistical: those important for tractability

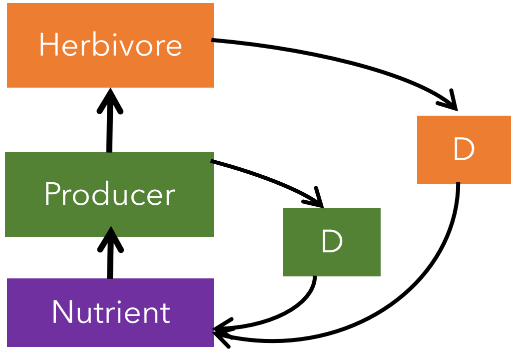
(Servedio et al. 2014)

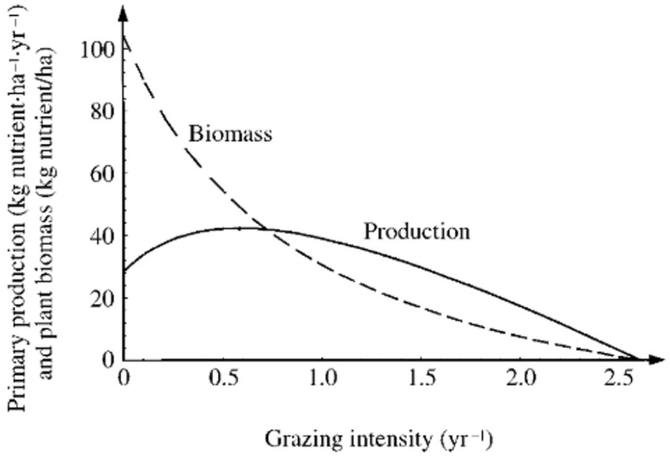
1. What system? What question? What hypotheses?

System + Question → Scale → What can we ignore? **→ What assumptions do we make?**
→ Variable + Processes

Question: *Can grazing increase primary production?* (de Mazancourt et al. 1998 Ecology)

Hypothesis: *Herbivory can maximize primary production if herbivore recycling path is faster than plant ones*



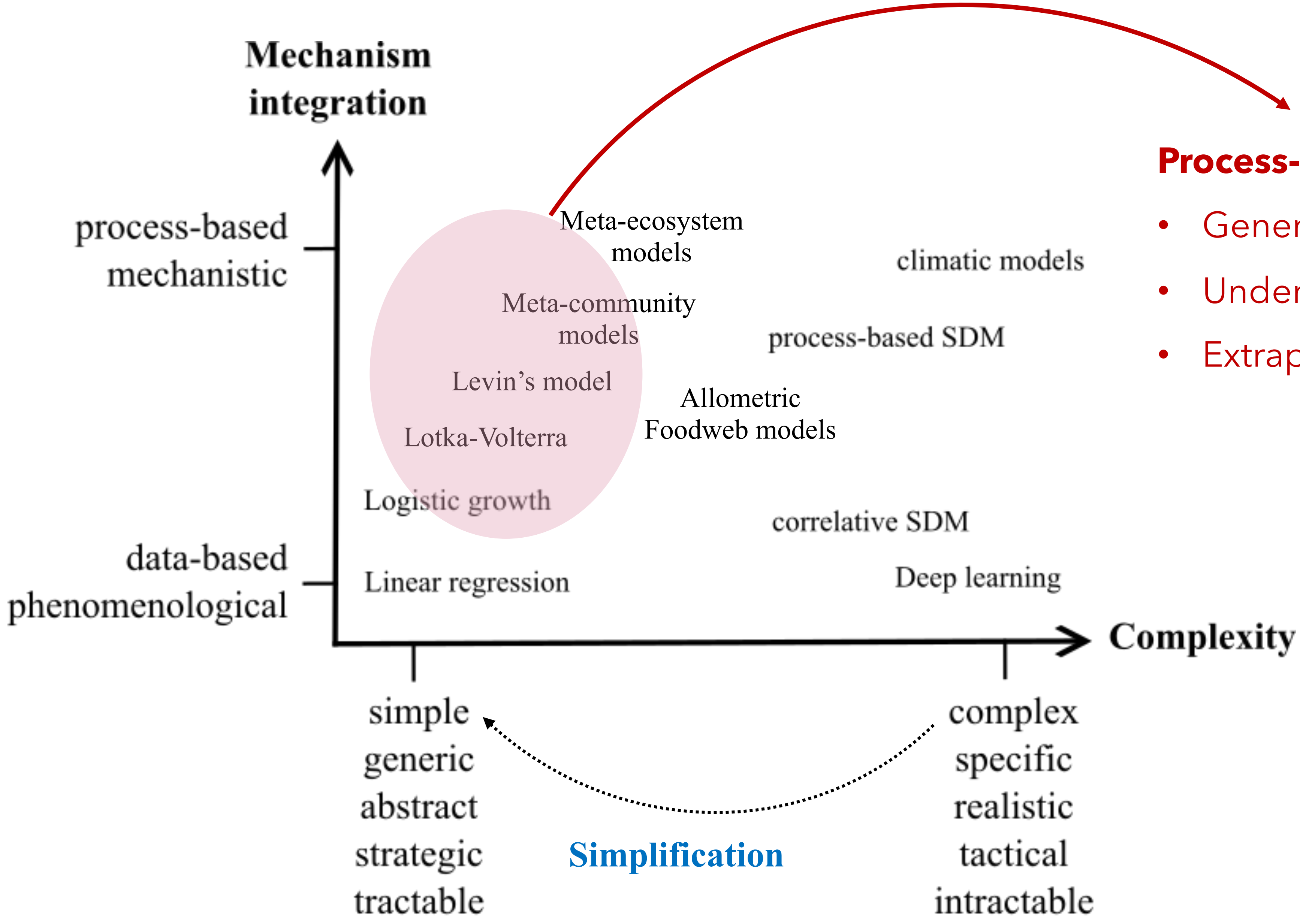


Types of assumptions

- critical: crucial to test the verbal hypothesis => 2 paths of recycling
- exploratory: important to vary and test but not core to the verbal hypothesis => functional response (donor vs recipient controlled)
- logistical: those important for tractability => ODE deterministic

(Servedio et al. 2014)

1. What model type?



Process-based [simple] models

- Generalize
- Understand
- Extrapolate

Simplification approaches

- Weak processes
- Large number theory
- Fast-slow processes

2. What model formalism?

1. Do we need **deterministic or stochastic** dynamics?
2. Do you model time or not ? Are processes continuous or discrete in **time**?
3. Do we need to consider **space** explicitly?

2. What model formalism? (1) Stochastic /Deterministic

What is stochasticity?
What sort of stochasticity counts in ecology?

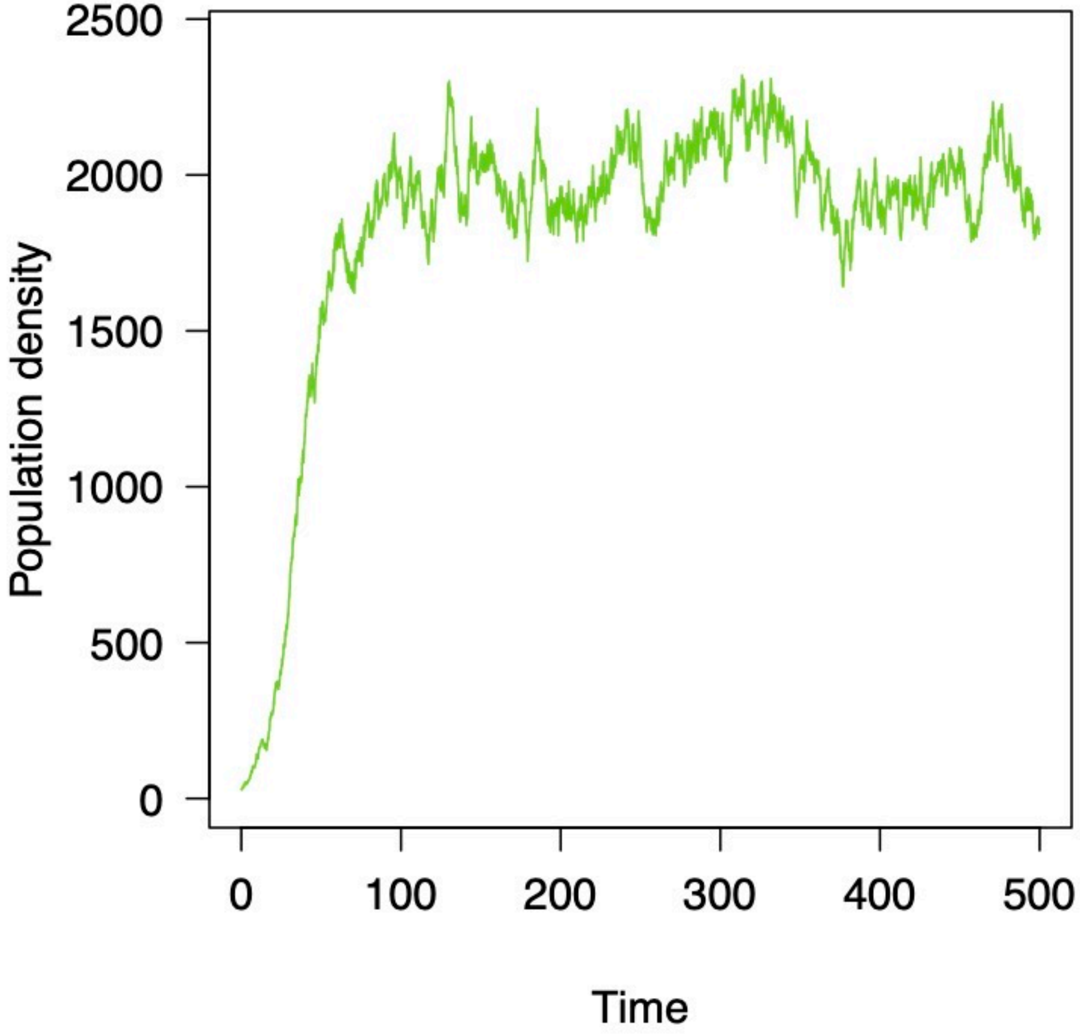
- demographic stochasticity

- environmental stochasticity

- trait variability

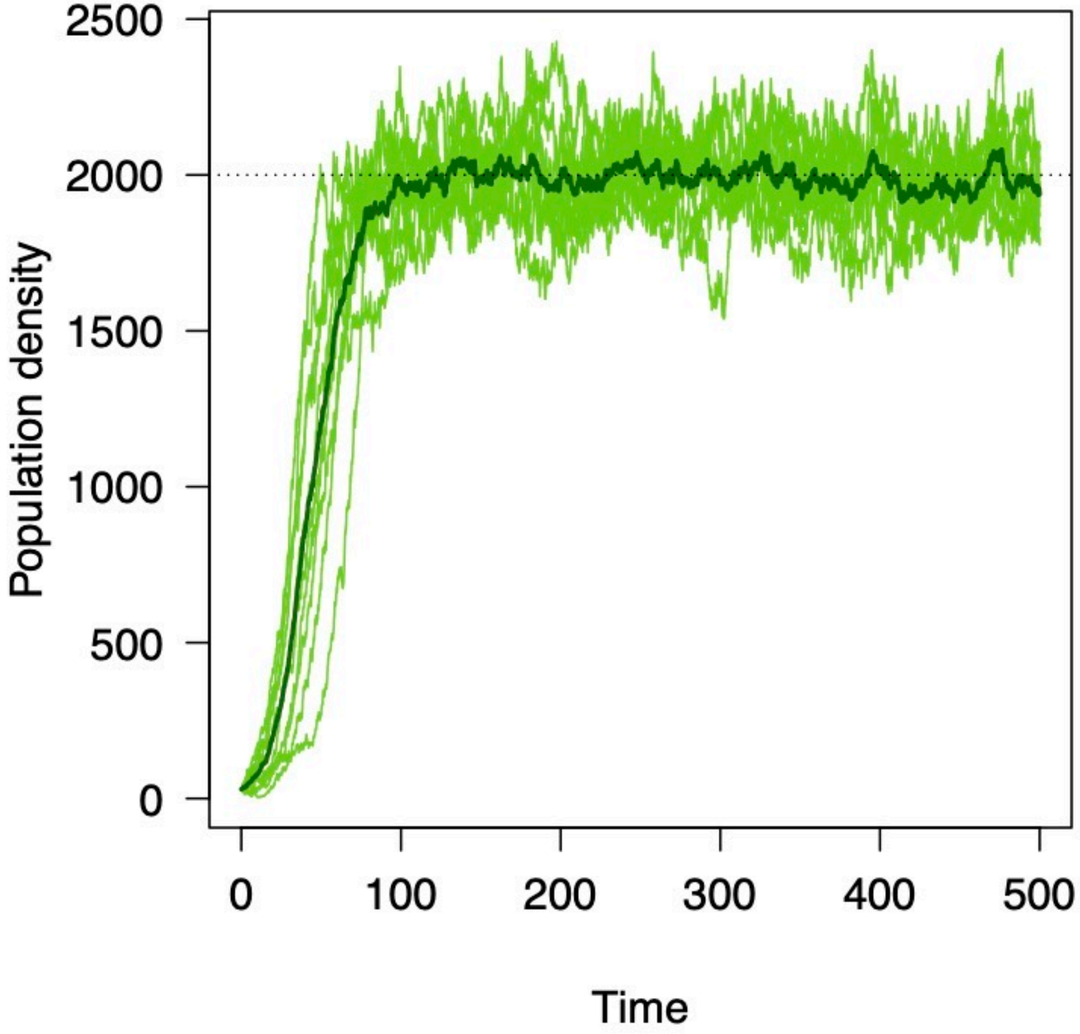
When should we account for it?

2. What model formalism? (1) Stochastic /Deterministic



Example: random demographic events

2. What model formalism? (1) Stochastic /Deterministic



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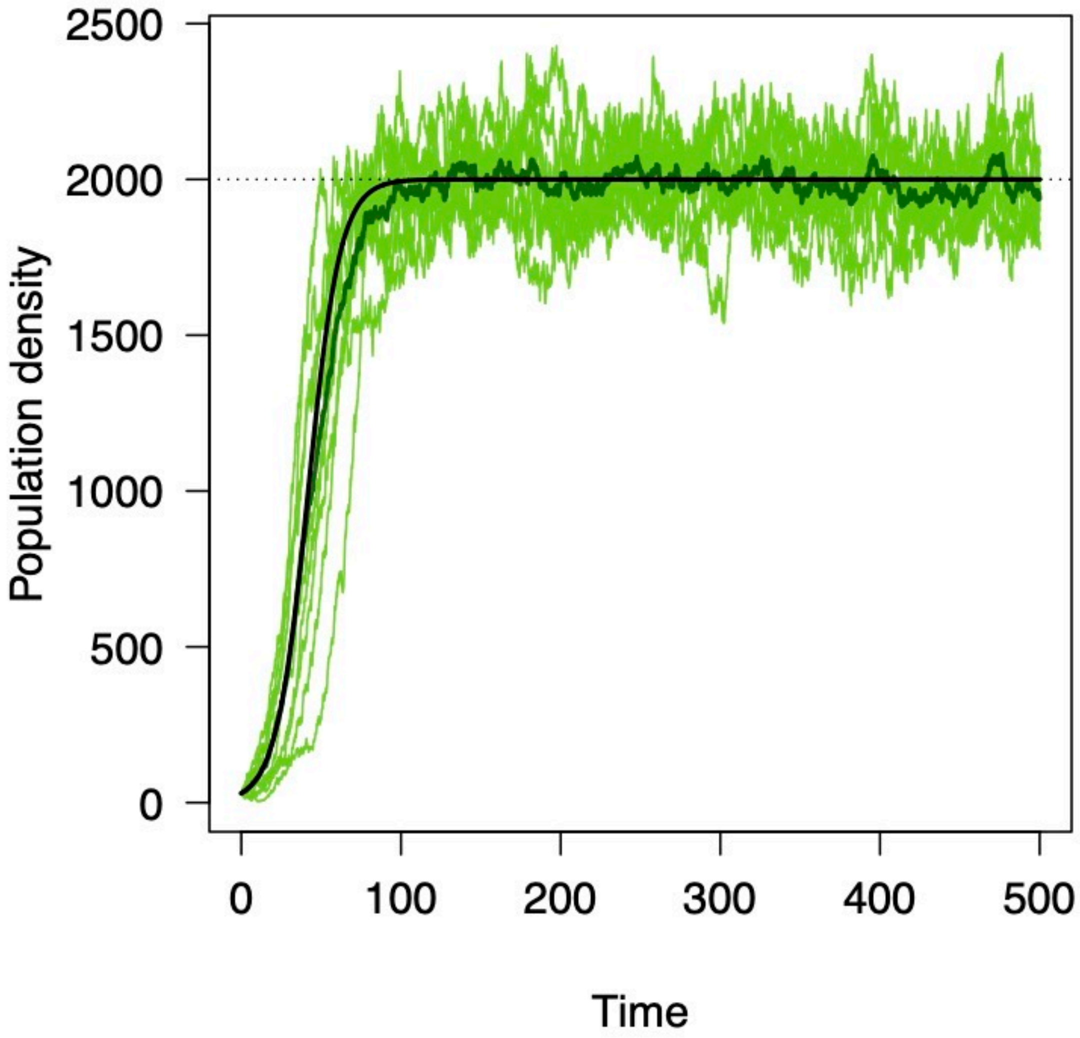
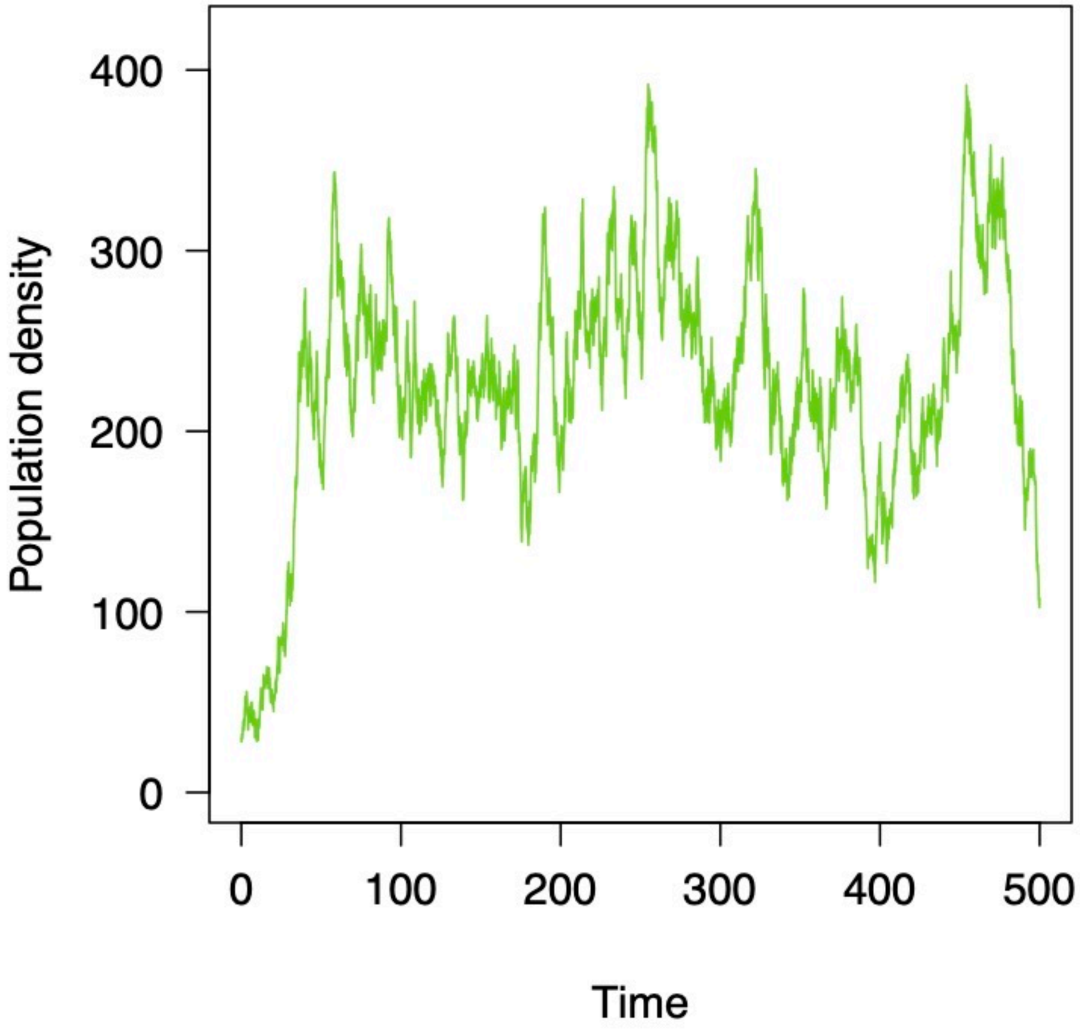


Example: random demographic events

→ care of the mean only
→ good approximation

2. What model formalism? (1) Stochastic /Deterministic



Example: random demographic events

- Randomness large compared to population size (e.g., small populations)

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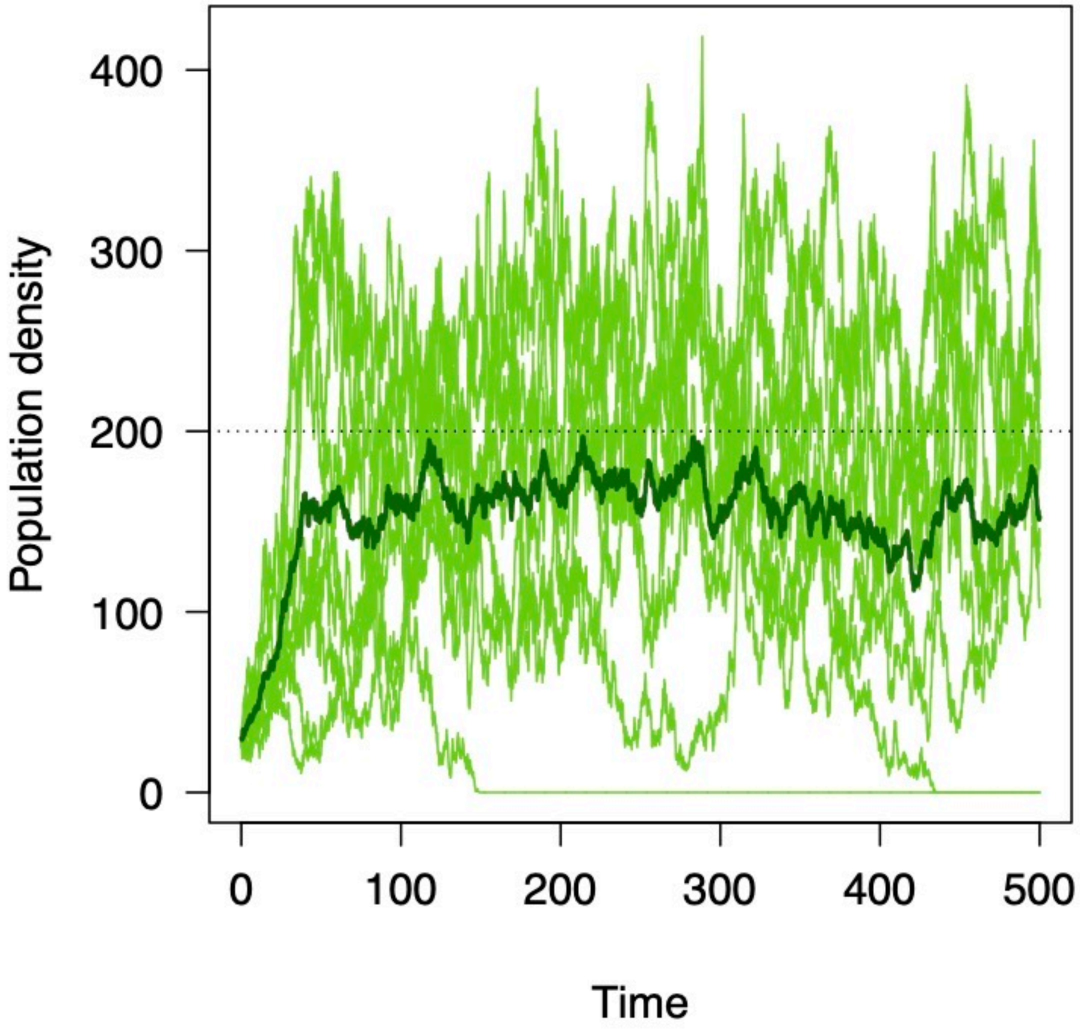

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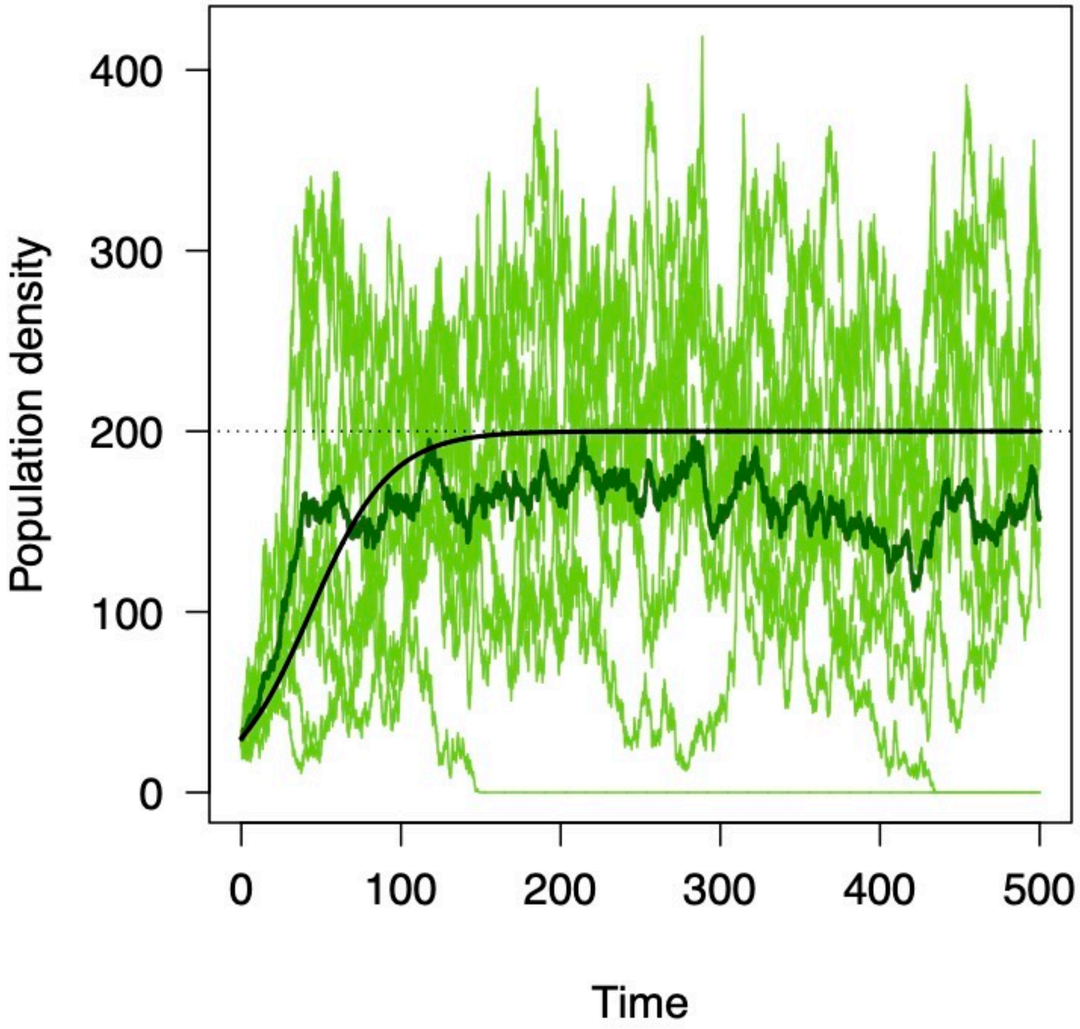


Example: random demographic events

- Randomness large compared to population size (e.g., small populations)

→ wrong prediction

2. What model formalism? (1) Stochastic /Deterministic

Stochastic models

Randomness of processes is important

When we have small numbers (integers relevant), which makes stochastic processes important relative to mean

→ Ex: Questions of viability of small populations

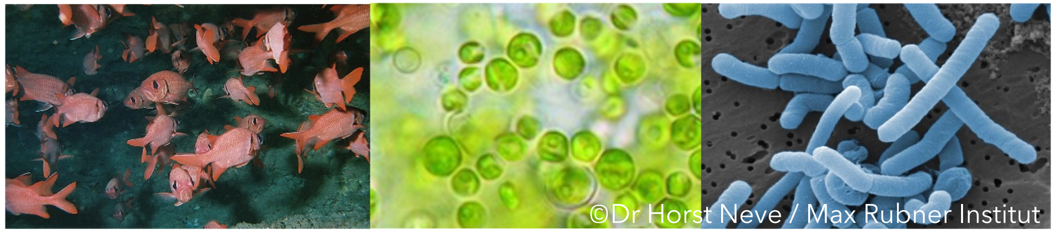
→ Ex: IBM models or SDE
See models in day 3 and 4 (Matthieu)

Deterministic models

The noise can be ignored

When processes can be summarised with average parameters, variance is small compared to mean: mean growth rate, mass action law

→ For large populations

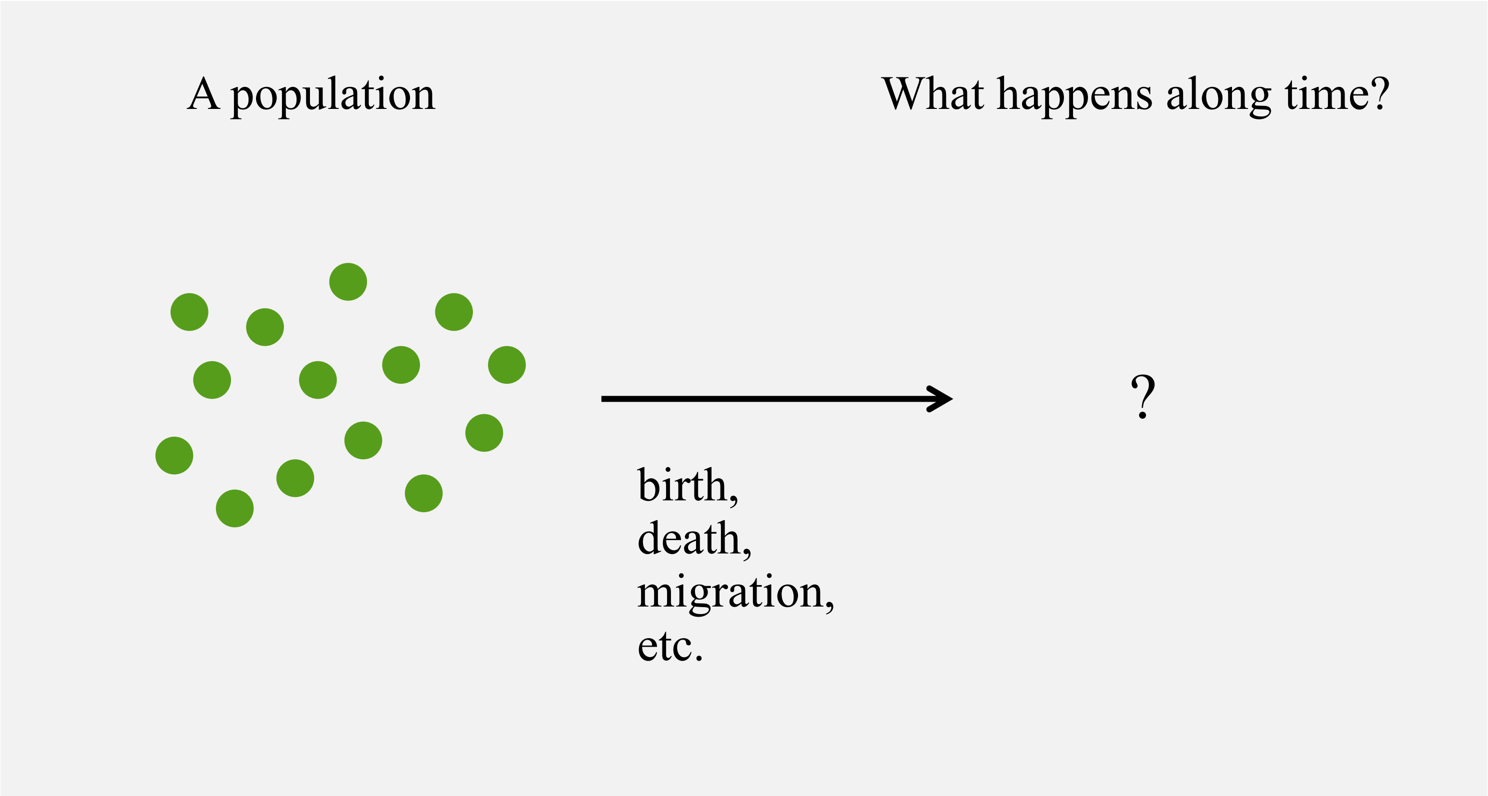


→ Ex: Deterministic ODE
See models in day 2 and 4

2. What model formalism? (2) Time

We have static versus dynamic models: does our question require time?
→ Ex: static trophic networks versus dynamic food web models (see day 4)

If dynamic, when might we use discrete or continuous-time formalism?



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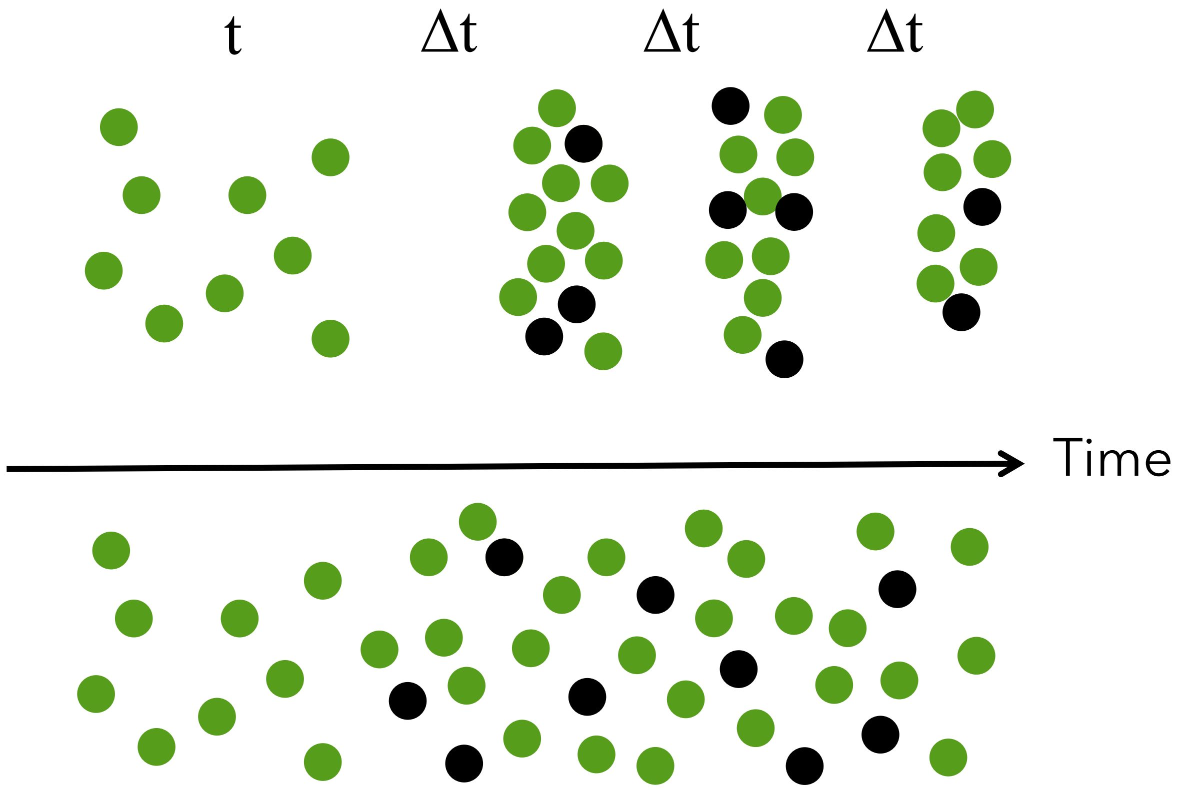


Discrete time

Synchronization of events

Continuous time

Events happen at any time

2. What model formalism? (2) Time

Discrete time models

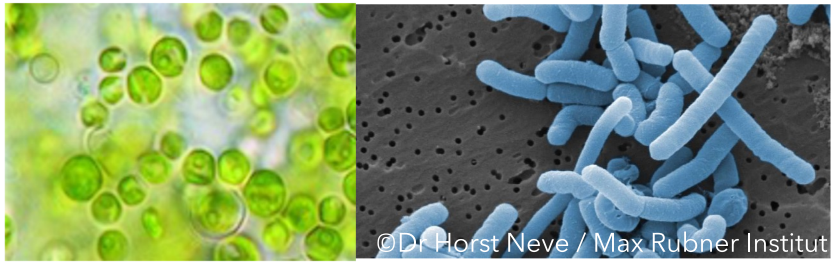
Events are synchronized

- Questions linked to the phenology
- Complex life cycles
- Synchronized generations
- Seasonal dynamics

Continuous time models

Everything can happen at any time

- Processes happen continuously
- Generations overlap



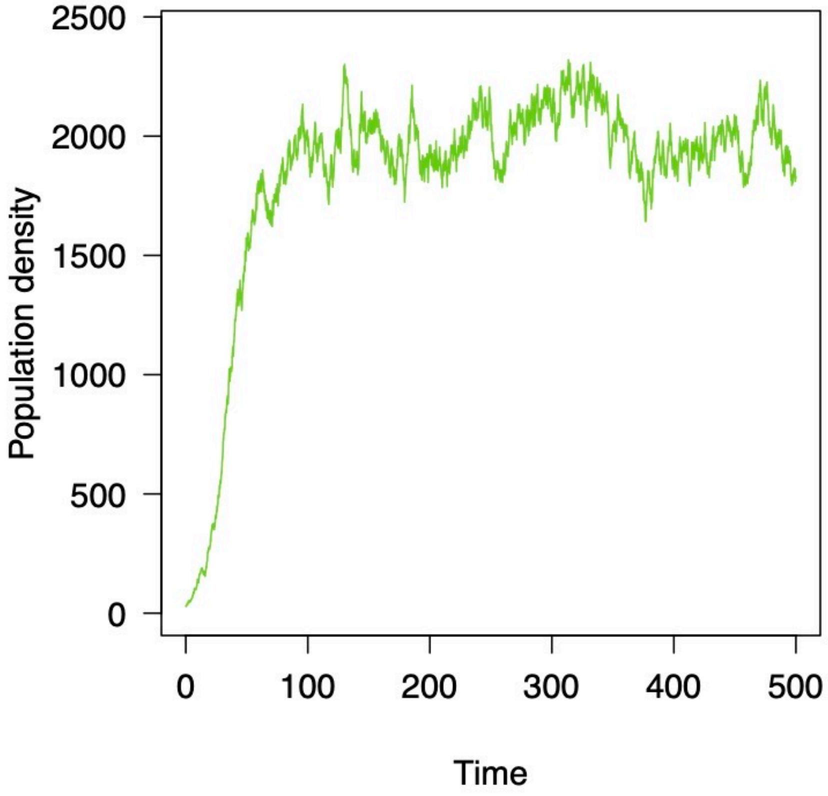
→ discrete time models where the time interval is very small boil down to continuous model

→ discrete or continuous time models can be either stochastic or deterministic

→ See models in day 2 (discrete), 3, 4 (continuous)

2. What model formalism? (3) Space

All ecological systems occur in space



In population models, space is often integrated in the unit, e.g., ind./km^2 or ind./m^3 or abundance in a given habitat of specific size

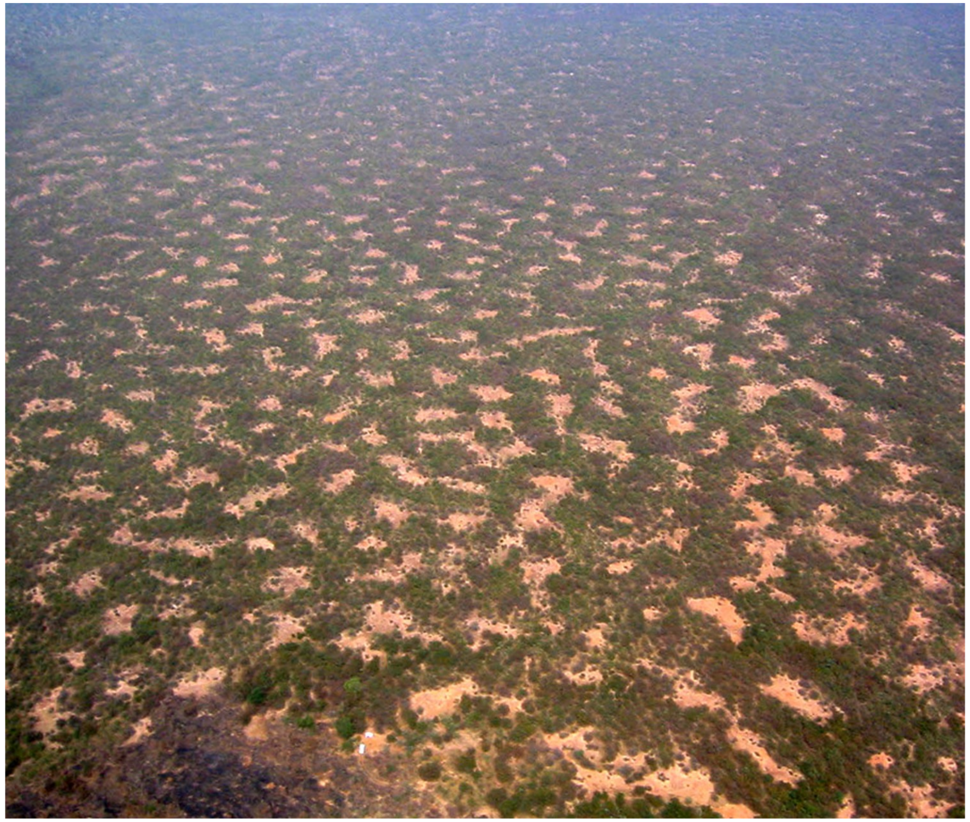
When is space important to describe your system and answer your question?

2. What model formalism? (3) Space

When interactions are localized, heterogeneously distributed in space.

Does diversity depend on spatial dynamics?

Does spatial patterns emerge from local dynamics?

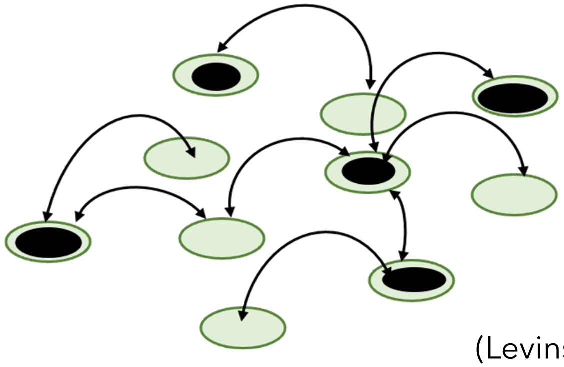


When is space important to describe your system and answer your question?

2. What model formalism? (3) Space

Does geographical position matter?

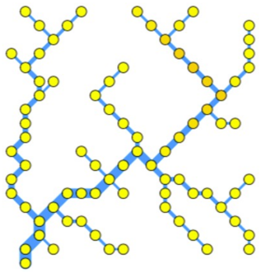
Space **implicit**: topology only



→ See models in day 3

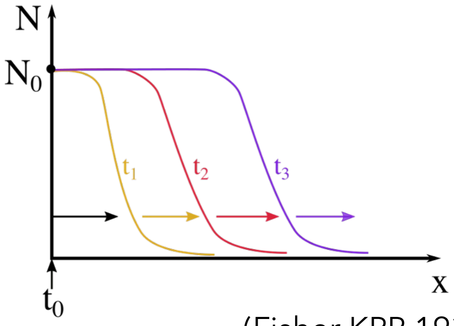
(Levins 1969, Leibold et al. 2004)

Space **explicit**: distances, geographical location



(Carraro et al 2020)

(Kéfi et al 2007)



(Fisher KPP 1937)

Discrete space → Continuous space

Distant locations

Fragmented landscapes

Connectivity structure effects

Grids

Spatial patterns

Continuous space (PDE)

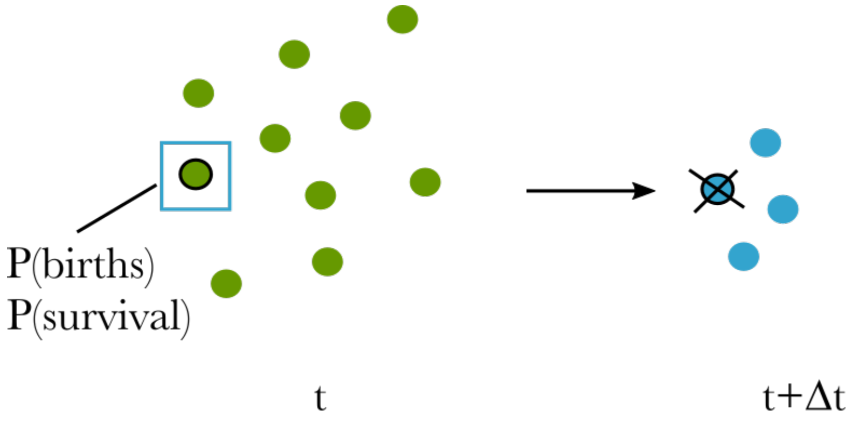
Environmental gradient, edge effects, invasion front

3. What technical choices?

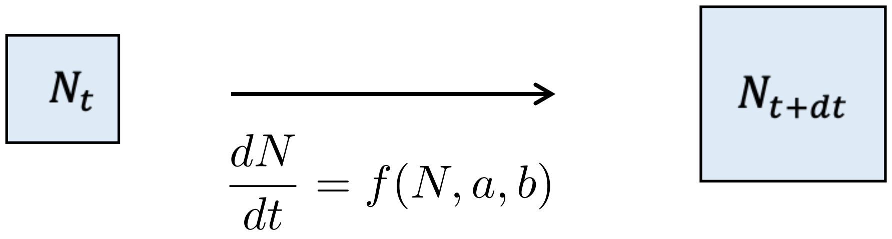
1. Agent Based Models vs Equations
2. Analytical vs Numerical

3. What technical choices? (1) rules vs maths

IBM – ABM



Dynamical equations

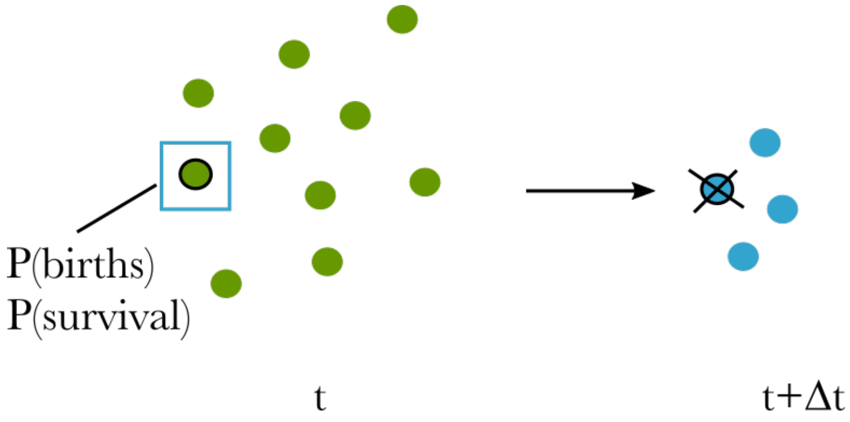


- Variables are individuals or agents (integers)
- Processes (birth, death, dispersal) are formulated as a series of rules involving probabilities, applied to each agent.

- Variables are population densities / biomasses (decimals)
- We use maths
- Processes are embedded into parameters

3. What technical choices? (1) rules vs maths

IBM - ABM



- Modelled objects & relations = assumptions (without approximations) → complex behavior easier to represent
- No need for math skills
- Computation time & resources
- Coding skills required

Dynamical equations

$$\boxed{N_t} \xrightarrow{\qquad\qquad} \boxed{N_{t+dt}}$$

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

- Simplification with math approximations
- Large analysis power for extreme case
- Fast computation: lower C footprint
- Easier to fit to data
- Imposed relations between variables
- Math skills required

3. What technical choices? (2) Analytical vs simulations

Analytical versus simulation models → Parsimony provides analytical power

Simple tractable models → Complex intractable models

A given model

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

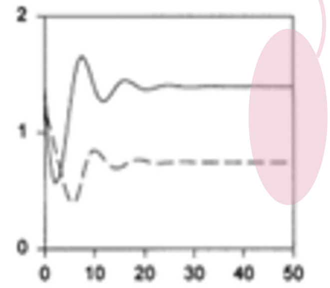
Analytically tractable ? → Yes → **a complete solution exists** (we fully know the model: almost never the case)

$$N = F(a, b, t, N_0)$$

Yes → **Equilibria** (we know long-term dynamics)

$$N^* = G(a, b)$$

$$\frac{dN}{dt} = 0$$



Analytically tractable ? → No → (results are specific to parameter values)

→ **Simulations** (many runs to explore parameter space)

→ Numerical integration (ODE)

→ Coding algorithm (ABM)

→ Simplifications → Equilibria

How to build a model?

Content

you

0. What is the question?

1. Sketch your system and choose your formalism

2. Identify the assumptions in a classical theoretical model

3. Code the model in R: principle of numerical integration

4. Explore the model

0. What is your question?

1. Sketch your system

What are your variables?

How are they connected? Which processes do you integrate?

And Choose your formalism

What formalisms in terms of stochasticity, time, space?

What assumptions on modelled processes?

2. Identify assumptions in theoretical models

Rosenzweig-MacArthur model (1963)

$$
\begin{cases}
\dfrac{dP}{dt} = r_0 P(1 - \dfrac{P}{K}) - \dfrac{aPH}{1 + ahP} \\
\dfrac{dH}{dt} = \varepsilon \dfrac{aPH}{1 + ahP} - mH
\end{cases}
$$

$\boldsymbol{r_0}$ growth rate

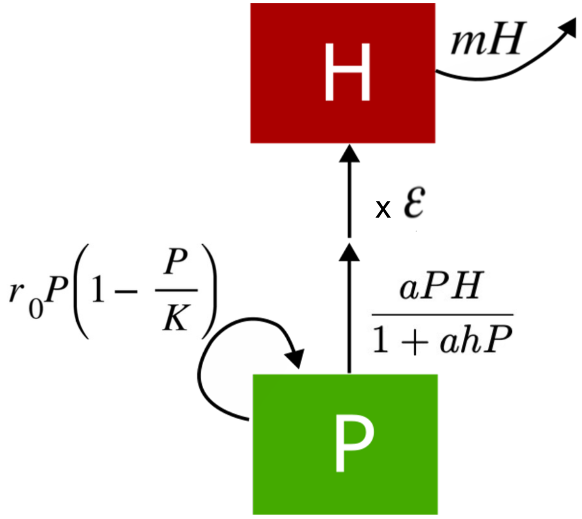
$\boldsymbol{K}$ carrying capacity

$\boldsymbol{a}$ attack rate

$\boldsymbol{h}$ handling time

$\boldsymbol{m}$ mortality rate

$\boldsymbol{\varepsilon}$ conversion efficiency



General assumptions from formalism

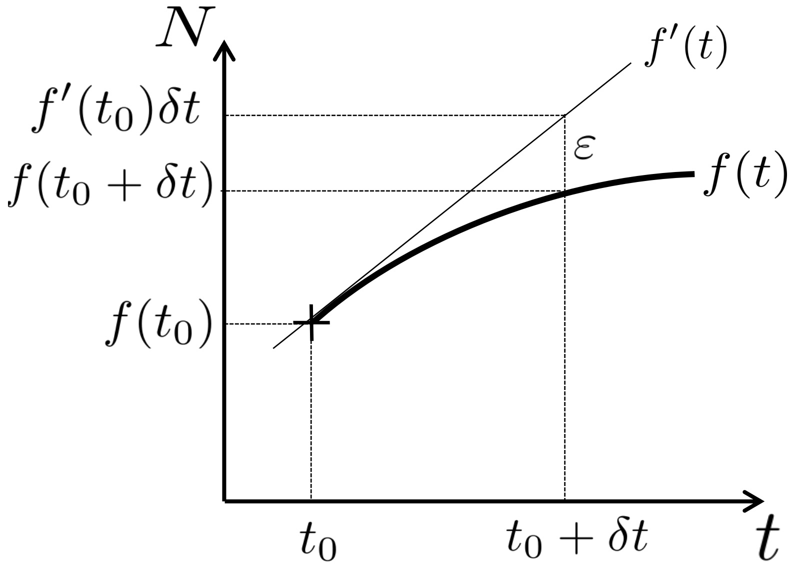
- Populations are sufficiently large for their biological rates to be approximated with averaged parameters: within a population, all individuals identical
- Generations overlaps in time
- Space is homogeneous

Assumptions from mathematical formulations

- Resources for producers are limited and resource dynamics are much faster than population dynamics
- There is no recycling feedback
- Mass action law: encounter rates are proportional to densities
- Herbivore consumption saturates through time needed to manipulate food
- Herbivores dies without producers (metabolic needs)
- Only a part of herbivore consumption is converted into new biomass

3. Code the model: principle of numerical integration

A given dynamics $N = f(t)$ $\quad \dfrac{dN}{dt} = f'(t)$



- Numerical integration is a recursive process:

  approximate the system from the previous time step

- A simple algorithm for ODEs: the Euler method

$$f(t_0 + \delta t) = f(t_0) + f'(t_0)\delta t + \varepsilon$$

- The error depends on time interval and the type of dynamics

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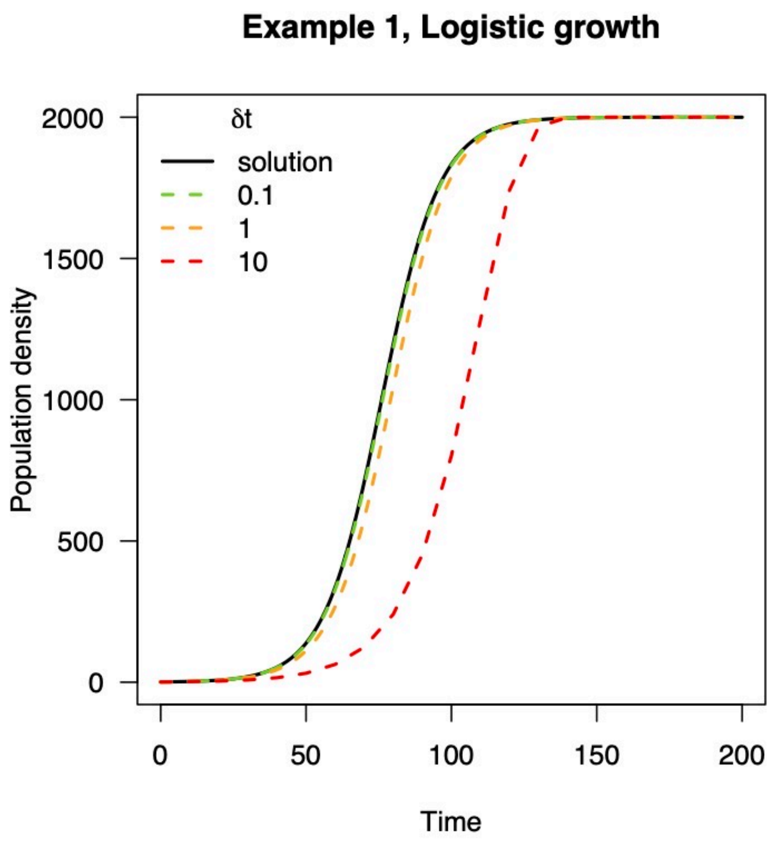

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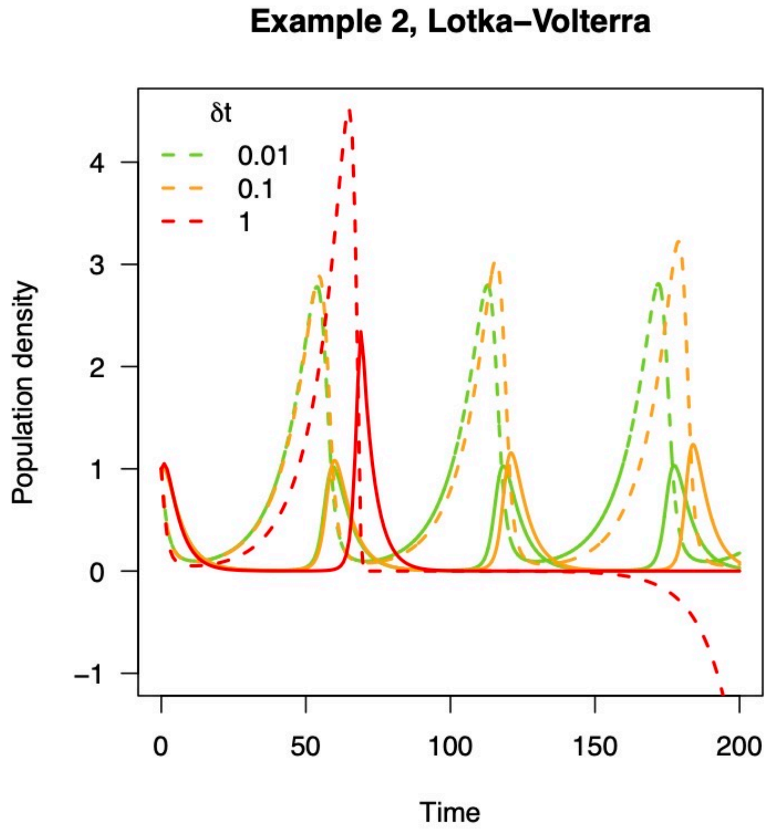

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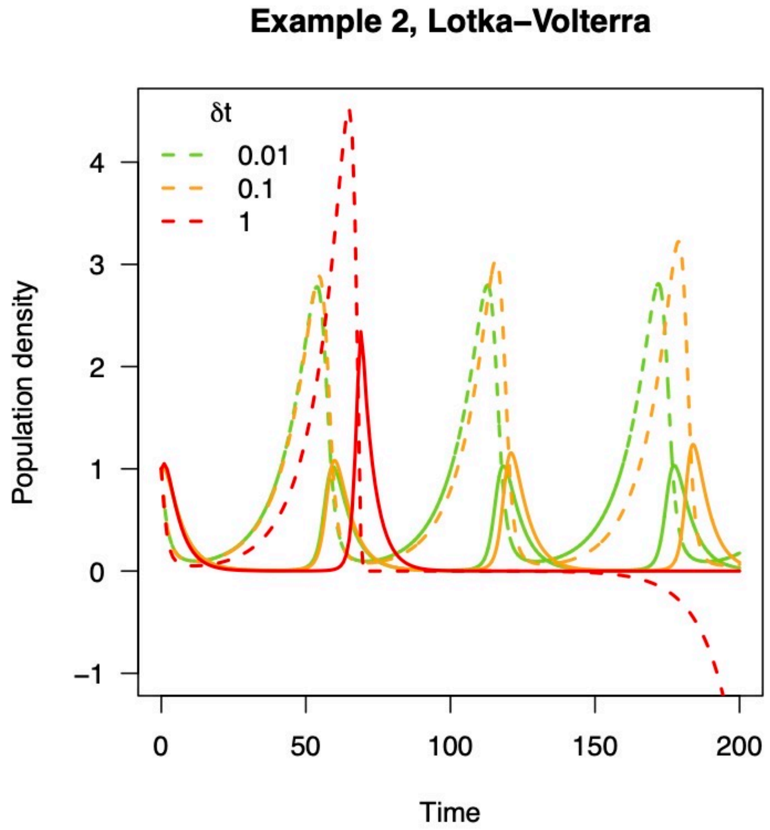

- Mathematicians proposed different algorithms to minimize the error depending on the problem.

- These algorithms are implemented into solvers. Some have adaptive time steps with error tolerance.

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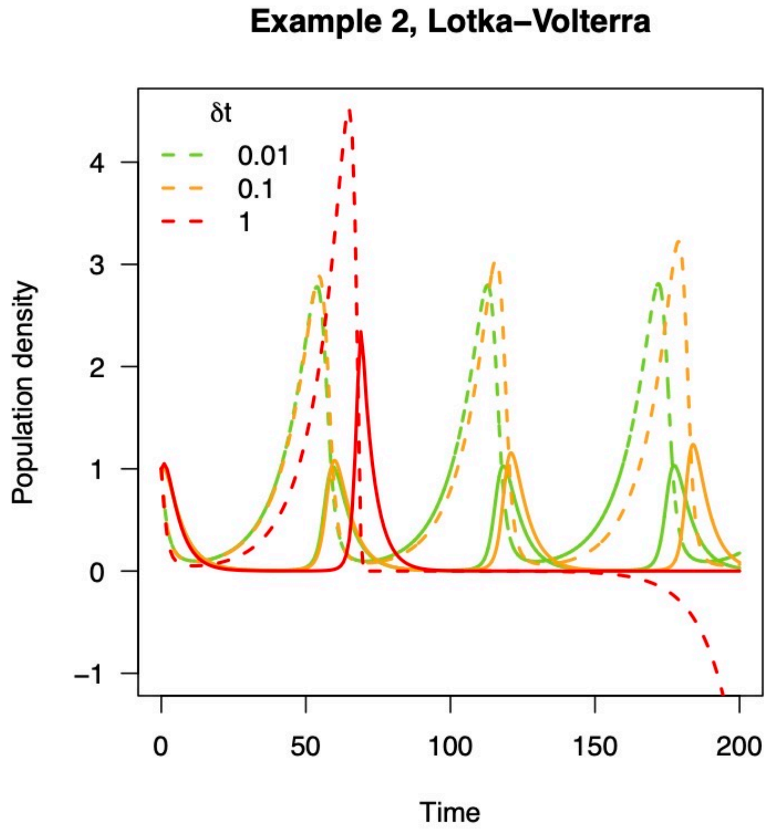

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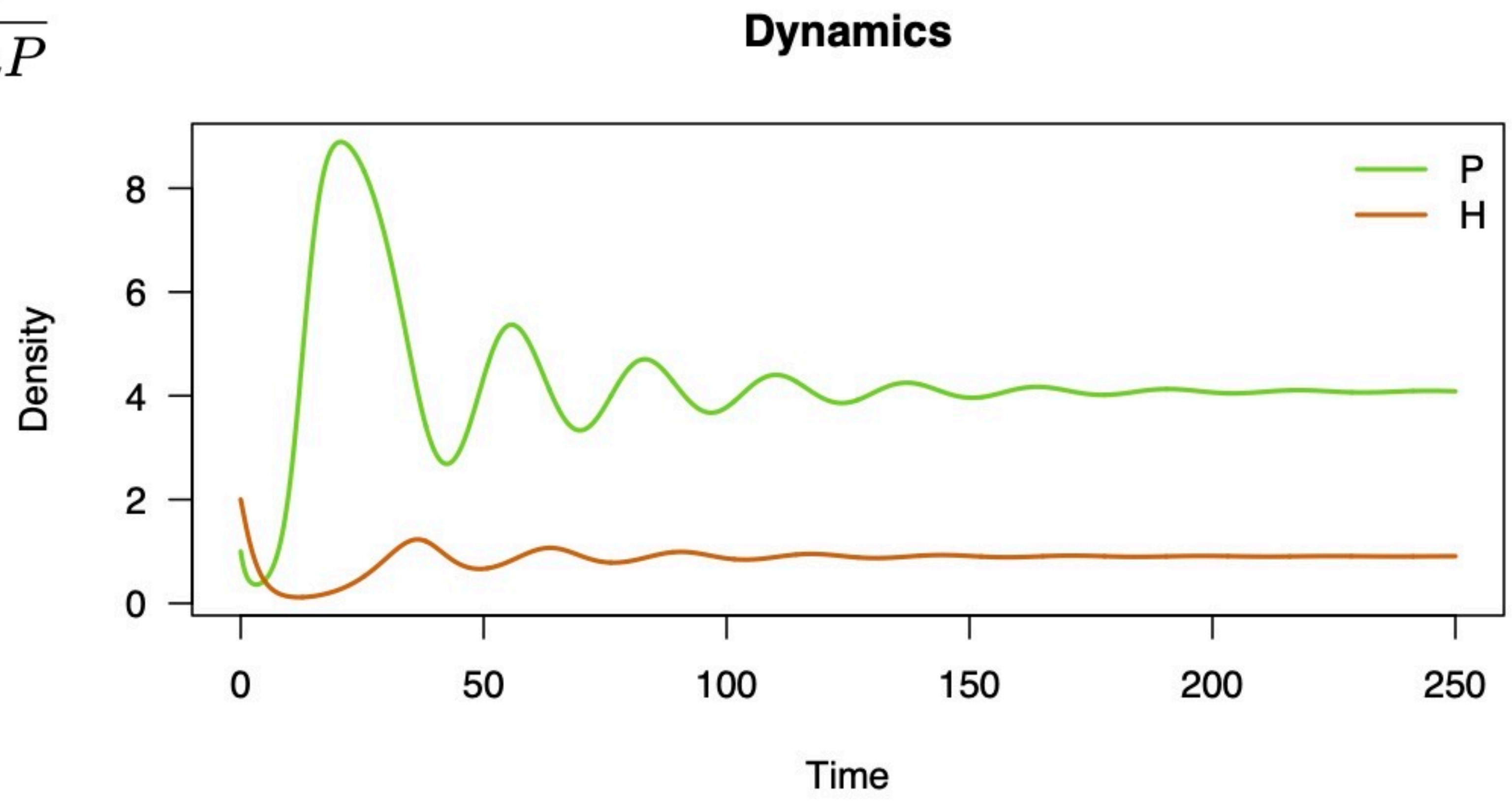
- These algorithms are implemented into solvers. Some have adaptive time steps with error tolerance.

- In R we can use the function `ode` of the package `deSolve`

3. Code the model: principle of numerical integration

Rosenzweig-MacArthur model (1963)

$$\begin{cases} \dfrac{dP}{dt} = r_0 P(1 - \dfrac{P}{K}) - \dfrac{aPH}{1 + ahP} \\ \dfrac{dH}{dt} = \varepsilon \dfrac{aPH}{1 + ahP} - mH \end{cases}$$



- In R we can use the function `ode` of the package `deSolve`

4. Explore the model

- Modify the initial conditions. Is the long term result changing?

- Modify the parameters

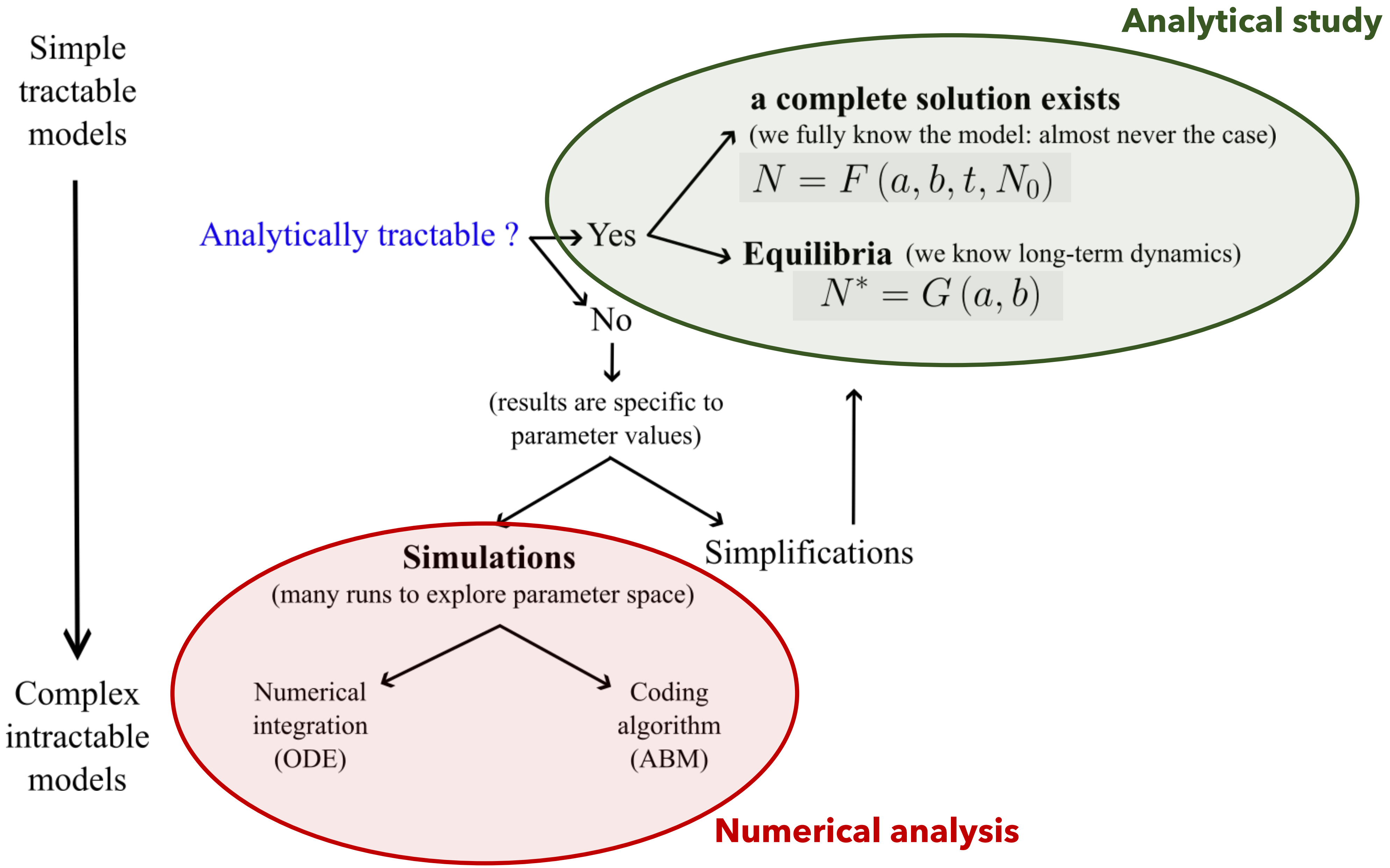
- **Which strategy to explore the model and answer our question?**

How to analyse a theoretical model?

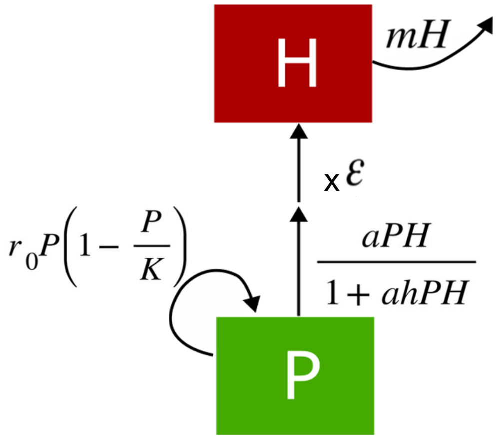
Content

1. General analysis
   - Equilibria
   - Local stability analysis (Jacobian matrix)
   - Bifurcation diagrams
   - Dependence to initial conditions

2. Simulation strategies
   - Parameter exploration
   - Model comparison
   - Experiments with synthetic data
   - Robustness of conclusions


Analytical study
Simple
tractable
models
a complete solution exists
(we fully know the model: almost never the case)
$N = F(a, b, t, N_0)$
Analytically tractable ?
Yes
Equilibria (we know long-term dynamics)
$N^* = G(a, b)$
No
(results are specific to
parameter values)
Simulations
(many runs to explore parameter space)
Simplifications
Numerical
integration
(ODE)
Coding
algorithm
(ABM)
Complex
intractable
models
Numerical analysis

1. General analysis (1) Equilibria



The Rosenzweig-MacArthur model (1963)

$$\frac{dP}{dt} = r_0 P\left(1 - \frac{P}{K}\right) - \frac{aPH}{1 + ahP}$$

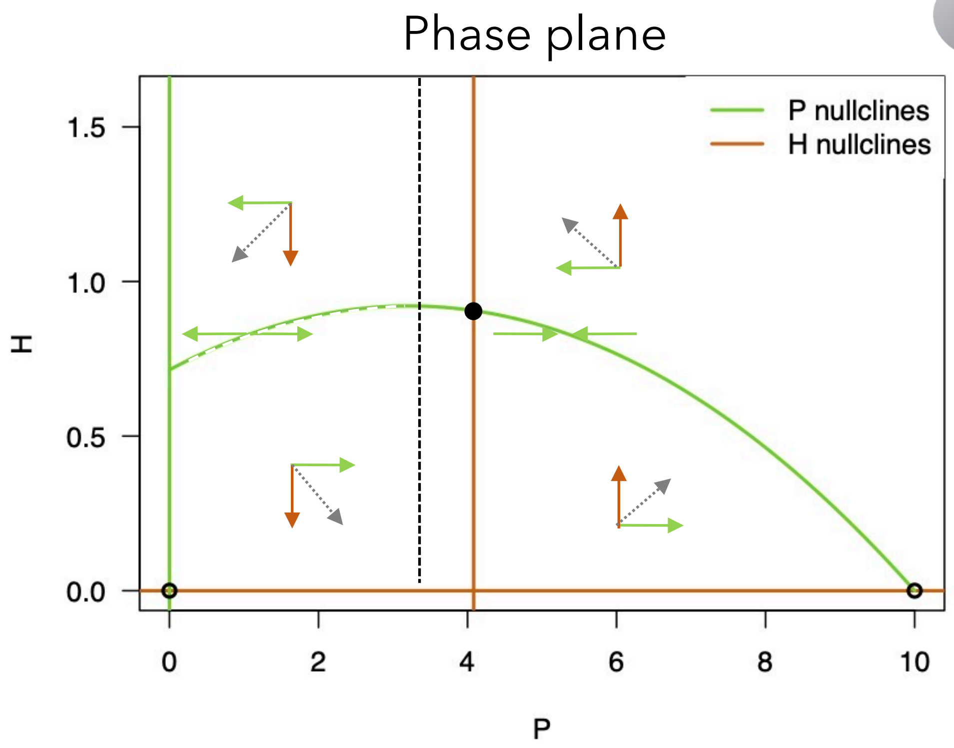
$$\frac{dH}{dt} = \varepsilon \frac{aPH}{1 + ahP} - mH$$

- First Step : Determine the Equilibria, solve: $\begin{cases} \dfrac{dP}{dt} = 0 \\ \dfrac{dH}{dt} = 0 \end{cases}$
- Graphically it's nullclines intersections:
  - for P growth $P = 0$

    $$H = r_0\left(\frac{1 + ahP}{a}\right)\left(1 - \frac{P}{K}\right)$$

  - for H growth $H = 0$

    $$P = \frac{m}{a(\varepsilon - hm)}$$



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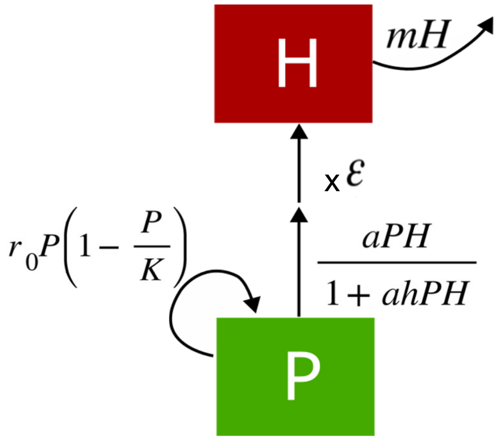

The Rosenzweig-MacArthur model (1963)

$$\frac{dP}{dt} = r_0P(1-\frac{P}{K}) - \frac{aPH}{1+ahP}$$

$$\frac{dH}{dt} = \varepsilon\frac{aPH}{1+ahP} - mH$$

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- Graphically it's nullclines intersections:
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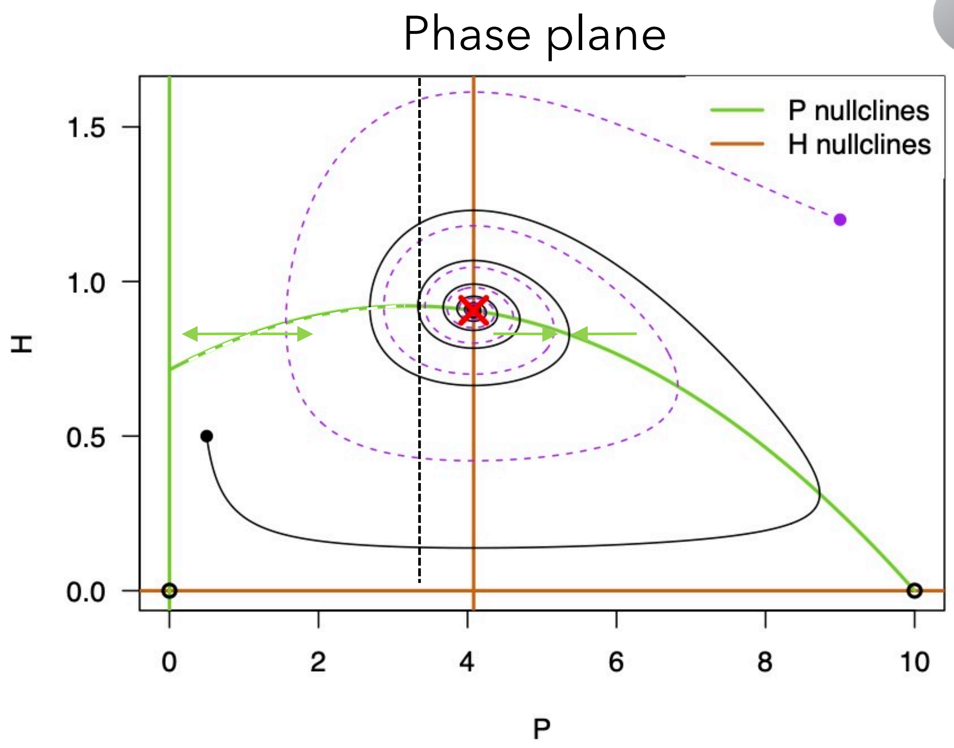
    $P=\dfrac{m}{a(\varepsilon-hm)}$



1. General analysis (1) Equilibria

The Rosenzweig-MacArthur model (1963)

$$\frac{dP}{dt} = r_0 P(1 - \frac{P}{K}) - \frac{aPH}{1 + ahP}$$

$$\frac{dH}{dt} = \varepsilon \frac{aPH}{1 + ahP} - mH$$

- First Step : Determine the Equilibria, solve: $\begin{cases} \frac{dP}{dt} = 0 \\ \frac{dH}{dt} = 0 \end{cases}$
- Symbolic calculus (Maxima, Mathematica, Matlab)
- In R we can get the numerical calculation of equilibria with the function `stode` of the package `rootSolve` or with the function `searchZeros` of the package `nleqslv`

When tractable, expresses P^* and H^* with the parameters (symbols) → general expression

$$\boxed{\begin{array}{l} \{ P^* = 0,\ H^* = 0 \} \\ \{ P^* = K,\ H^* = 0 \} \\ \begin{cases} P^* = \dfrac{m}{a(\varepsilon - hm)} \\ H^* = \dfrac{\varepsilon r_0 (aK(\varepsilon - hm) - m)}{a^2 K(\varepsilon - hm)^2} \end{cases} \end{array}}$$

- **Feasibility criteria**
- **Interpretation on parameters**

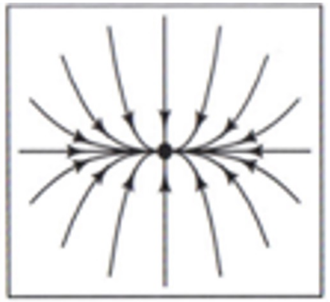
1. General analysis (1) Equilibria

For a 2-equation system in continuous time

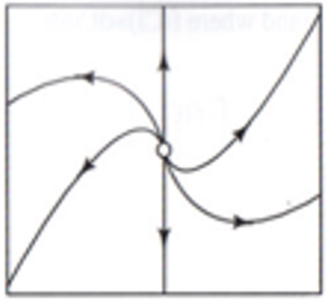
Phase portraits, typology of trajectories and stability for 2-equations models, some examples:

Monotonous trajectories

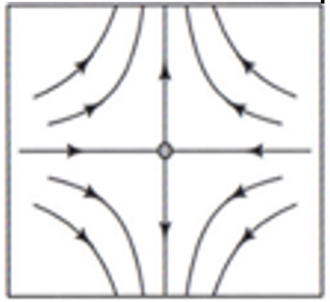
Stable node



Unstable node

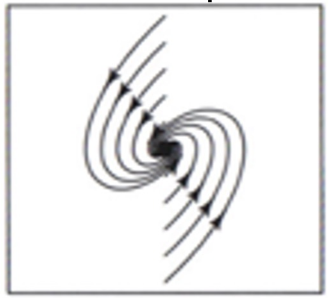


Unstable saddle point



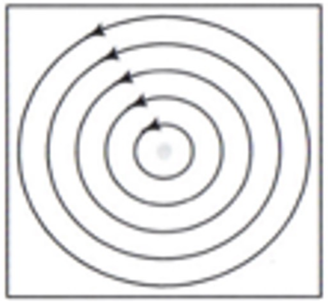
Oscillatory trajectories

Stable spiral

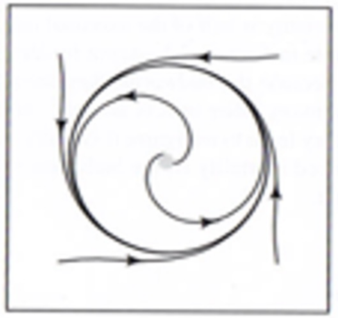


Unstable spiral

Neutral center

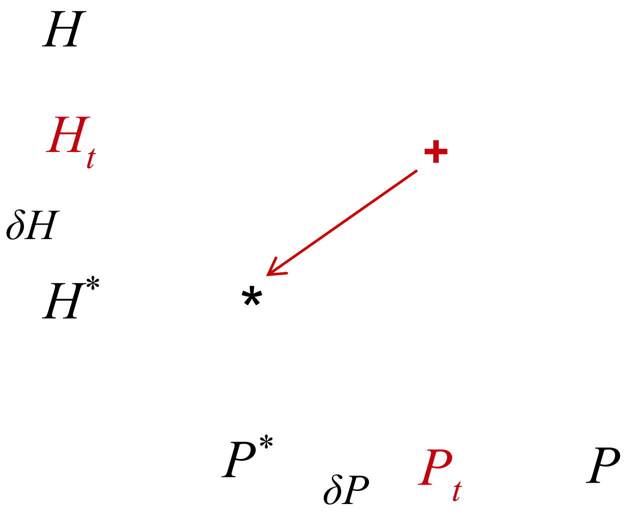


Limit cycle



1. General analysis (2) Local stability analysis

Determine the stability of each equilibrium by analyzing the Jacobian matrix at the equilibrium



$$\begin{pmatrix} \dfrac{dP_t}{dt} \\ \dfrac{dH_t}{dt} \end{pmatrix} = J \cdot v_t \quad \text{with} \quad v_t = \begin{pmatrix} \delta P \\ \delta H \end{pmatrix}$$

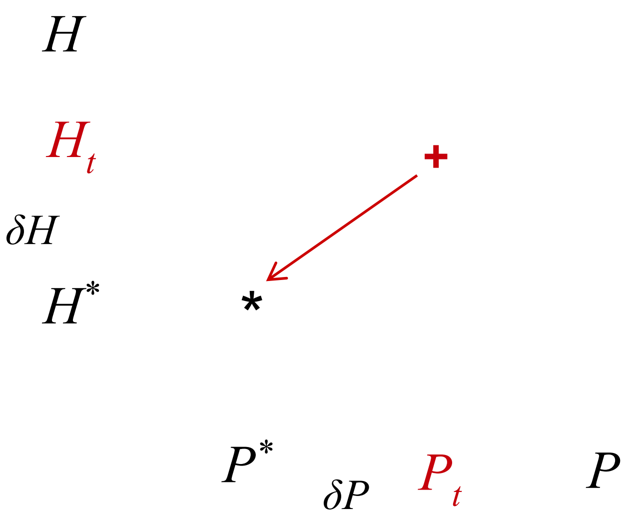
$$J = \begin{bmatrix} \dfrac{\partial \frac{dP}{dt}}{\partial P} & \dfrac{\partial \frac{dP}{dt}}{\partial H} \\ \dfrac{\partial \frac{dH}{dt}}{\partial P} & \dfrac{\partial \frac{dH}{dt}}{\partial H} \end{bmatrix}_{P^*,\, H^*}$$

Stability analysis = examining eigenvalues of J (real or complex numbers)

Stability criterium: Stable when the real parts of eigenvalues are negative

1. General analysis (2) Local stability analysis

Determine the stability of each equilibrium by analyzing the Jacobian matrix at the equilibrium



Equilibrium	**Eigenvalues**
$\{P^* = 0,\ H^* = 0\}$	$\{-m, r_0\}$
$\{P^* = K,\ H^* = 0\}$	$\{\frac{a\varepsilon K}{1+ahK} - m, -r_0\}$
$\left\{ P^* = \frac{m}{a(\varepsilon - hm)},\ H^* = \frac{\varepsilon r_0 (aK(\varepsilon - hm) - m)}{a^2 K (\varepsilon - hm)^2} \right.$	

Stability analysis = examining eigenvalues of J (real or complex numbers)

Stability criterium: Stable when the real parts of eigenvalues are negative

J from the function `fully.jacobian` and λ from the function `eigen` (package `rootSolve`)

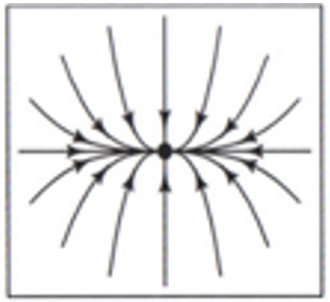
1. General analysis (2) Local stability analysis

For a 2-equation system in continuous time

Monotonous trajectories

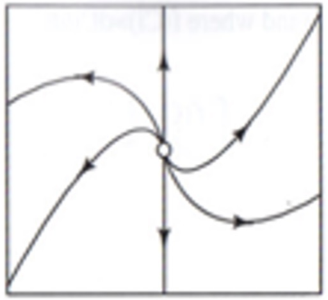
eigenvalues are real ($\lambda \in \mathbb{R}$,)

Stable node



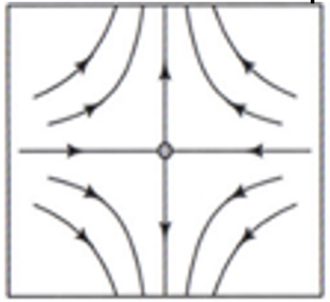
$-$	$-$

Unstable node



$+$	$+$

Unstable saddle point

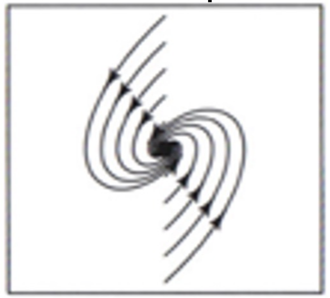


$-$	$+$

Oscillatory trajectories

eigenvalues are complex ($\lambda \in \mathbb{C}$)

Stable spiral

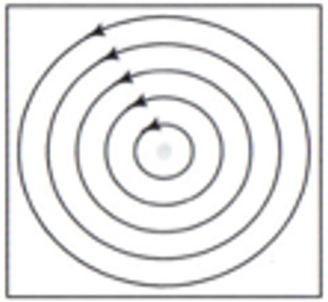


$-a \pm ib$	$-a \pm ib$

Unstable spiral

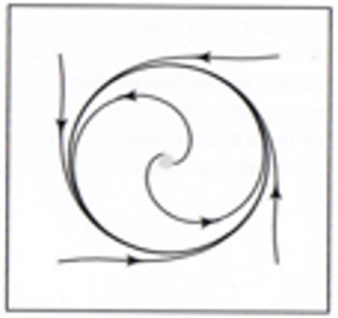
$+a + ib$	$+a \pm ib$

Neutral center



$0 \pm ib$	$0 \pm ib$

Limit cycle

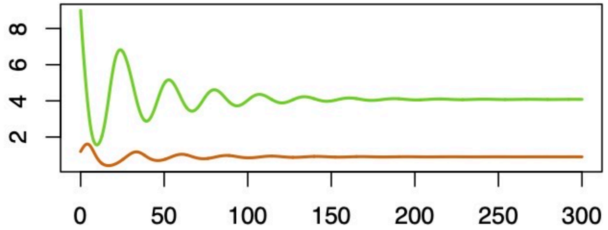


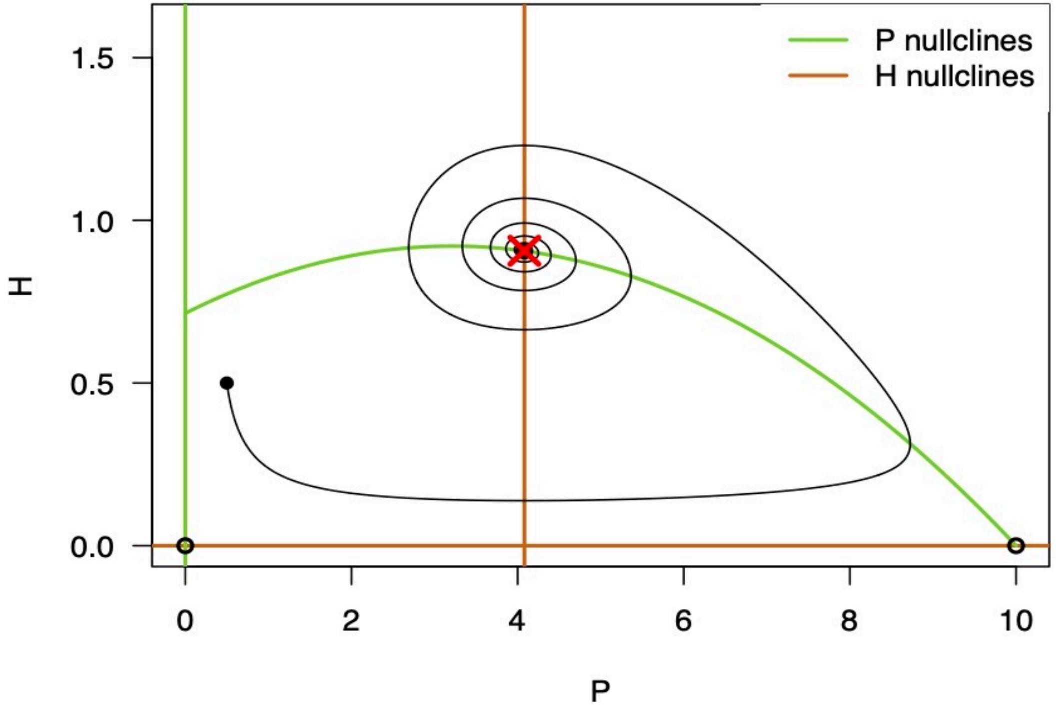
$+a \pm ib$	$+a \pm ib$

1. General analysis (2) Local stability analysis

Stable equilibrium

$m = 4$





(1) $\left\{ P^* = 0,\ H^* = 0 \right.$ $\lambda_1 = 0.5 \quad \lambda_2 = -0.4$

(2) $\left\{ P^* = K,\ H^* = 0 \right.$ $\lambda_1 = -0.5 \quad \lambda_2 = 0.153$

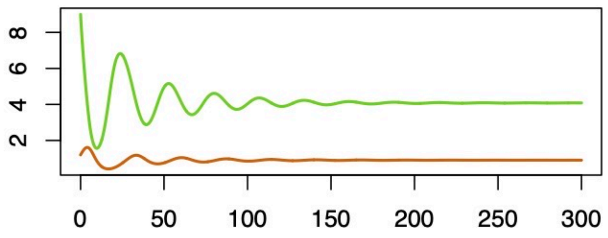
(3) $$\left\{ \begin{aligned} P^* &= \frac{m}{a(\varepsilon - hm)} \\ H^* &= \frac{\varepsilon r_0 (aK(\varepsilon - hm) - m)}{a^2 K(\varepsilon - hm)^2} \end{aligned} \right.$$

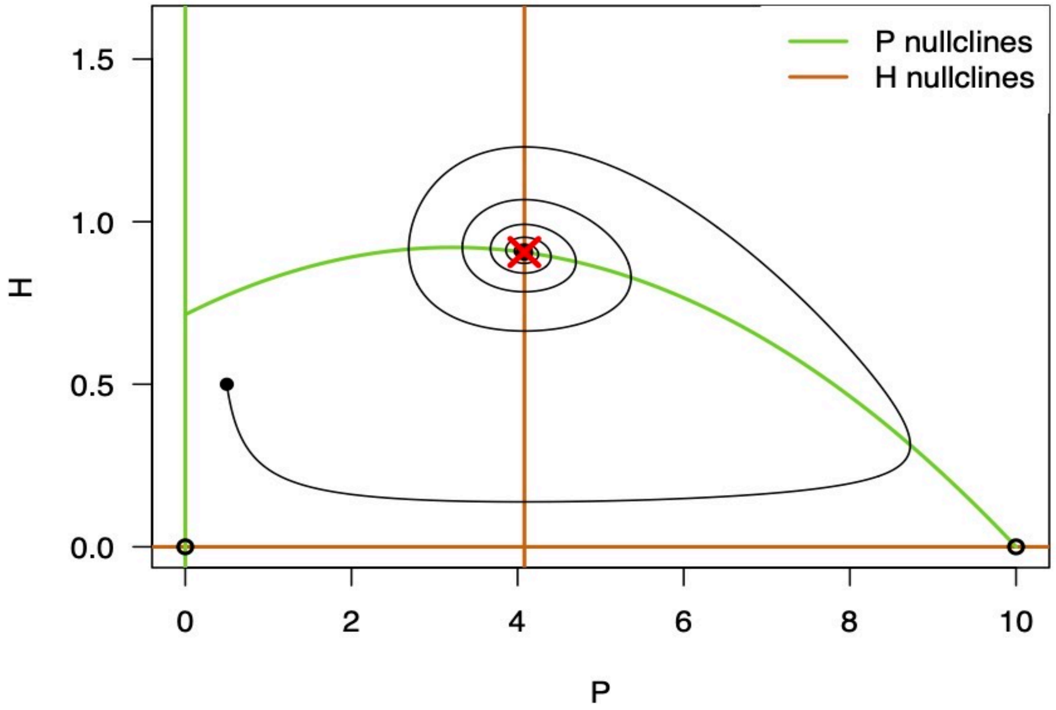
$\lambda_1 = -0.023 + i0.234$
$\lambda_2 = -0.023 - i0.234$

1. General analysis (2) Local stability analysis

Stable equilibrium

$m = 4$

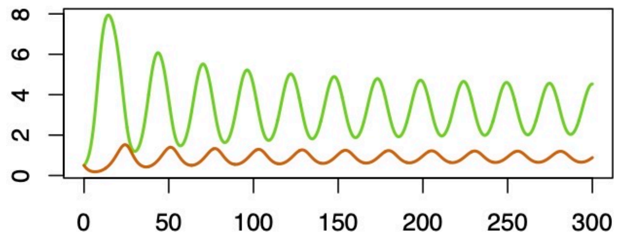


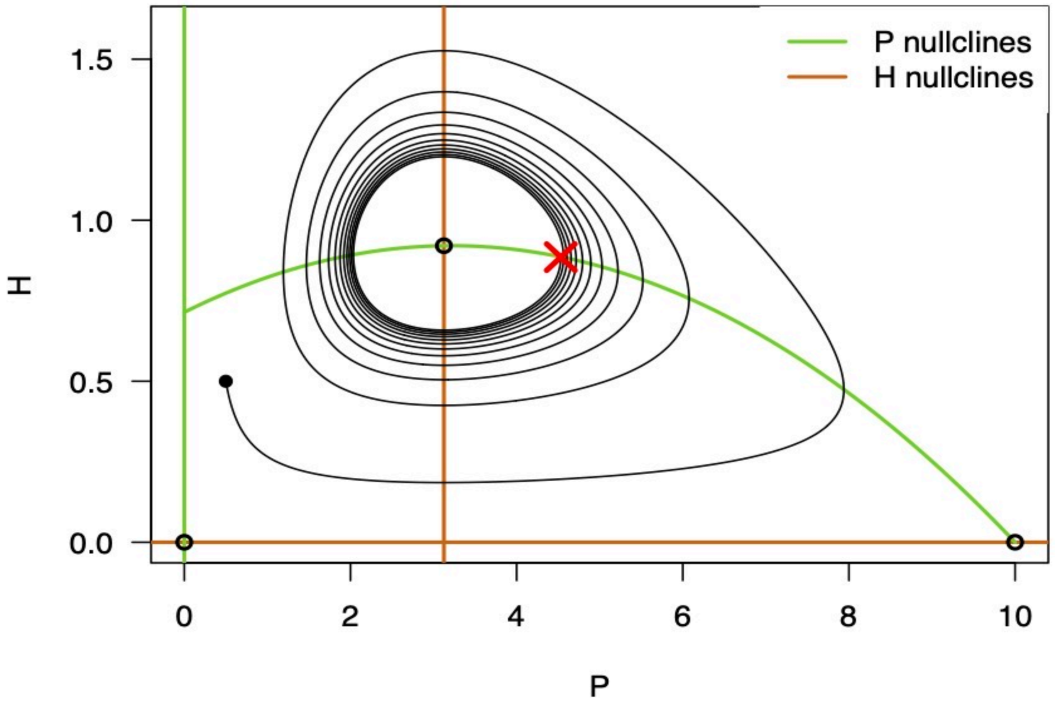


$$\lambda_1 = -0.023 + i0.234$$
$$\lambda_2 = -0.023 - i0.234$$

Limit cycle

$m = 3.5$



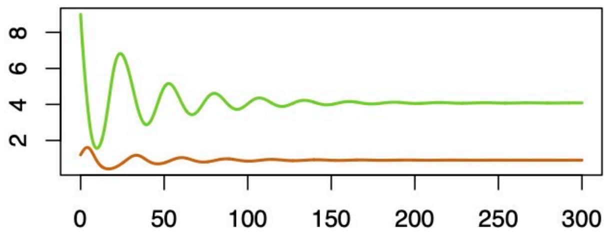


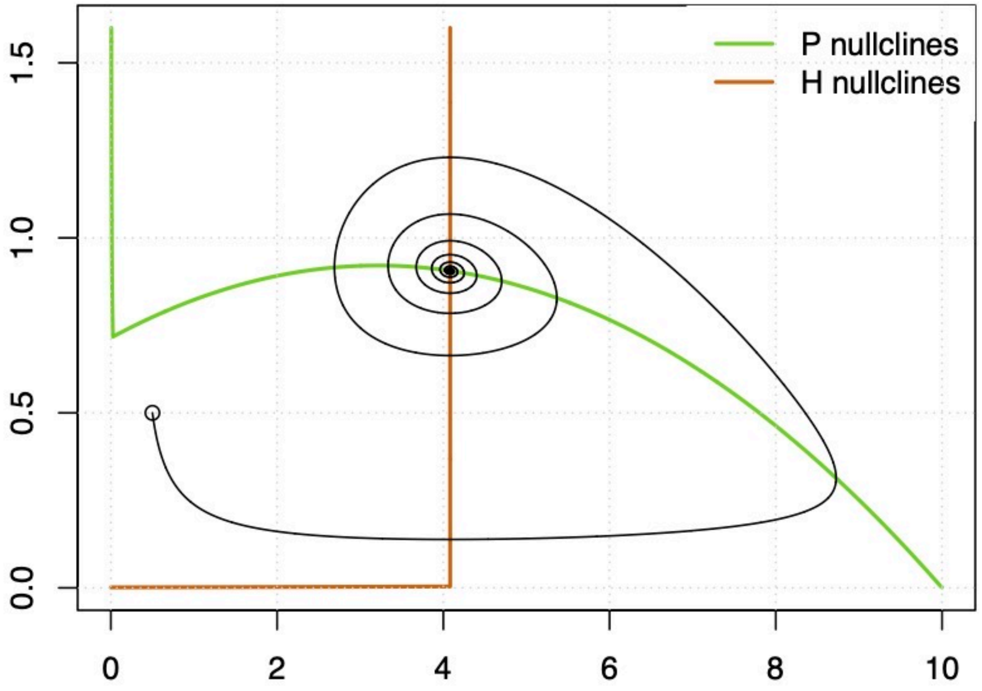
$$\lambda_1 = +0.002 + i0.253$$
$$\lambda_2 = +0.002 - i0.253$$

1. General analysis (2) Local stability analysis

Stable equilibrium

$m = 4$

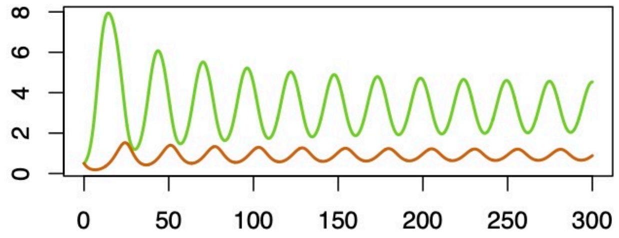


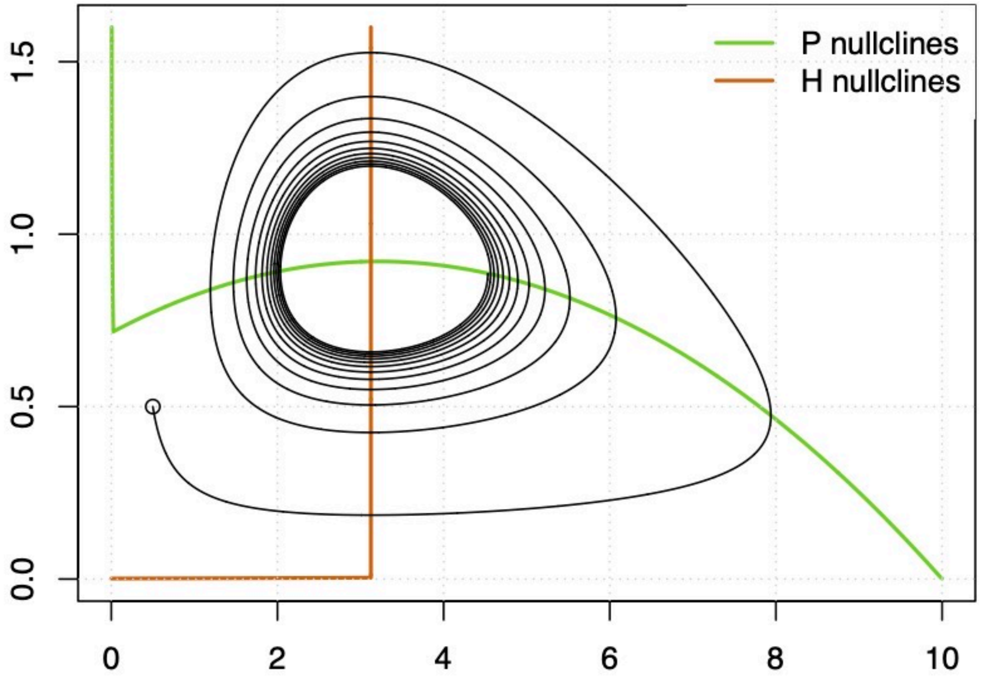


$$\lambda_1 = -0.023 + i0.234$$
$$\lambda_2 = -0.023 - i0.234$$

Limit cycle

$m = 3.5$



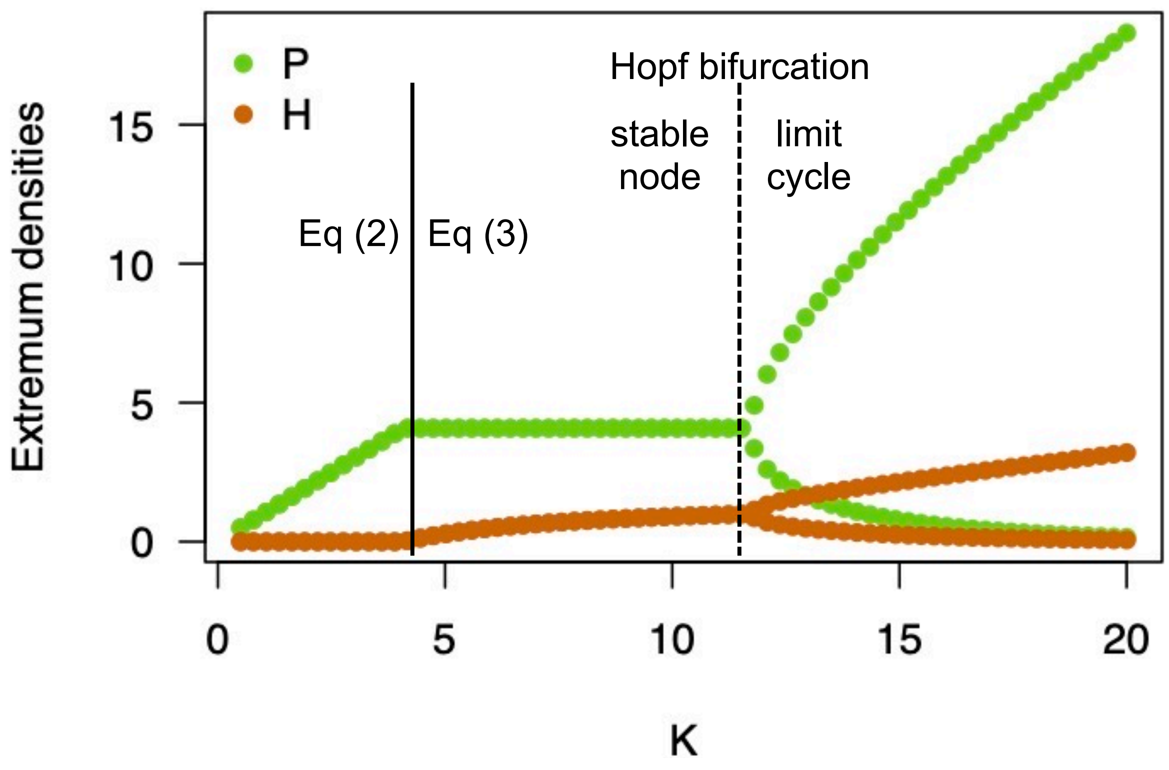


$$\lambda_1 = +0.002 + i0.253$$
$$\lambda_2 = +0.002 - i0.253$$

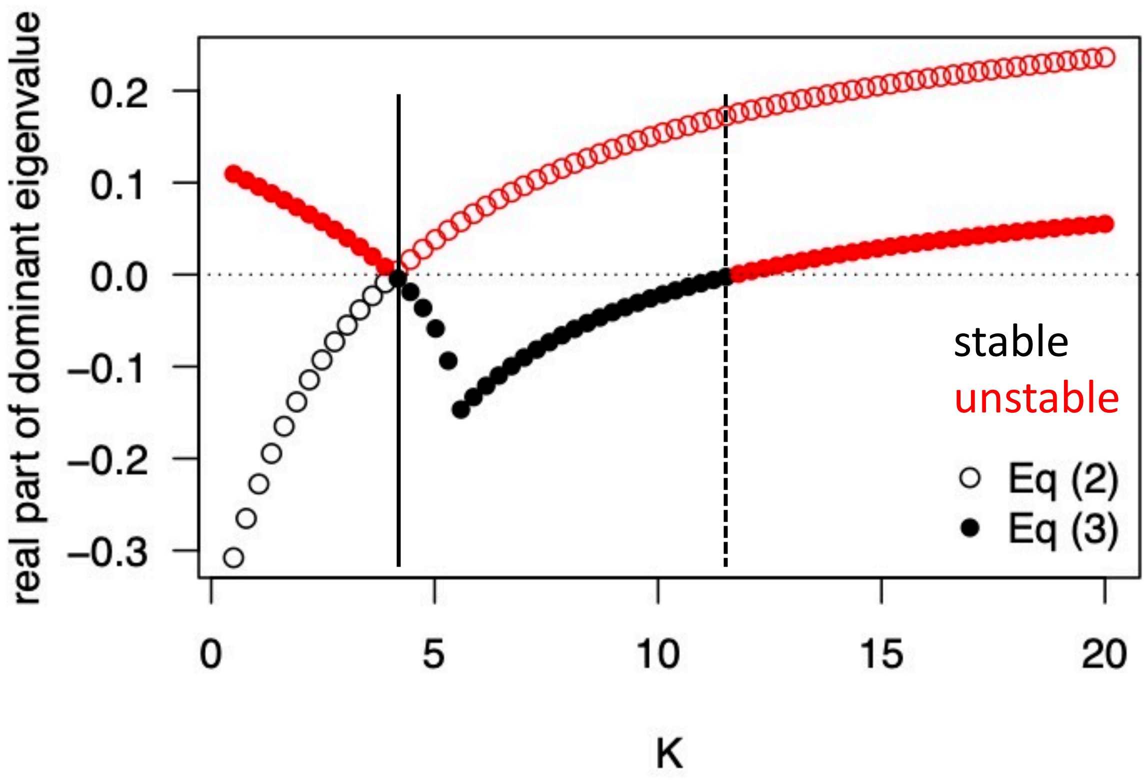
1. General analysis (3) Bifurcation diagrams

How does long-term (asymptotic) behaviour of the system vary with one parameter ?

Variables



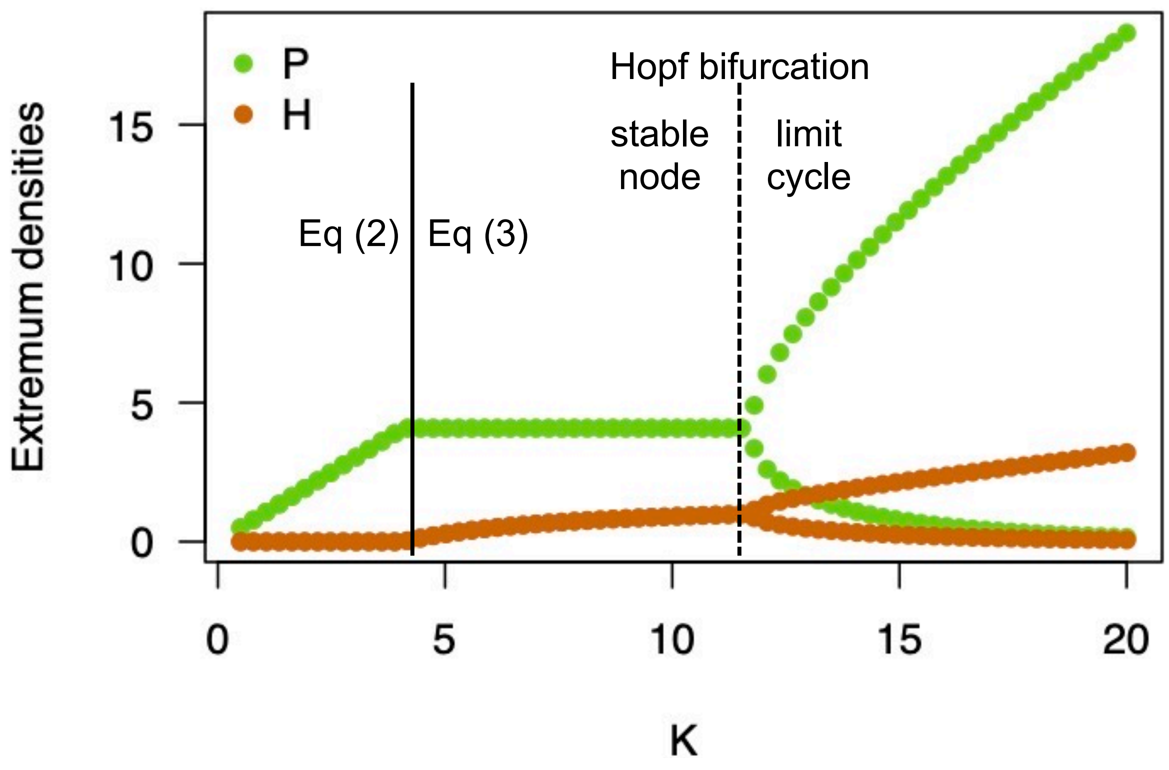
Stability



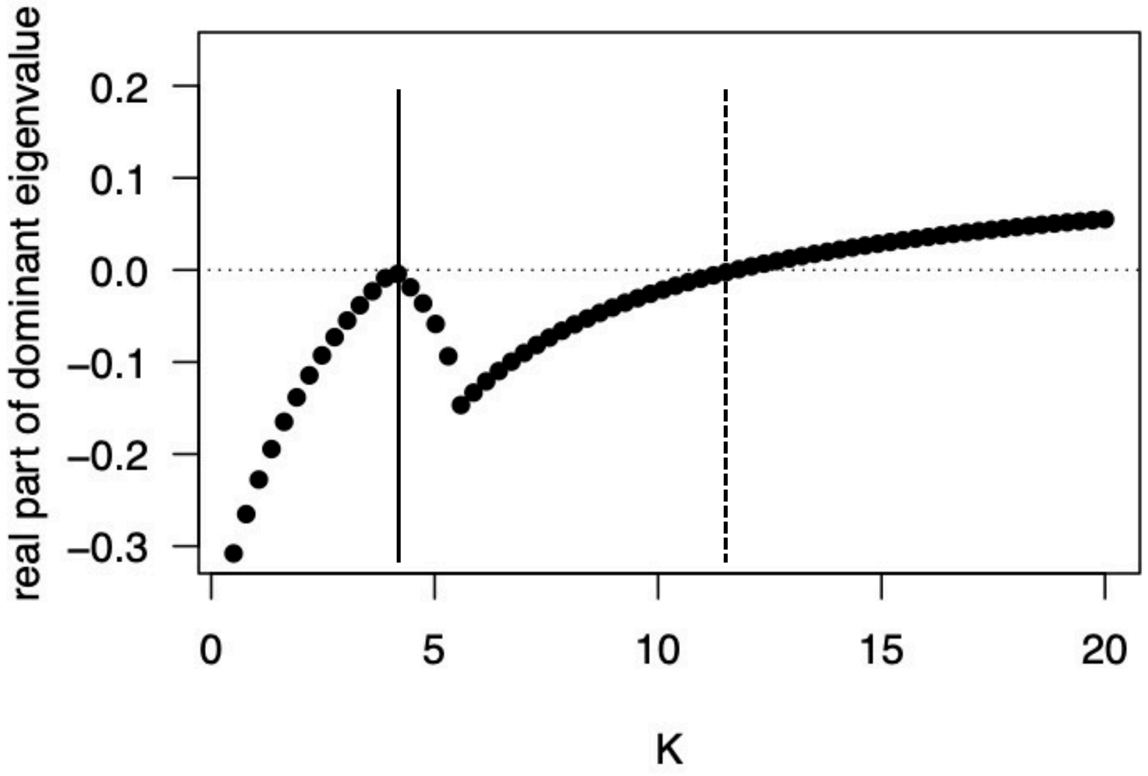
1. General analysis (3) Bifurcation diagrams

How does long-term (asymptotic) behaviour of the system vary with one parameter ?

Variables

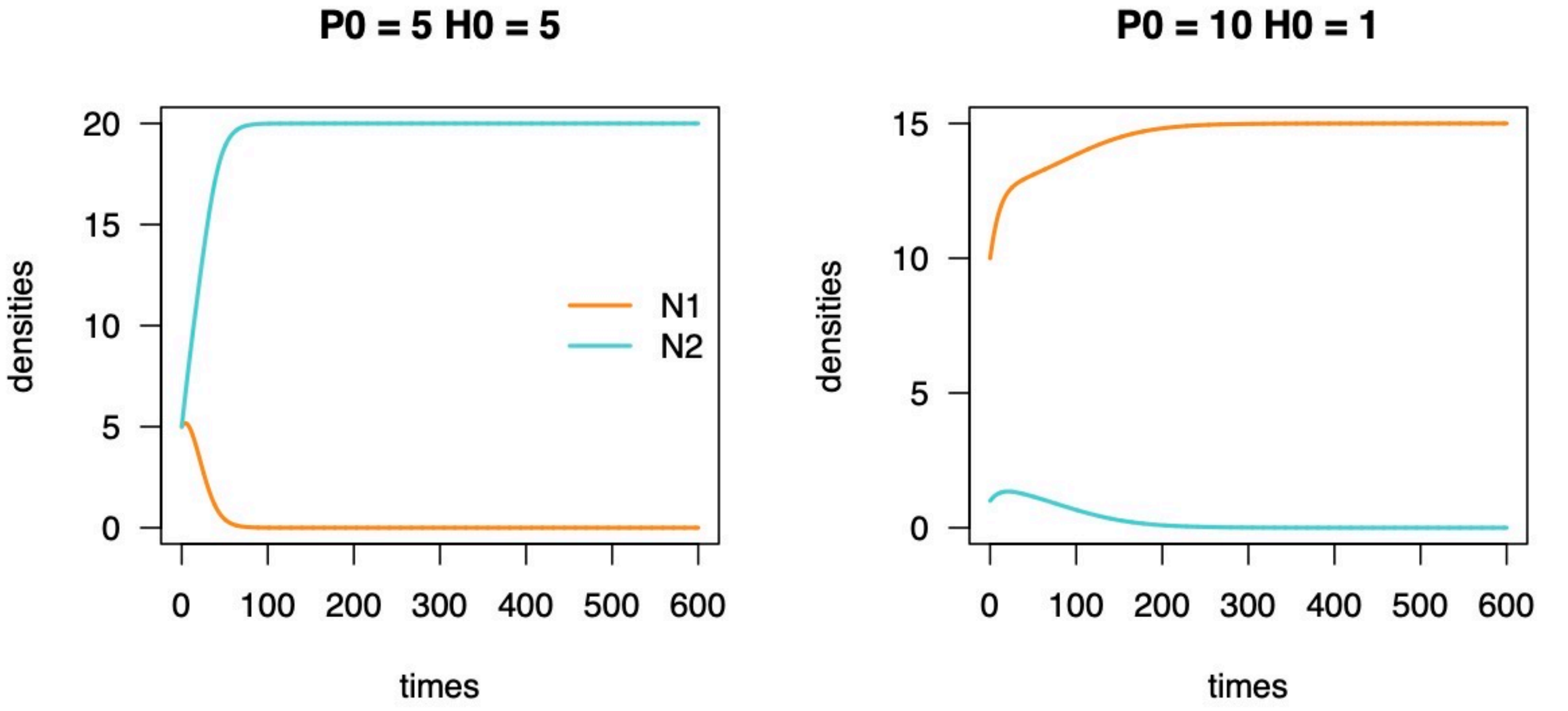


Stability



1. General analysis (4) Dependance to initial conditions

- We can observe several equilibrium points for the same parameters (historical effects)
- Example of Lotka-Volterra competition only initial densities differing:



- Screen series of initial densities to find all the equilibria using `searchZeros` in `nleqslv`

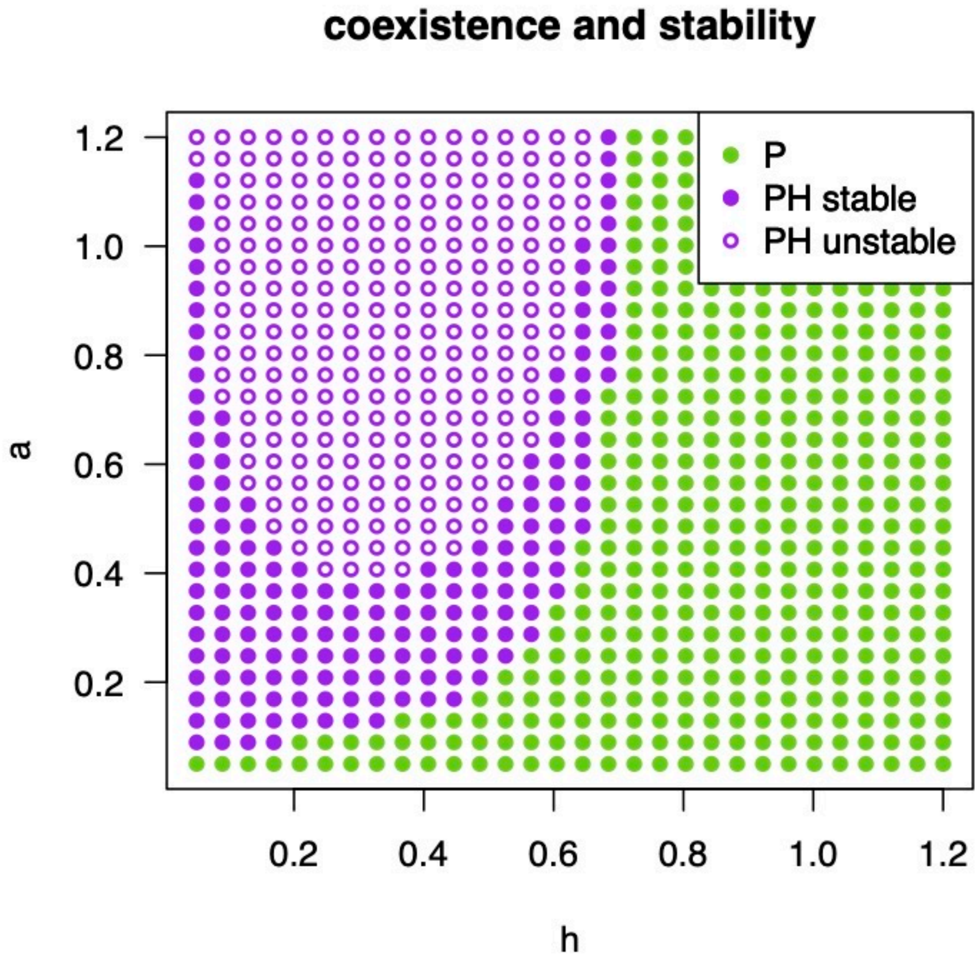
2. What simulation strategy?

1. Parameter exploration
2. Model comparison
3. Robustness of conclusions
4. *in sillico* experiment on synthetic data

2. Simulation strategy (1) Parameter exploration

- Generalisation of bifurcation diagrams with 2-D parameter space exploration.
- The aim is to identify all the possible behaviors of the model
  within 'reasonable' parameter ranges

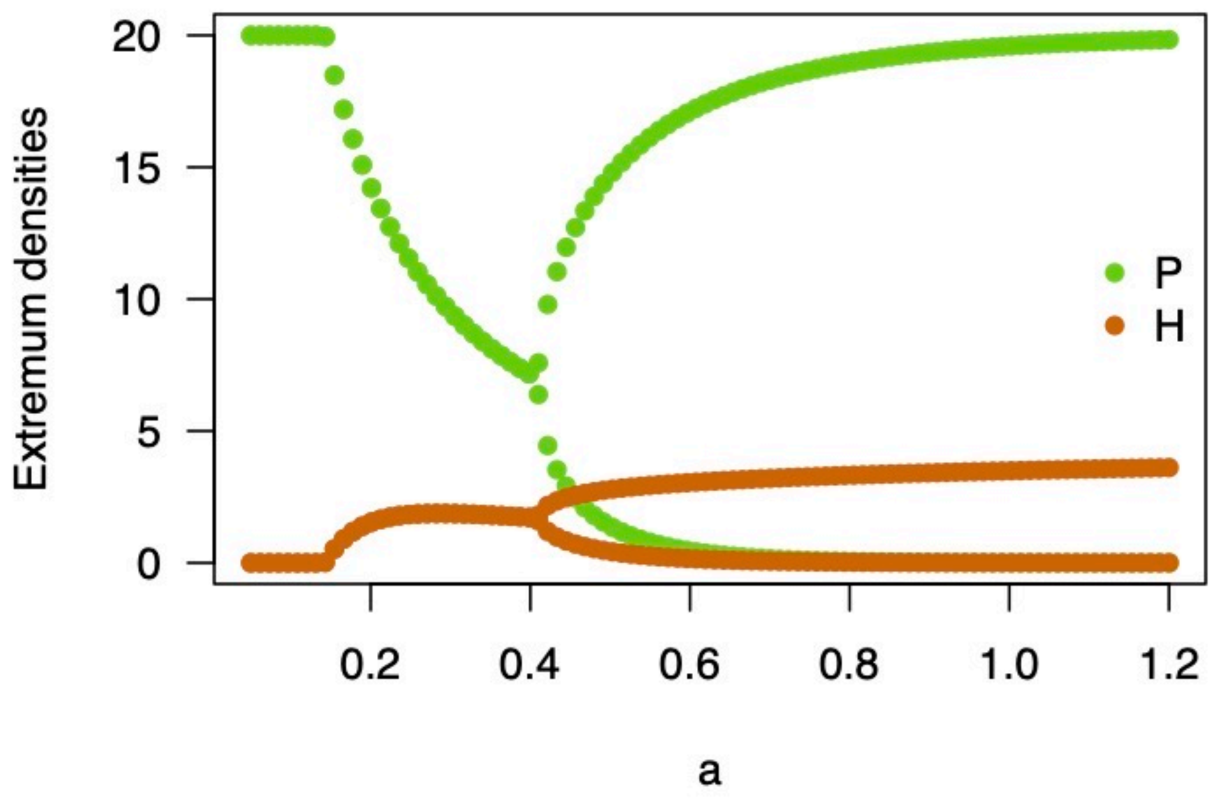
Here we vary h the handling time and
a the grazing rate

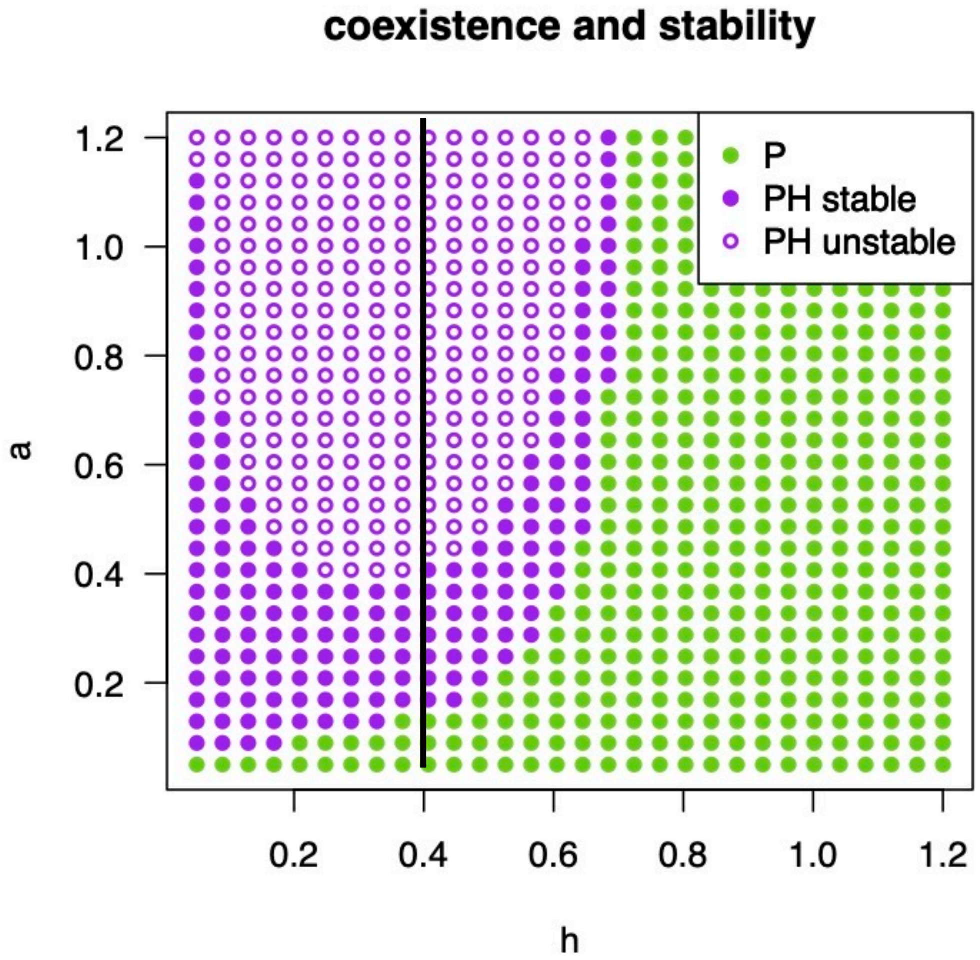


- h should be sufficiently small, for H to persist
- Increasing a allows to compensate high h
- Increasing a destabilizes the system

2. Simulation strategy (1) Parameter exploration

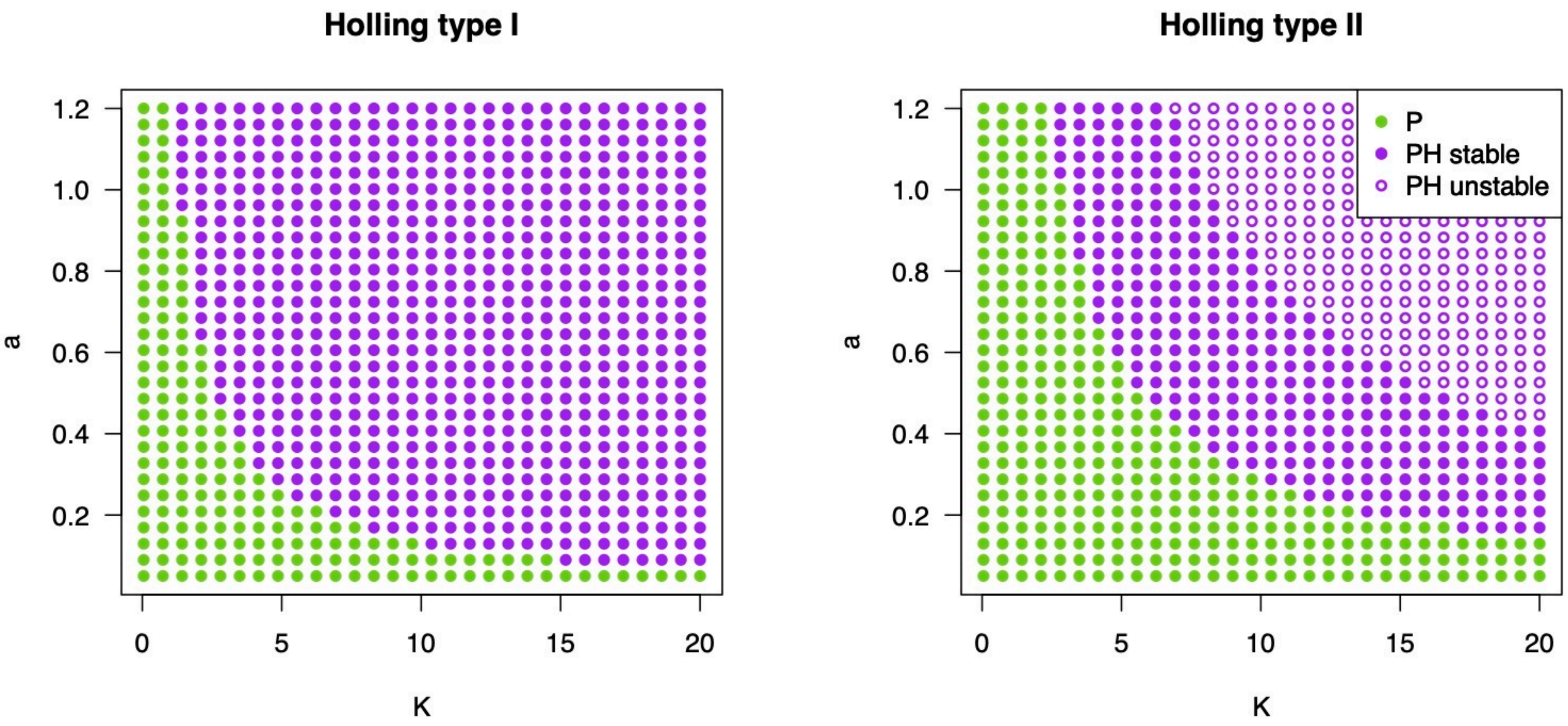
- Generalisation of bifurcation diagrams with 2-D parameter space exploration.
- The aim is to identify all the possible behaviors of the model
  within 'reasonable' parameter ranges





2. Simulation strategy (2) Model comparison

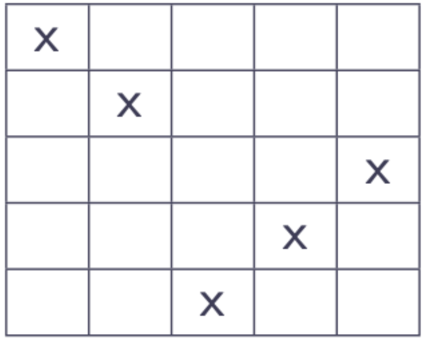
Here we compare models with different functional responses for the herbivore



In our system a type I (linear) increases persistence and stability compared to a type II (saturating) functional response because it creates a lag between P and H growths.

2. Simulation strategy (3) Robustness of conclusions

- Sampling strategies (coverage / interpretability / cost):
  - One factor at a time; empirical data fix some parameters or restrain ranges.
  - Complete plan
  - Latin Hypercube sampling / Sobol



- Sensitivity analysis:
  - Check the sensitivity of the results to variation in parameters ± 10%
  - Methods to discard factors for further experiments (Morris / Saltelli)

Refs: Saltelli et al. (2004). Sensitivity analysis in practice: a guide to assessing scientific models. *Chichester, England*.

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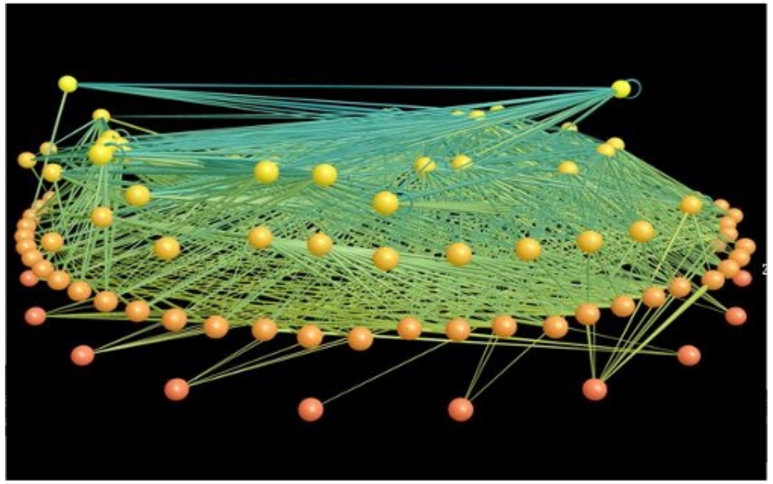
2. Simulation strategy (4) Experiments with synthetic data

Complex system experiments not feasible in nature → create realistic virtual data, for example food webs having the same general properties as natural food webs, to do perturbation experiments and observe how this would modify food we structure.



❖ Some useful references

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