Theory-driven analysis of Ecological data – Day 1

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

13:45-15:45 **How to build and analyze a model?**

Isabelle Gounand

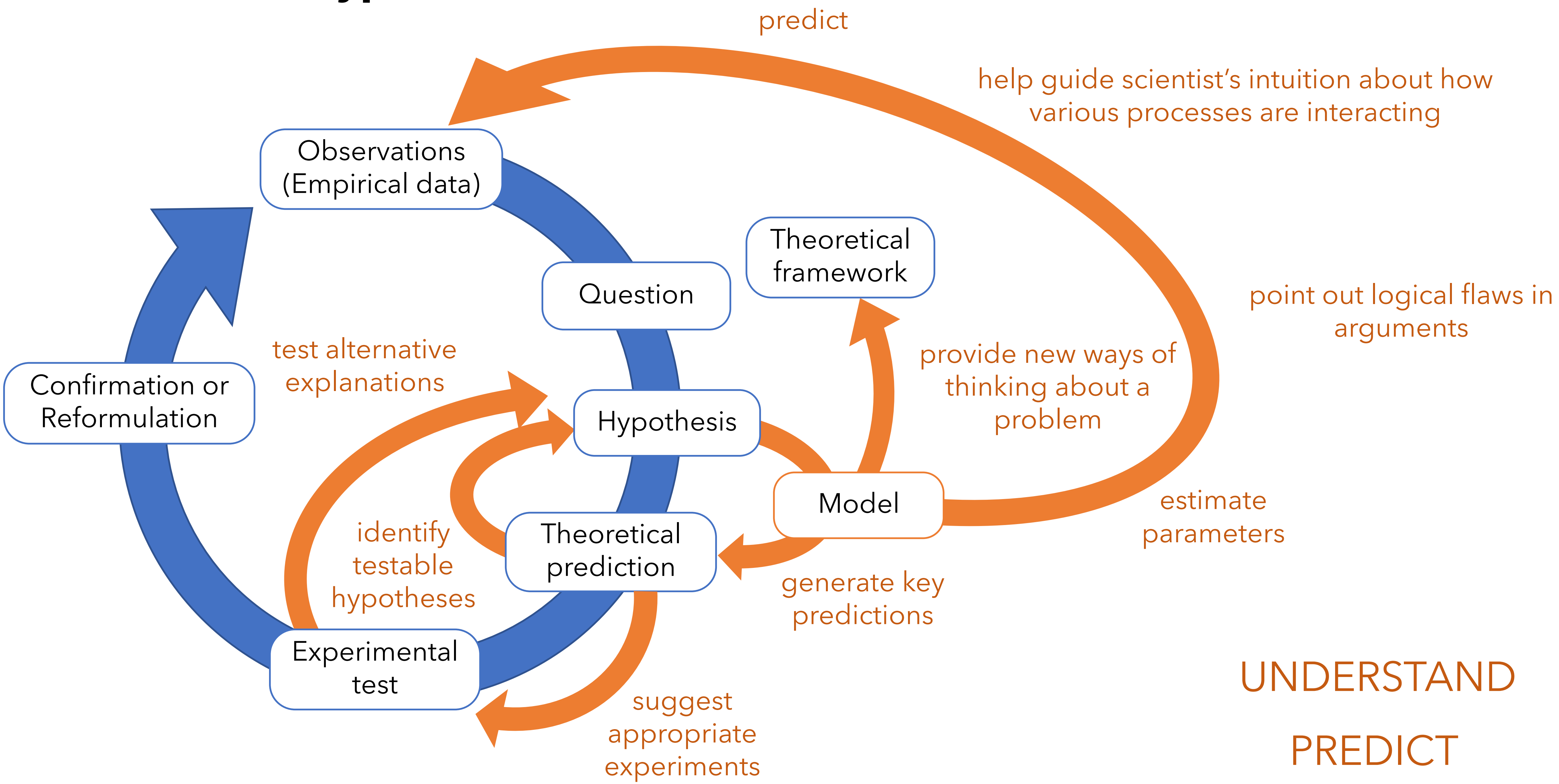
CESAB, Montpellier,
March 16, 2026

What types of theoretical models in ecology?

Content

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

1. What model type for what aim?

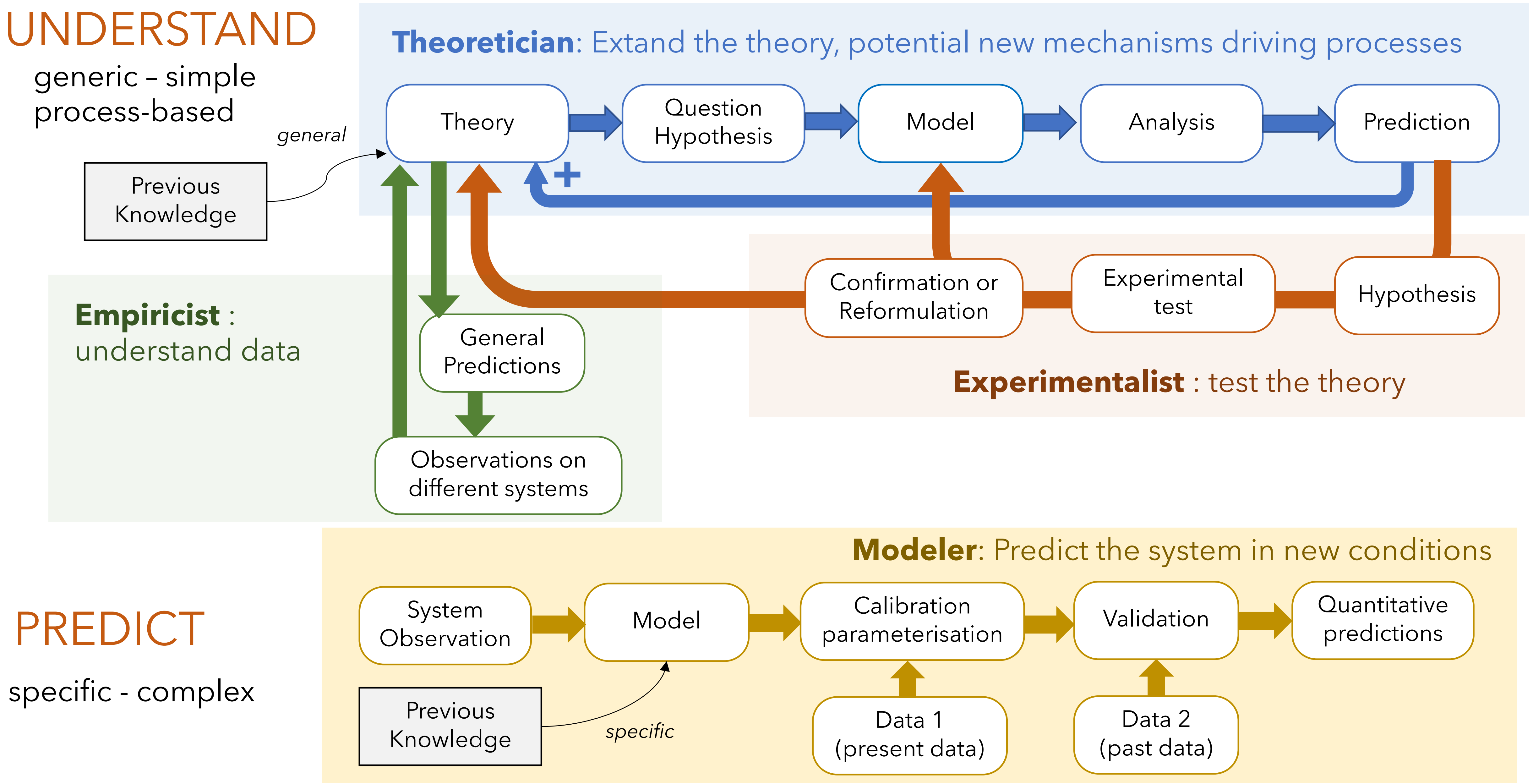


UNDERSTAND

PREDICT

adapted from Otto and Day 2007

1. What model type for what aim?

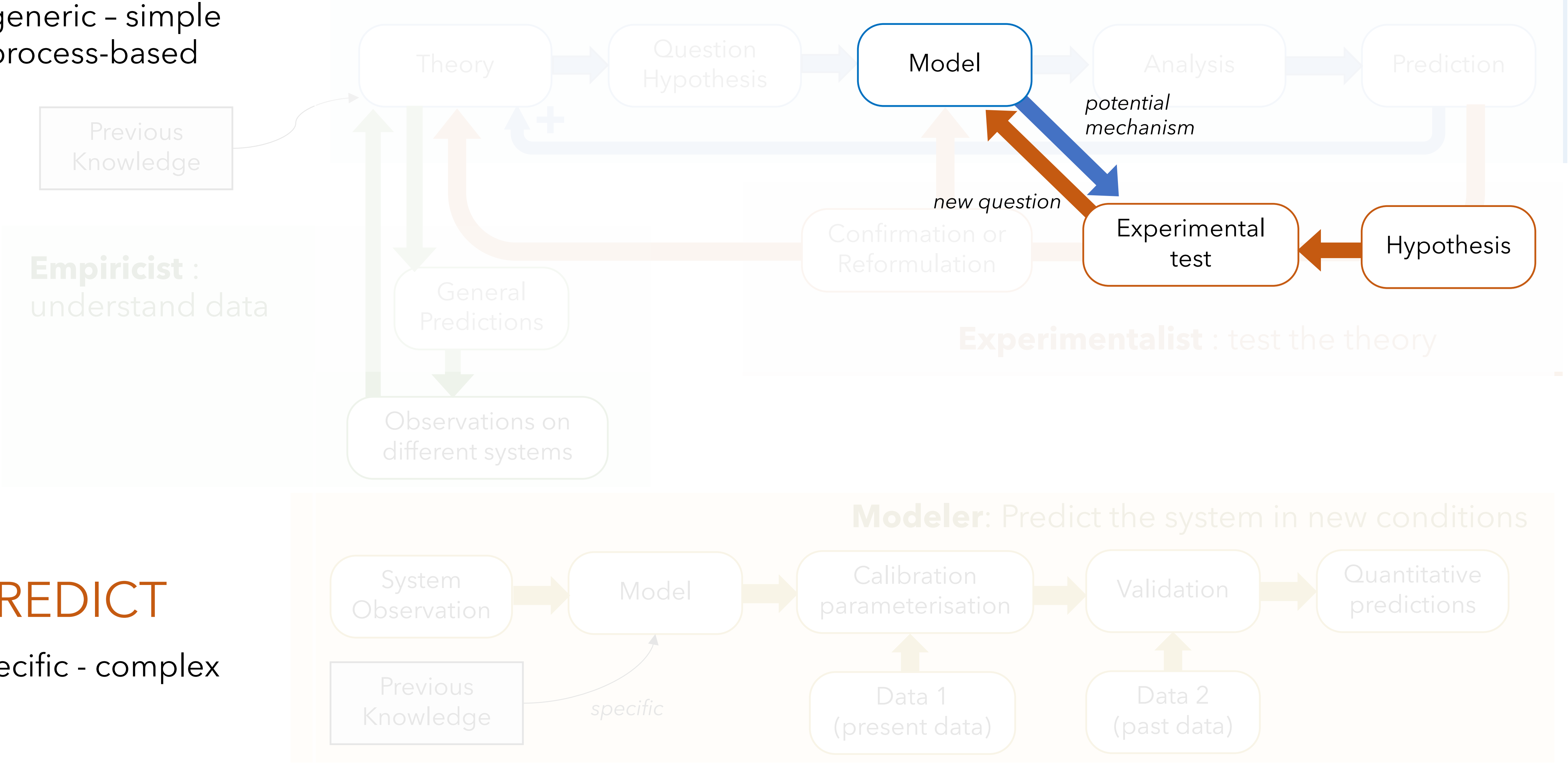


1. What model type for what aim?

UNDERSTAND

generic – simple
process-based

Theoretician - Experimentalist : understand experimental results



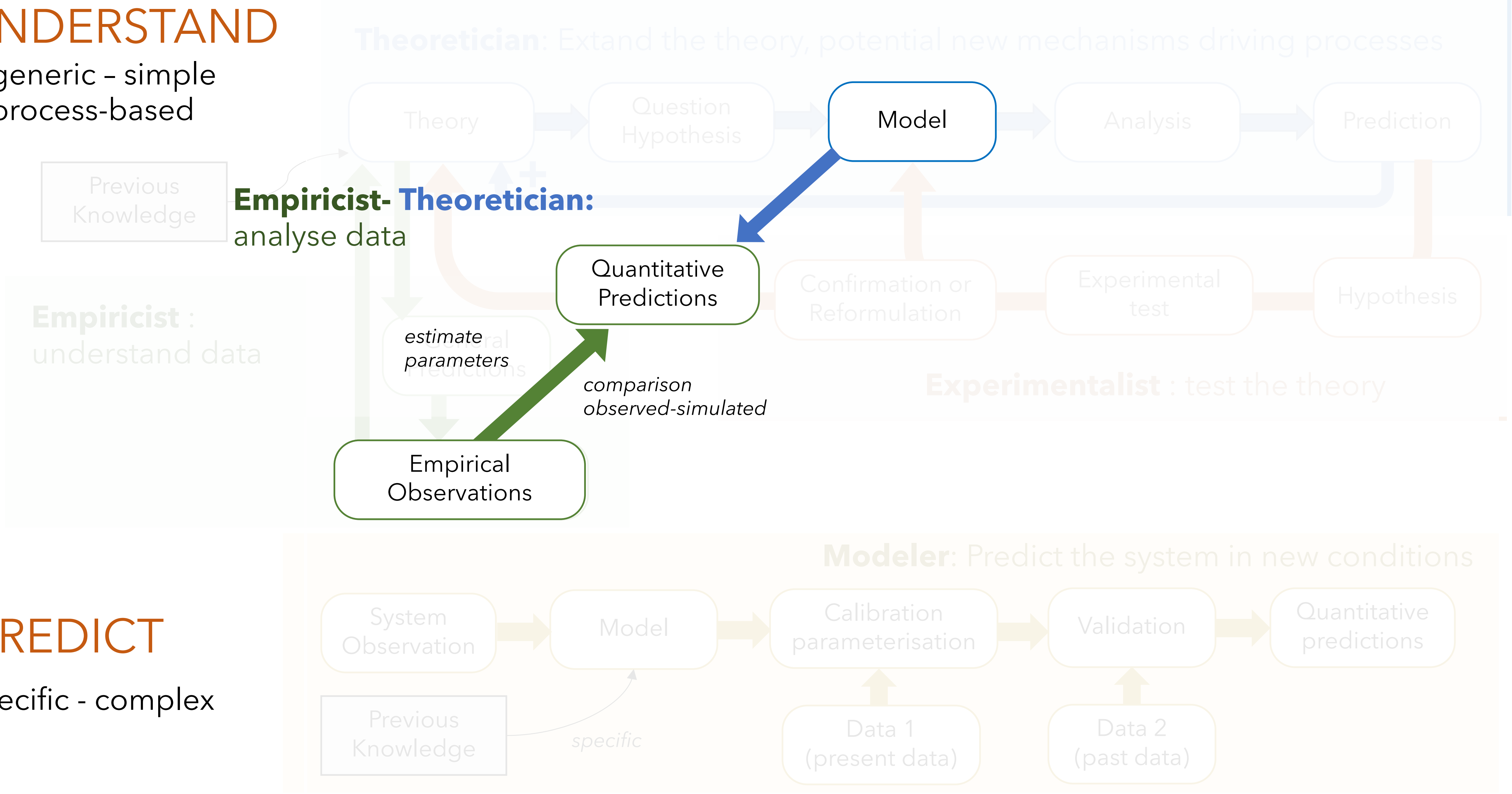
PREDICT

specific - complex

1. What model type for what aim?

UNDERSTAND

generic – simple
process-based

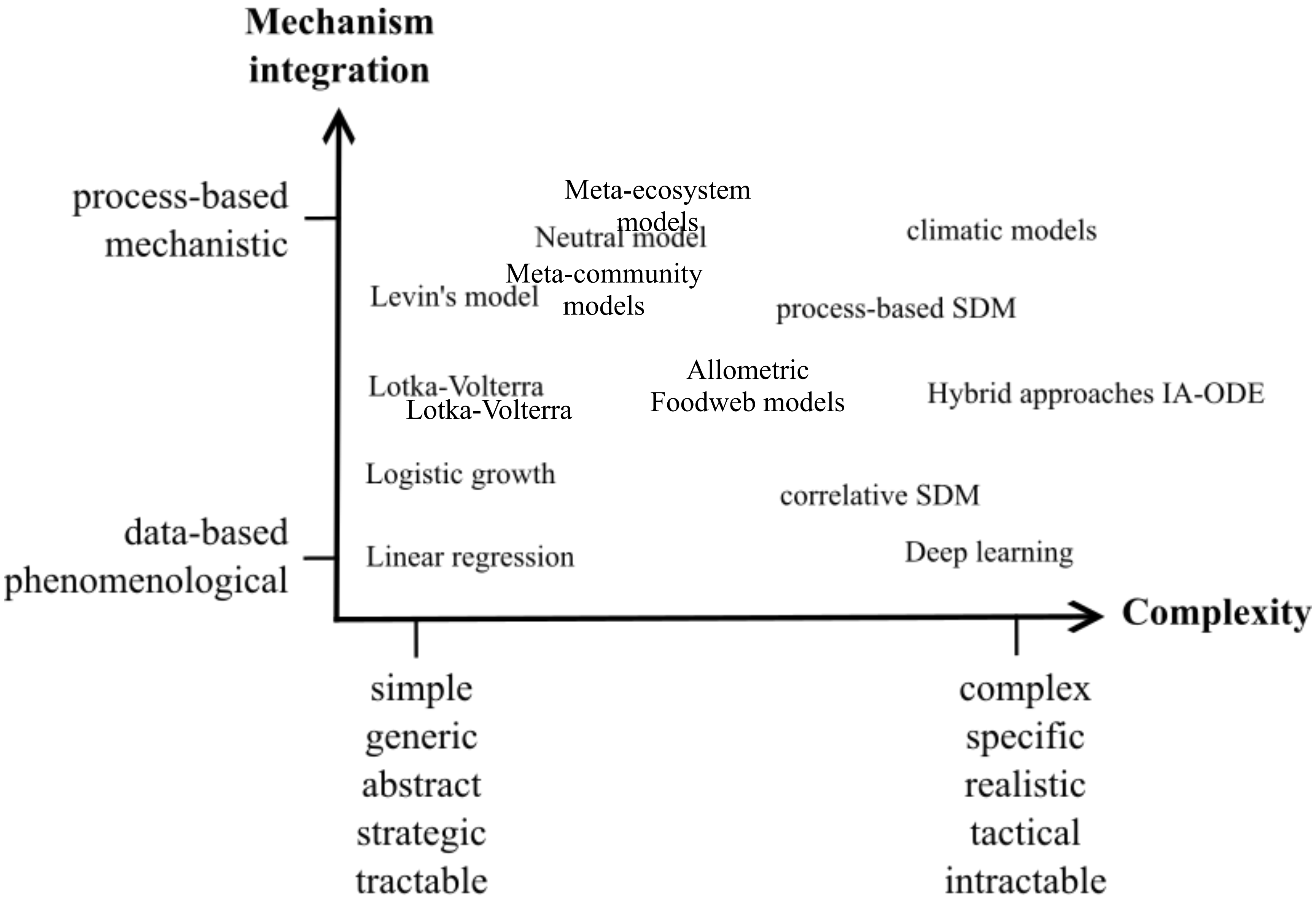


PREDICT

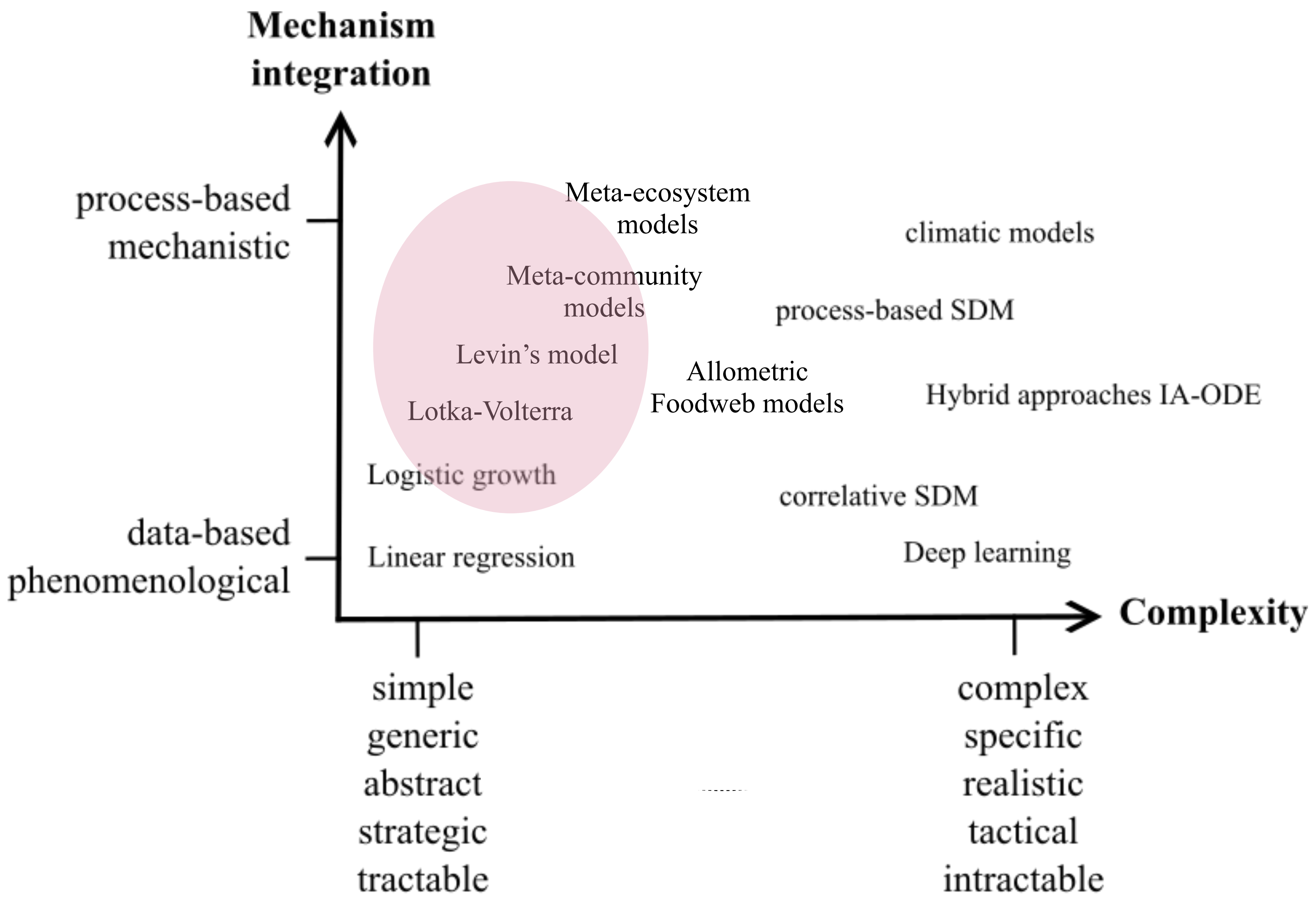
specific - complex

1. What model type for what aim?

Panorama of model types



1. What model type for what aim? Panorama of model types



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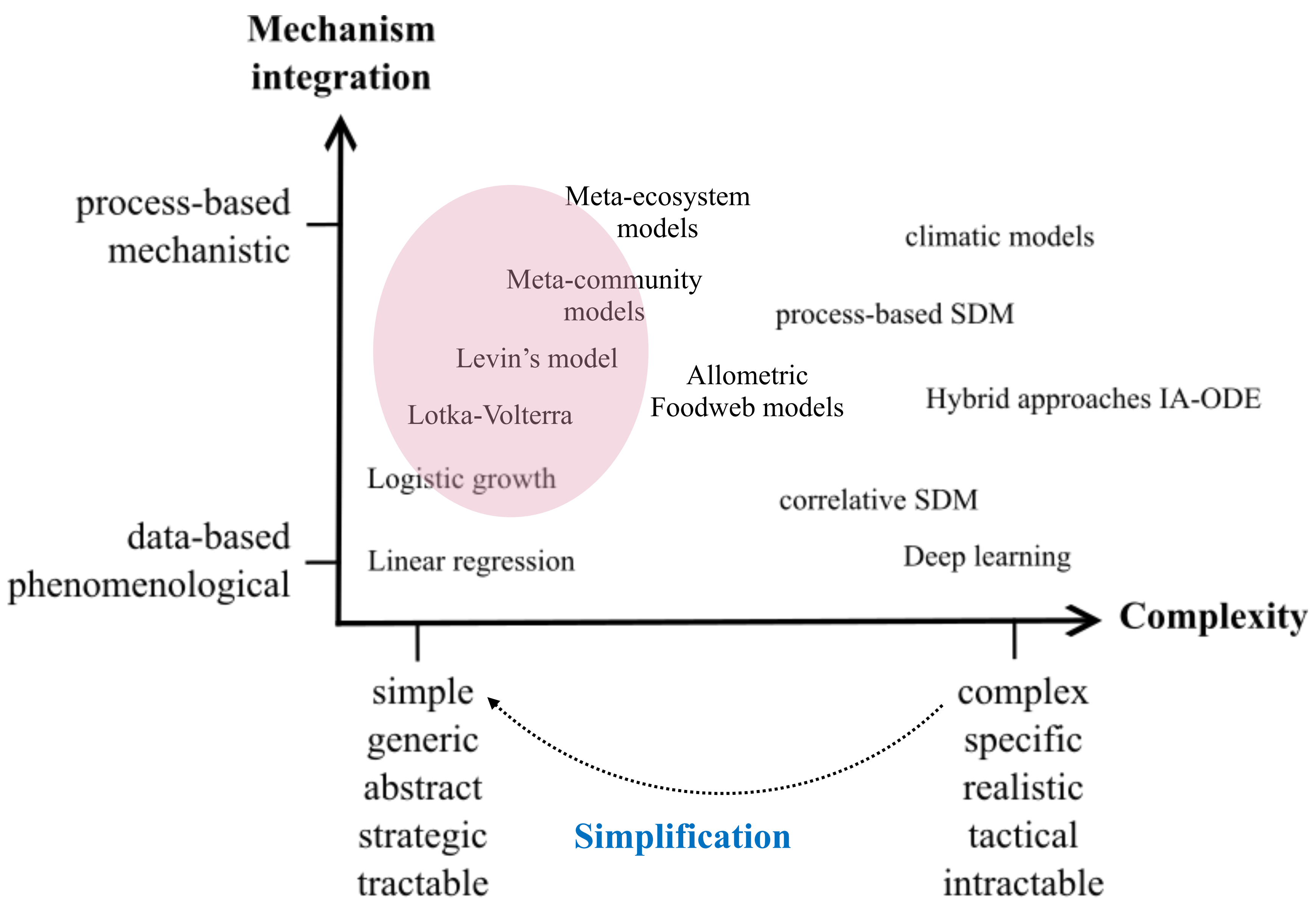

Simplification approaches

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

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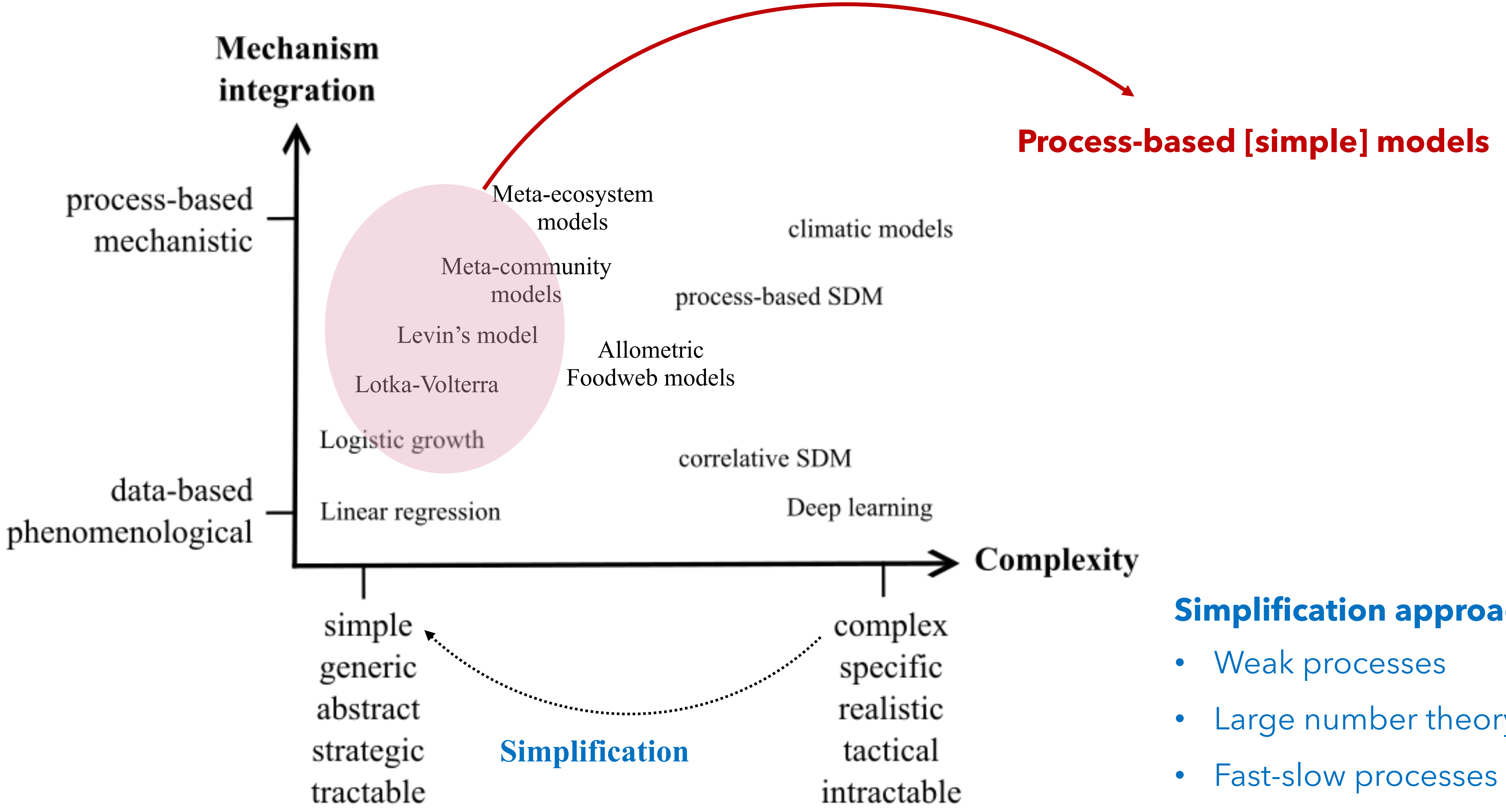
Panorama of model types



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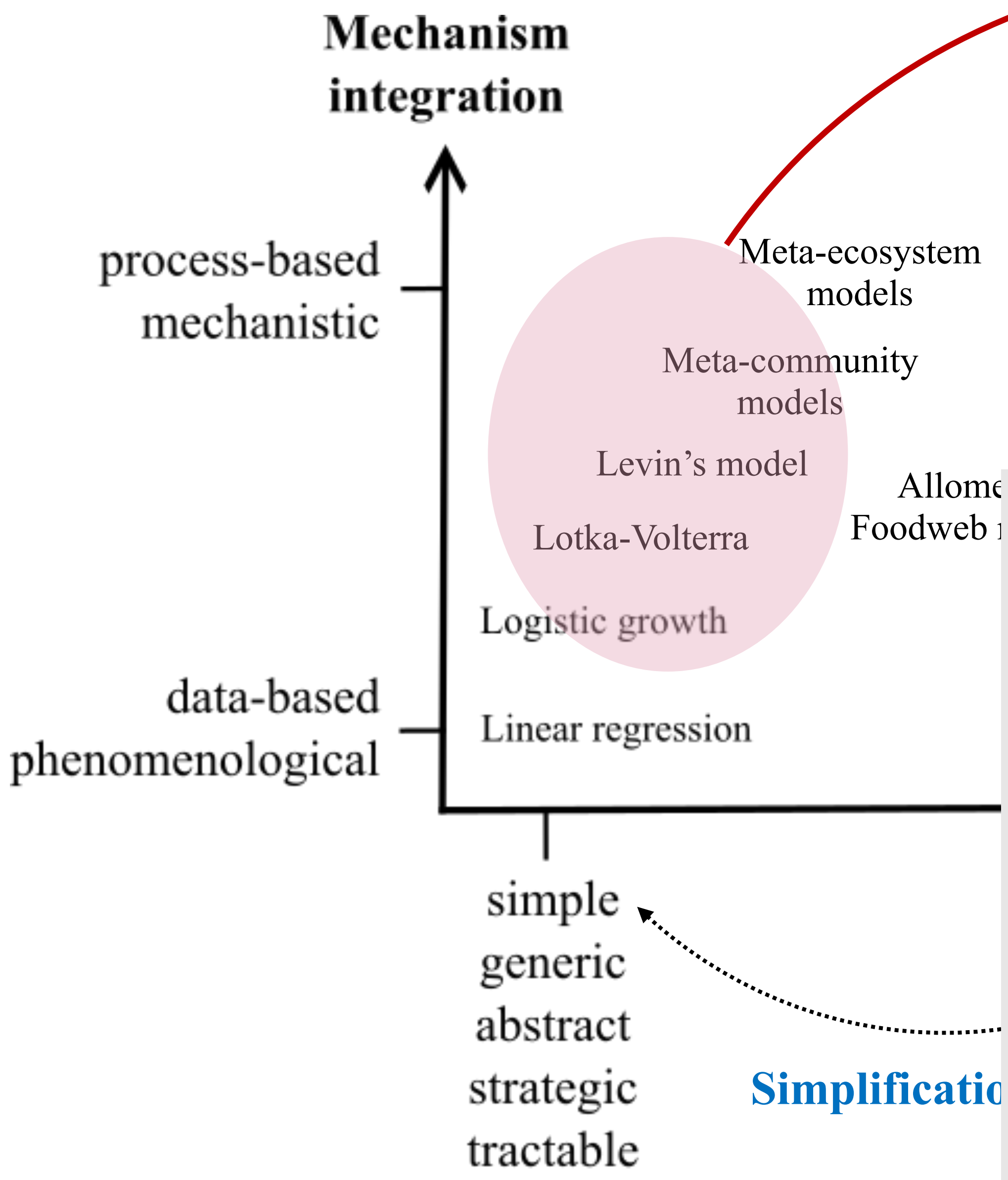
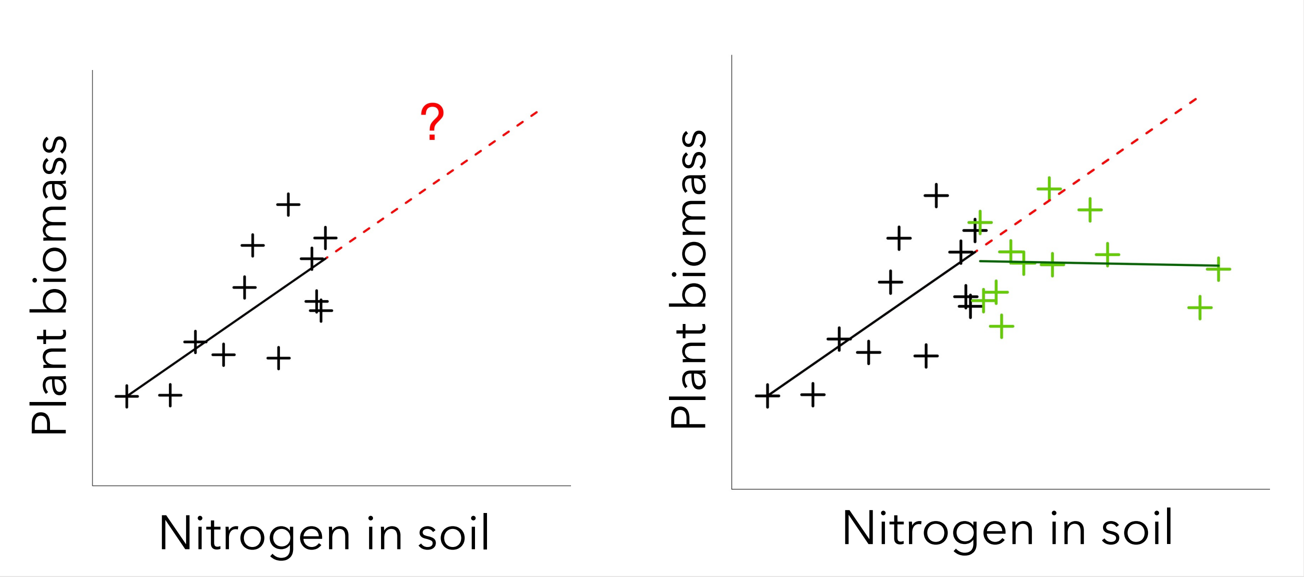


Process-based [simple] models

- Extrapolate
- Generalize
- Understand

A simple example of stats vs process-based model



2. 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?

2. What system? What question? What hypotheses?

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

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Landscape features and plant diversity

Can spatial heterogeneity promote plant diversity?

Scales: landscape, time scale of many generations

System features: spatial structure and connectivity

Variables: plant patch occupancy

Processes:
dispersal, species niche, trait evolution (?) etc.

2. What system? What question? What hypotheses?

System + Question → **Scale** → What can we ignore? → What assumptions do we make?
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Plant – herbivore interactions

Can grazing increase primary production?

Scales: ecosystem, demographic time scale

System features: trophic structure

Variables: plant and herbivore biomasses

Processes:
consumption fluxes, mortality, recycling etc.

2. What system? What question? What hypotheses?

System + Question → **Scale** → What can we ignore? → What assumptions do we make?
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Parasite physiology

Which factors determine individual development?

Scale: lifespan of an individual

System features: physiological paths, environment

Variables: individual stages or metabolic functions

Processes:
Physiology, morphology, behavior, life-cycle etc.

2. 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.

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)

2. What system? What question? What hypotheses?

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

Assumptions ⟶ Model ⟶ Analysis ⟶ Prediction

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

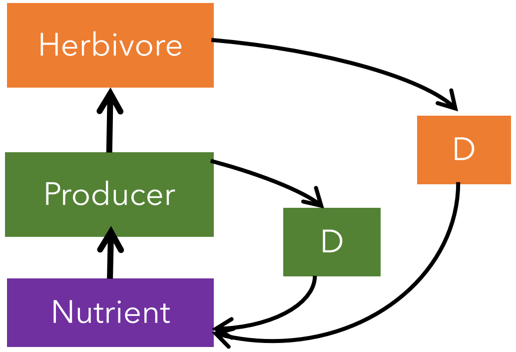
(Servedio et al. 2014)

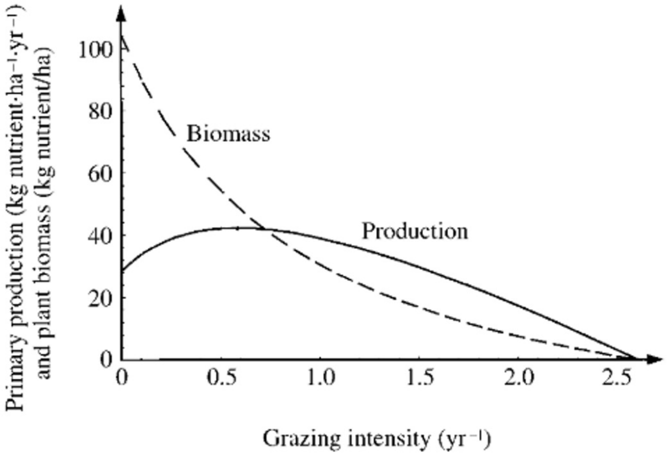
2. What system? What question? What hypotheses?

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)

2. What system? What question? What hypotheses?

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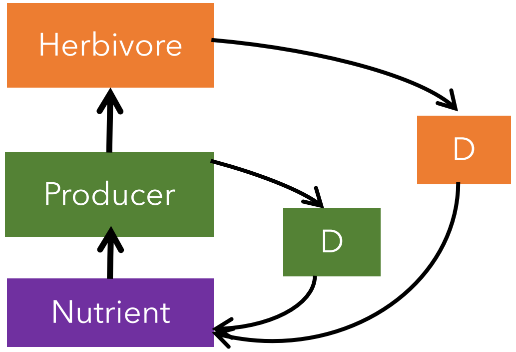
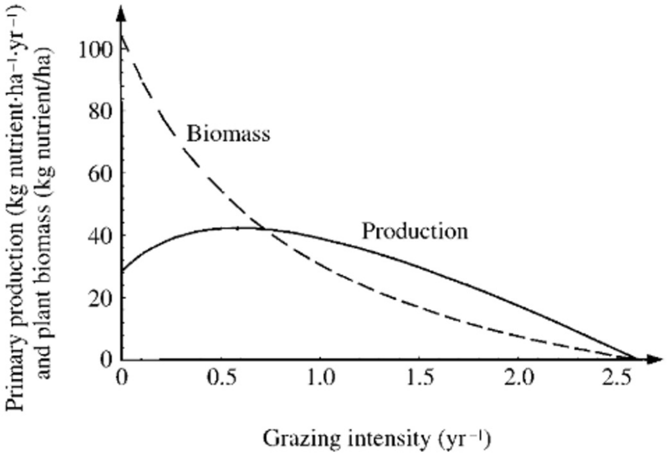




What does the study tell?

When producer and herbivore detritus is recycled into nutrients at different speeds, grazing can increase primary production despite it decreases producer biomass.

What it does NOT tell

Intermediate grazing intensity optimizes primary production.

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?

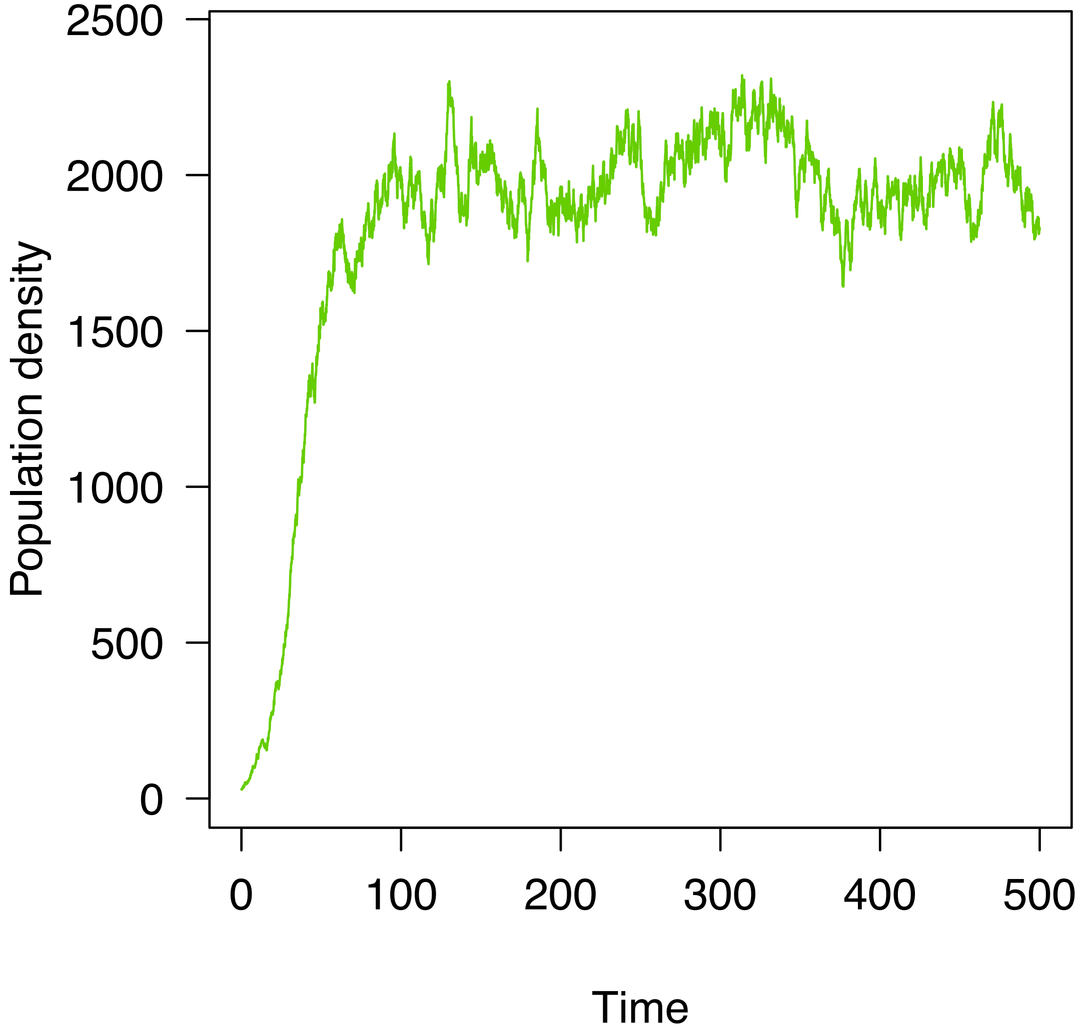
2. What model formalism? (1) Stochastic /Deterministic

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

- demographic stochasticity
- environmental stochasticity
- trait variability

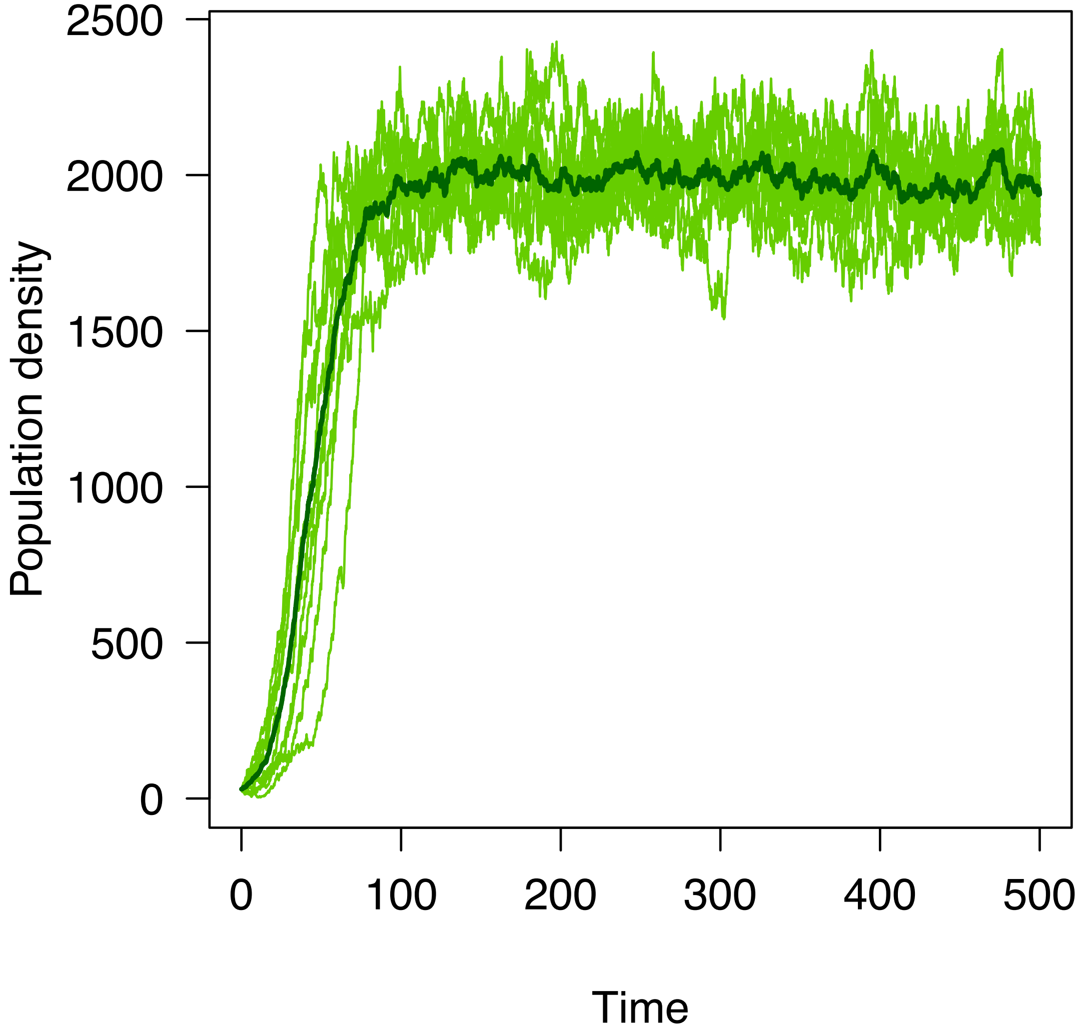
When should we account for it?

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



Example: random demographic events

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



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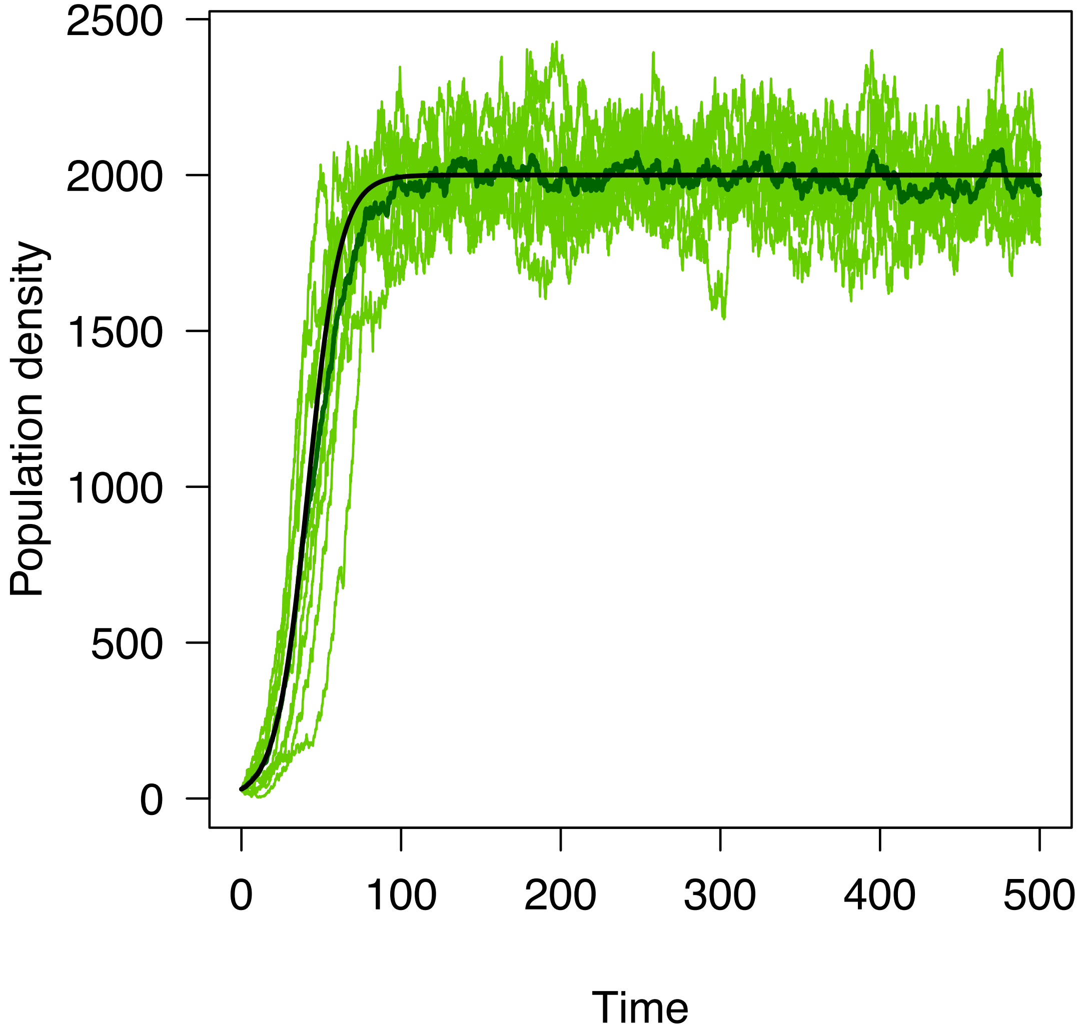
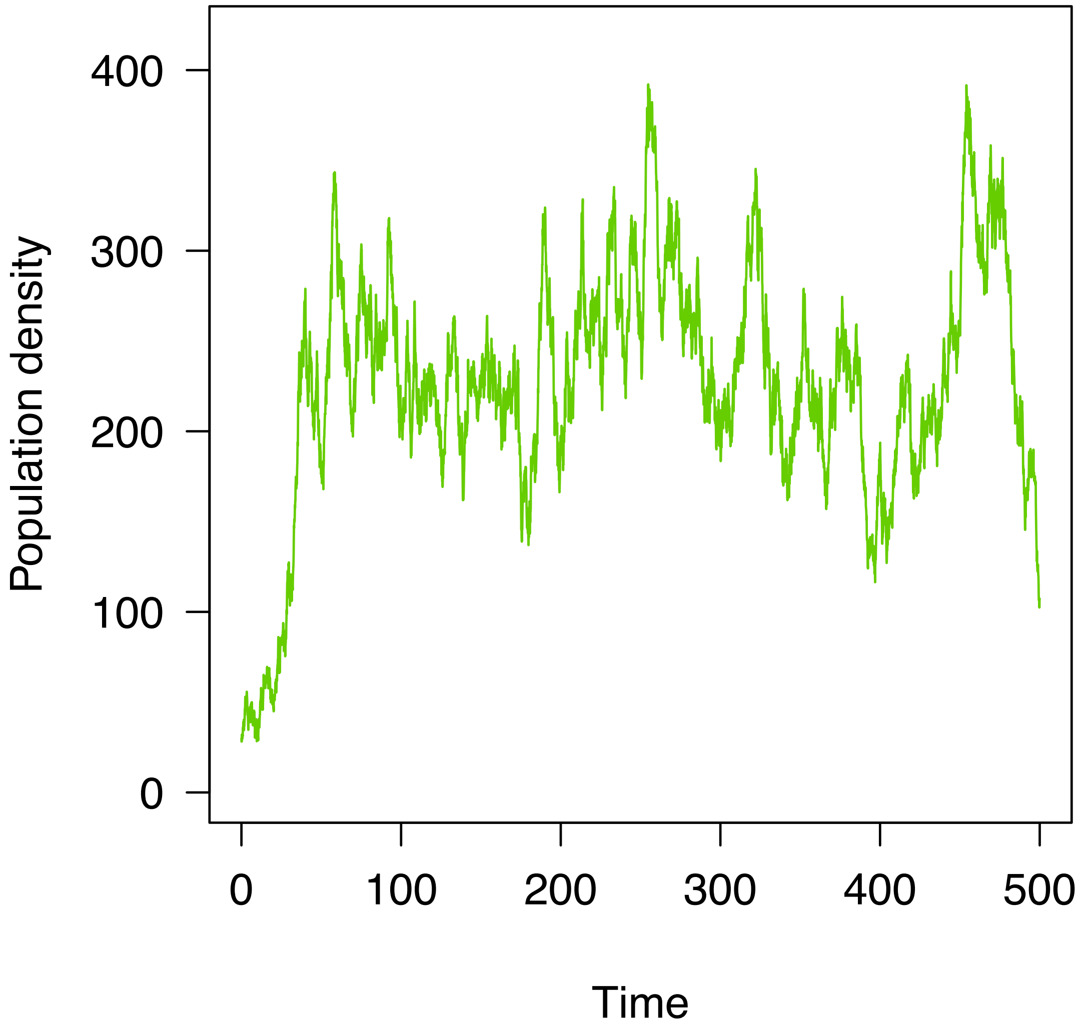


Example: random demographic events

→ care of the mean only
→ deterministic is a 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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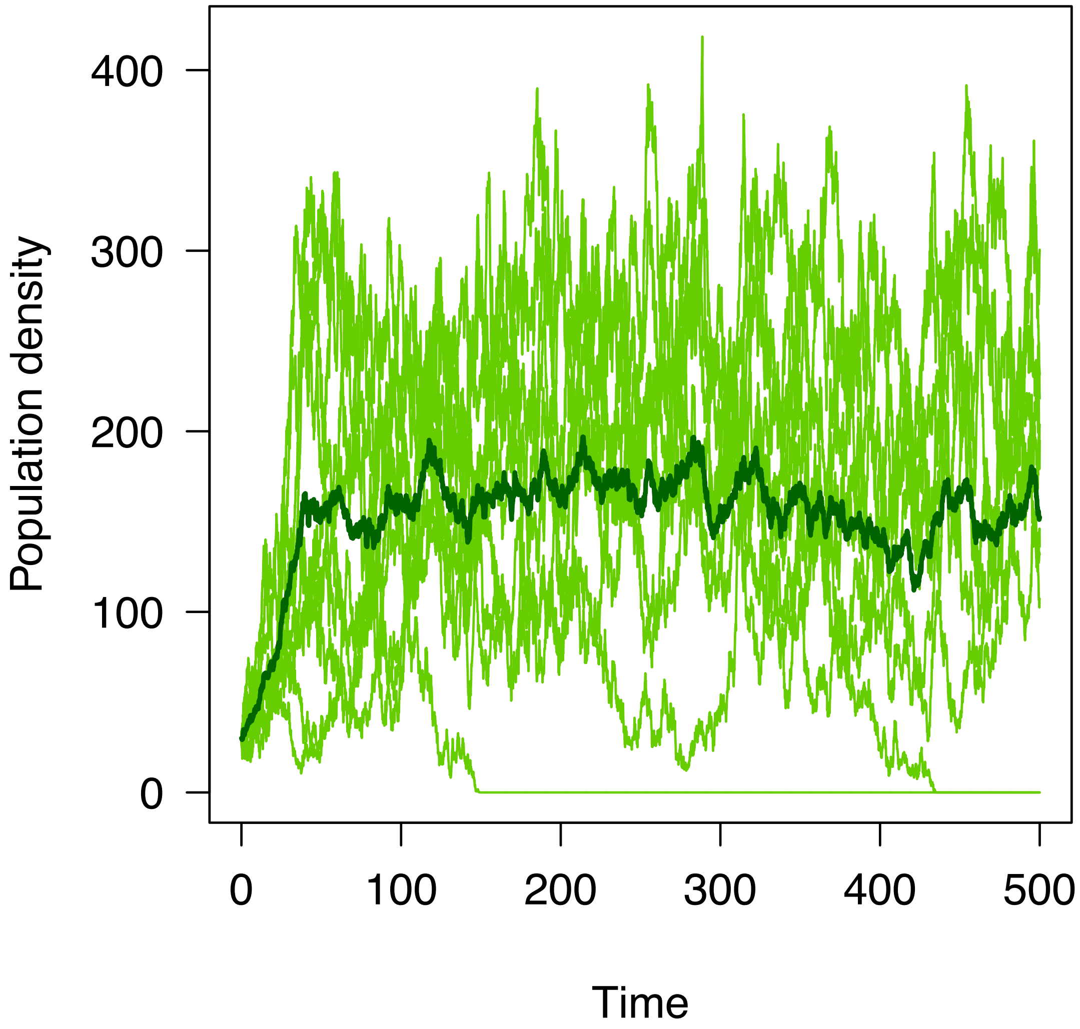

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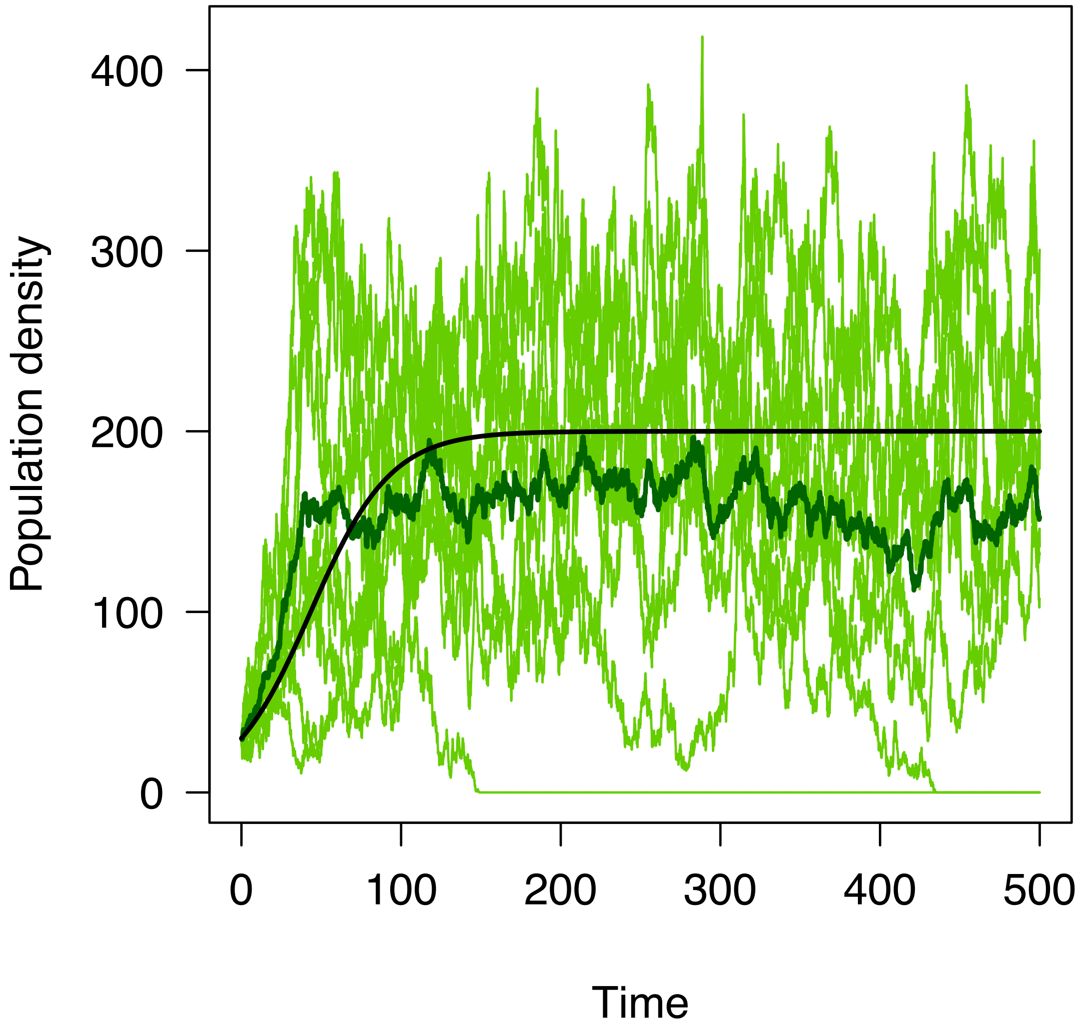


Example: random demographic events

- 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

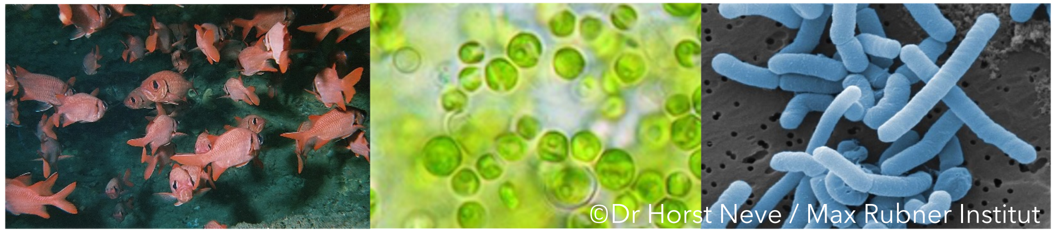
→ Ex: IBM models or SDE
See models in day 3 and 4 (Matthieu)

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

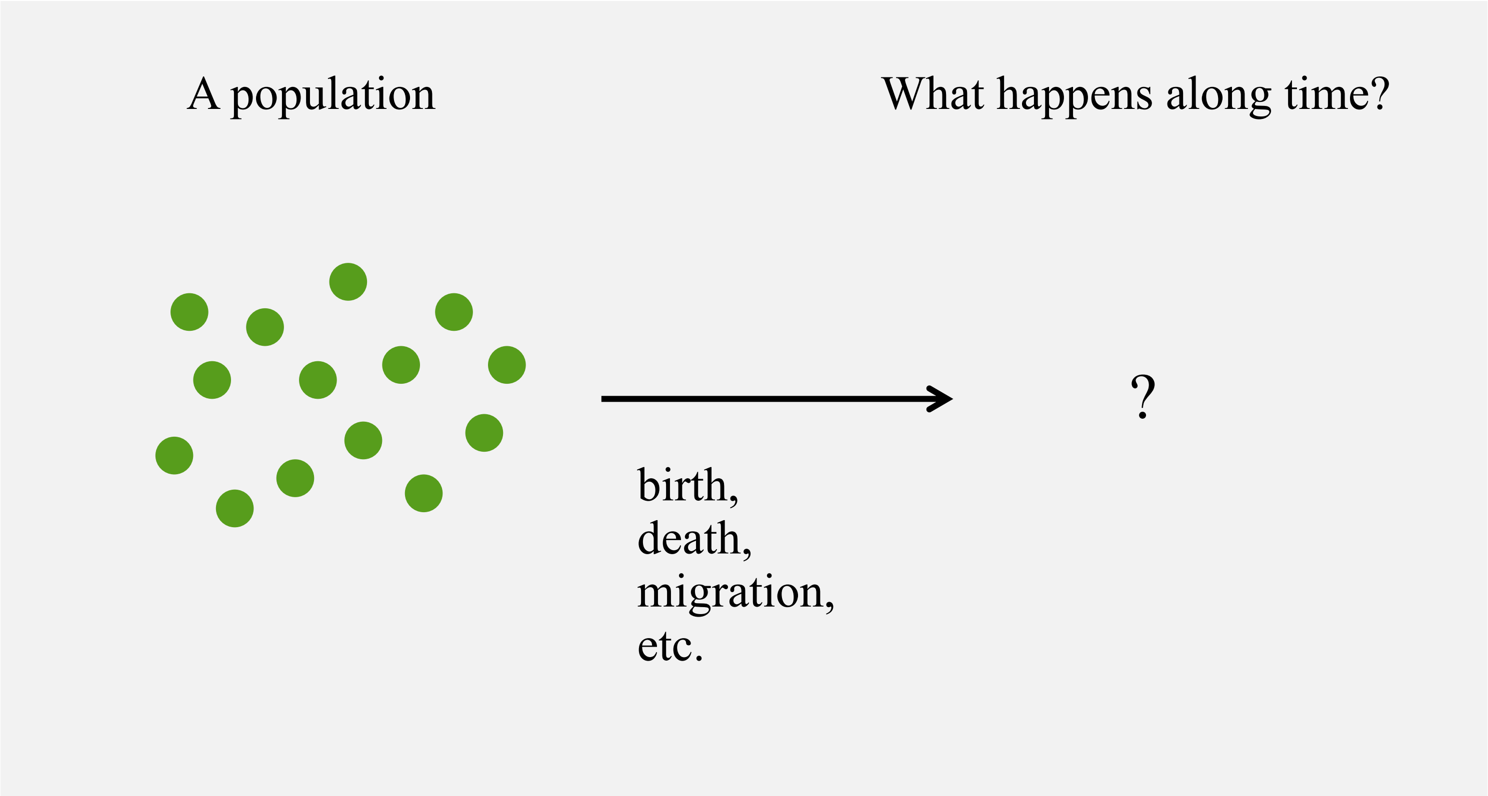


→ Ex: Deterministic ODE
See models in day 2 and 4

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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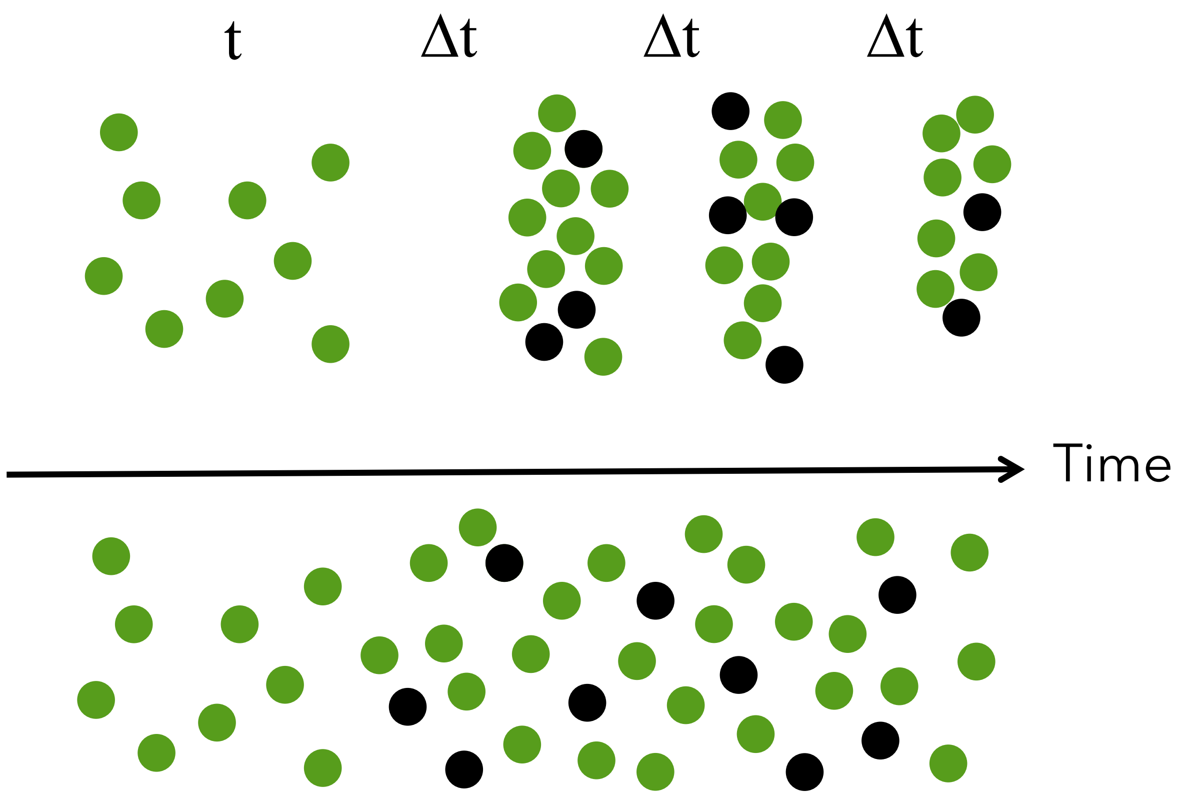


Discrete time $N_{t+1} = N_t + \cdots$

Synchronization of events

Continuous time $\frac{dN}{dt} = N * \;\ldots$

Events happen at any time

2. What model formalism? (2) Time

Discrete time models

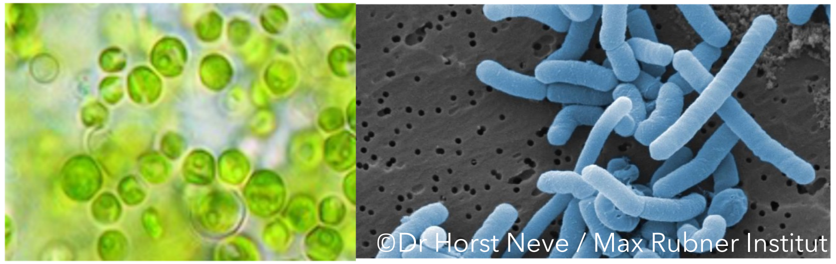
Events are synchronized

- 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



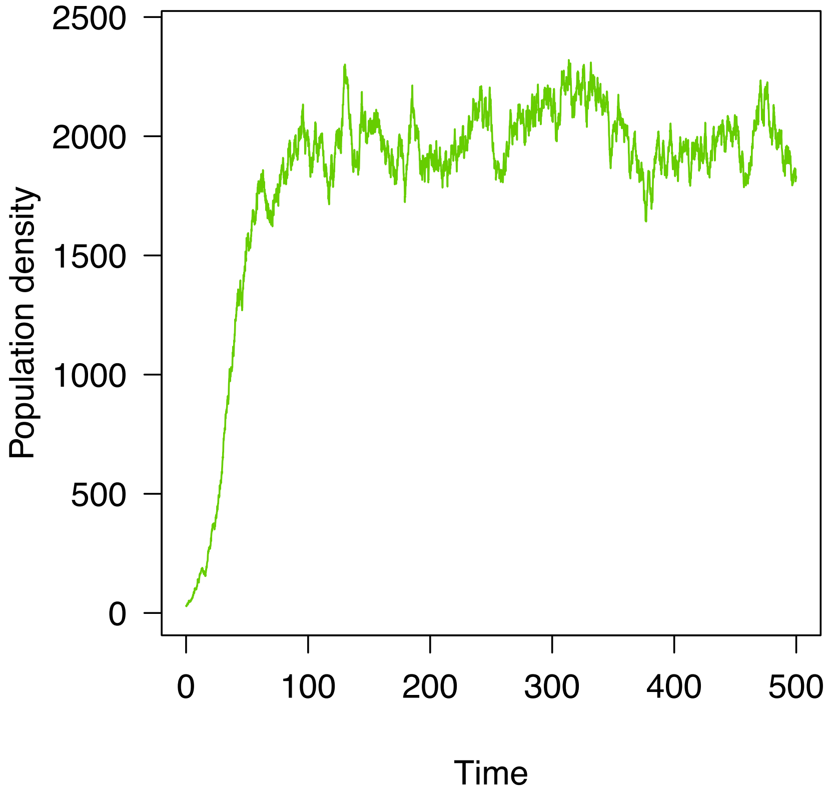
→ discrete time models where the time interval is very small boil down to continuous model

→ 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

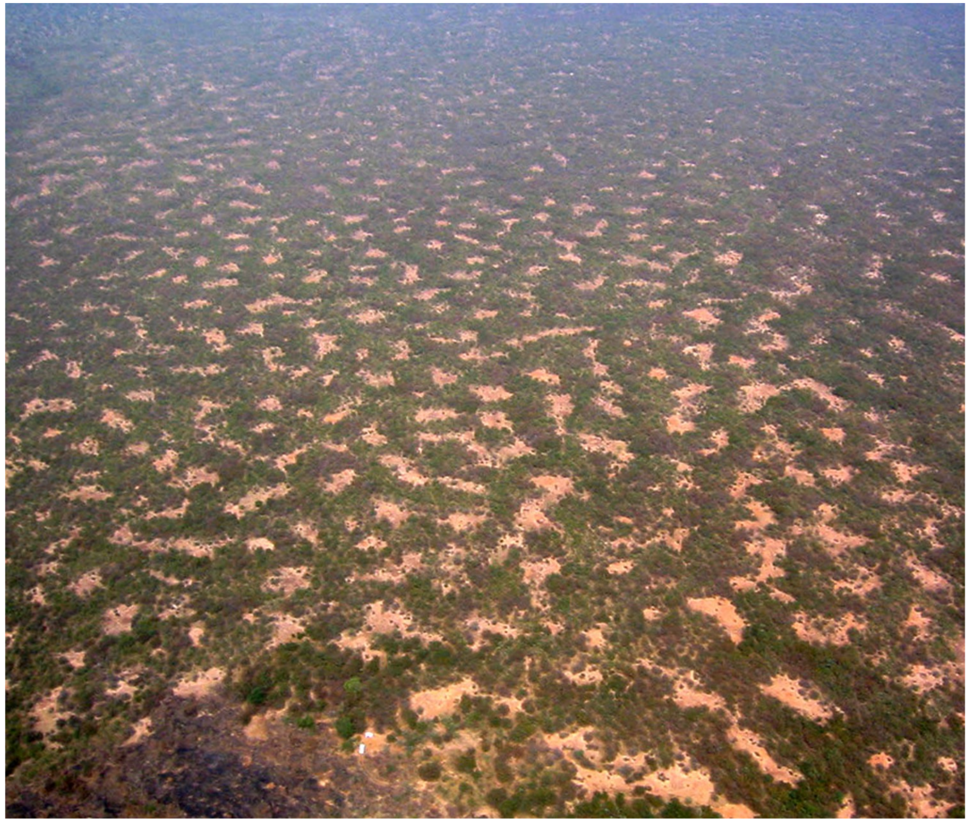
When is space important to describe your system and answer your question?

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?

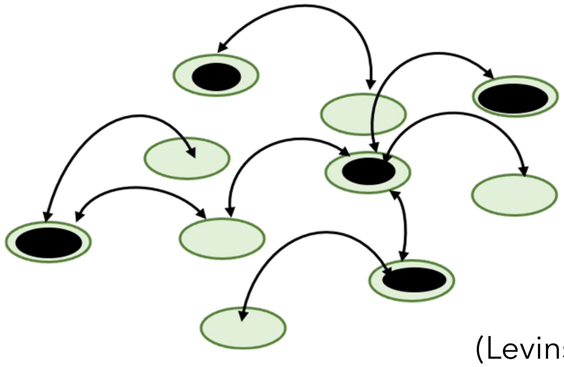


When is space important to describe your system and answer your question?

2. What model formalism? (3) Space

Does geographical position matter?

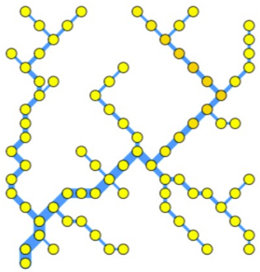
Space **implicit**: topology only



→ See models in day 3

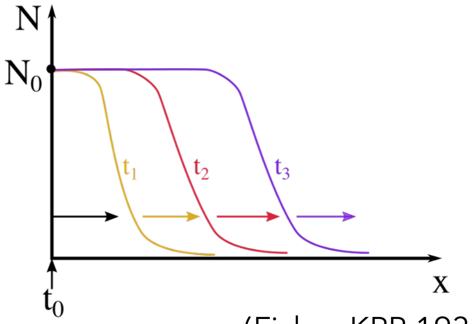
(Levins 1969, Leibold et al. 2004)

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)

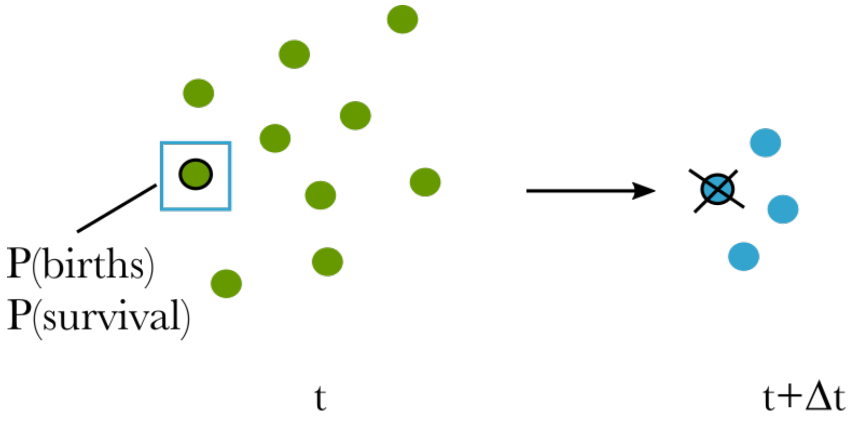
Environmental gradient, edge effects, invasion front

3. What technical choices?

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

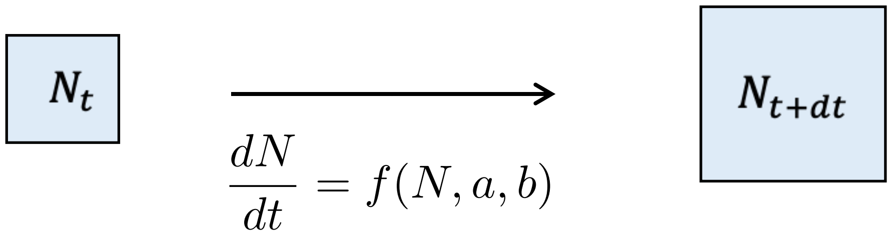
3. What technical choices? (1) rules vs maths

IBM – ABM



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

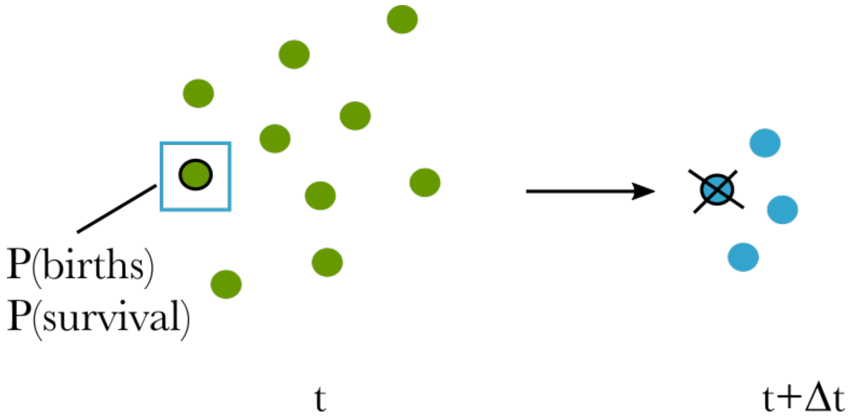
Dynamical equations



- Variables, *N*, are population densities / biomasses (decimals)
- We use maths
- Processes are embedded into parameters (*a, b*)

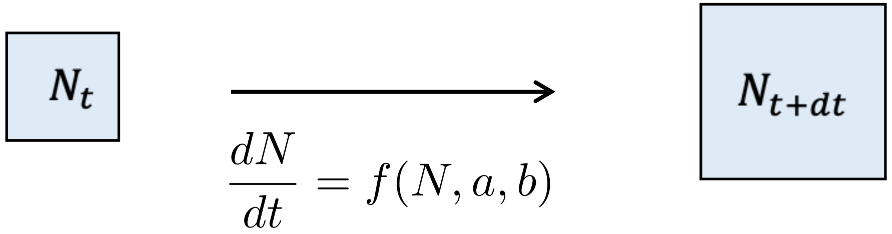
3. What technical choices? (1) rules vs maths

IBM – ABM



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

Dynamical equations



- Simplification with math approximations
- Large analysis power for extreme cases
- 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

A given model

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

Simple tractable models ↓ Complex intractable models

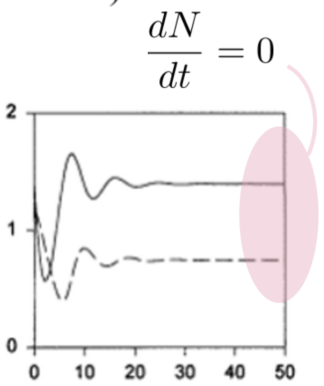
Analytically tractable ? → Yes

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)

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



Analytically tractable ? → No

↓

(results are specific to parameter values)

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

→ Numerical integration (ODE)

→ Coding algorithm (ABM)

→ Simplifications ↑

How to build a model?

Content

1. General principles
2. One example of approach in a theoretical study
3. Identify the assumptions in a classical theoretical model

1 . General principles

What is your question?

Formulate hypotheses: what are the possible explanations of observed patterns?

Sketch your system => simplification

What are your variables?

How are they connected? Which processes do you integrate?

Formulate mathematically

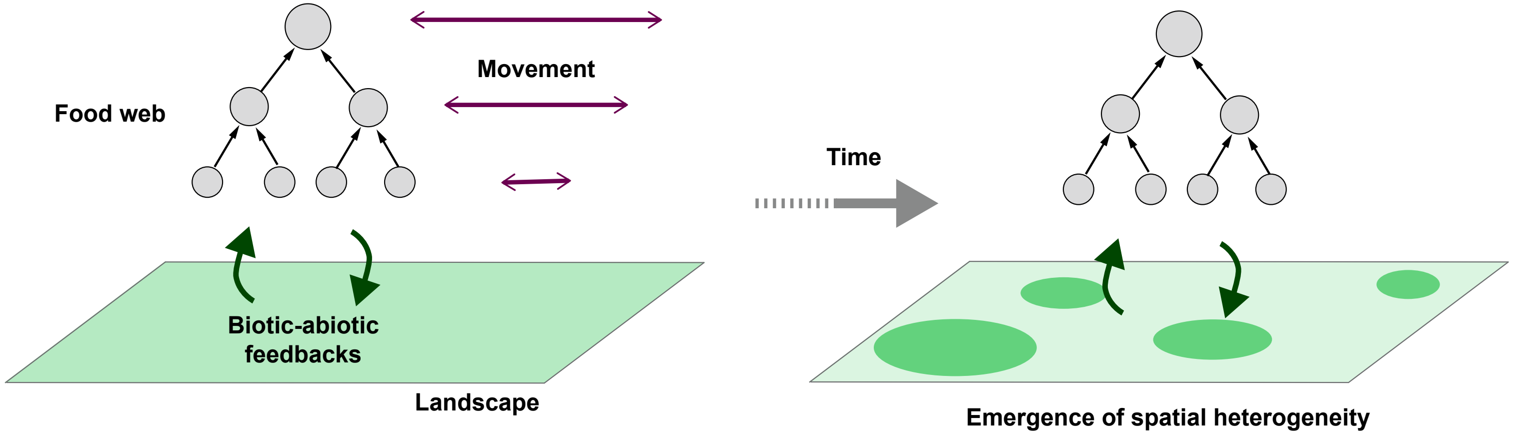
What formalisms in terms of stochasticity, time, space?

How do I formulate the processes : what assumptions on modelled processes and relations between variables ?

Analyse and interpret your results in the context of your assumptions

2. Example: RED-BIO project

How can biotic interactions generate resource spatial heterogeneity?



Exploratory approach to

- provide new ways of thinking about a problem
- help guide scientist's intuition about how various processes are interacting
- generate key predictions on underlying mechanisms
- point out logical flaws in arguments

2. Example: RED-BIO project

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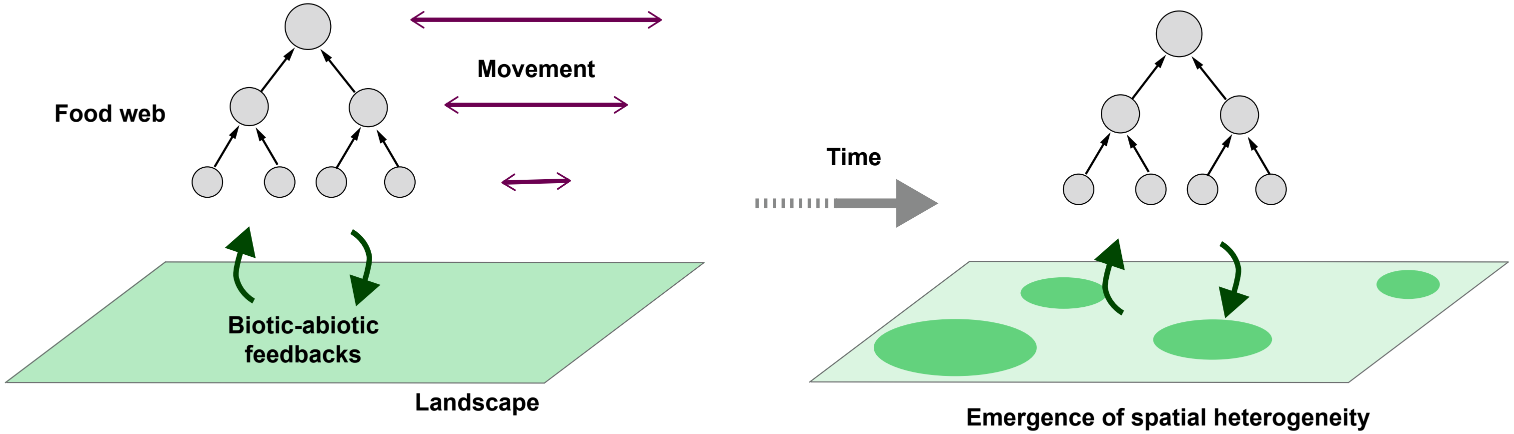

Hypotheses

- The scales of dispersal and foraging of producers & consumers affect nutrient patchiness
- Recycling level may modulate nutrient hot and cold spots created by species
- Consumers affect nutrient heterogeneity by both recycling and producer control

2. Example: RED-BIO project

How can biotic interactions generate resource spatial heterogeneity?

Sketch your system => simplification

What are the minimal ingredients to answer the question?

What scale?

What variables?

What processes?

Hypotheses

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Sketch your system => simplification

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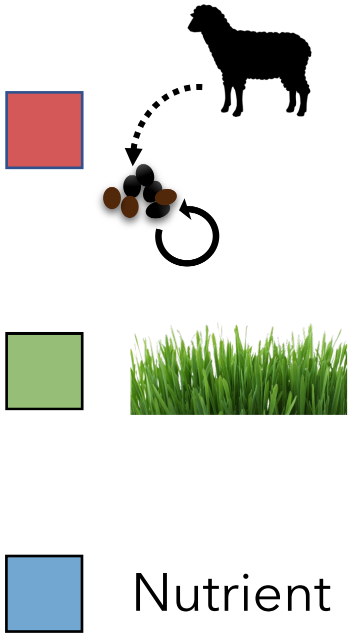

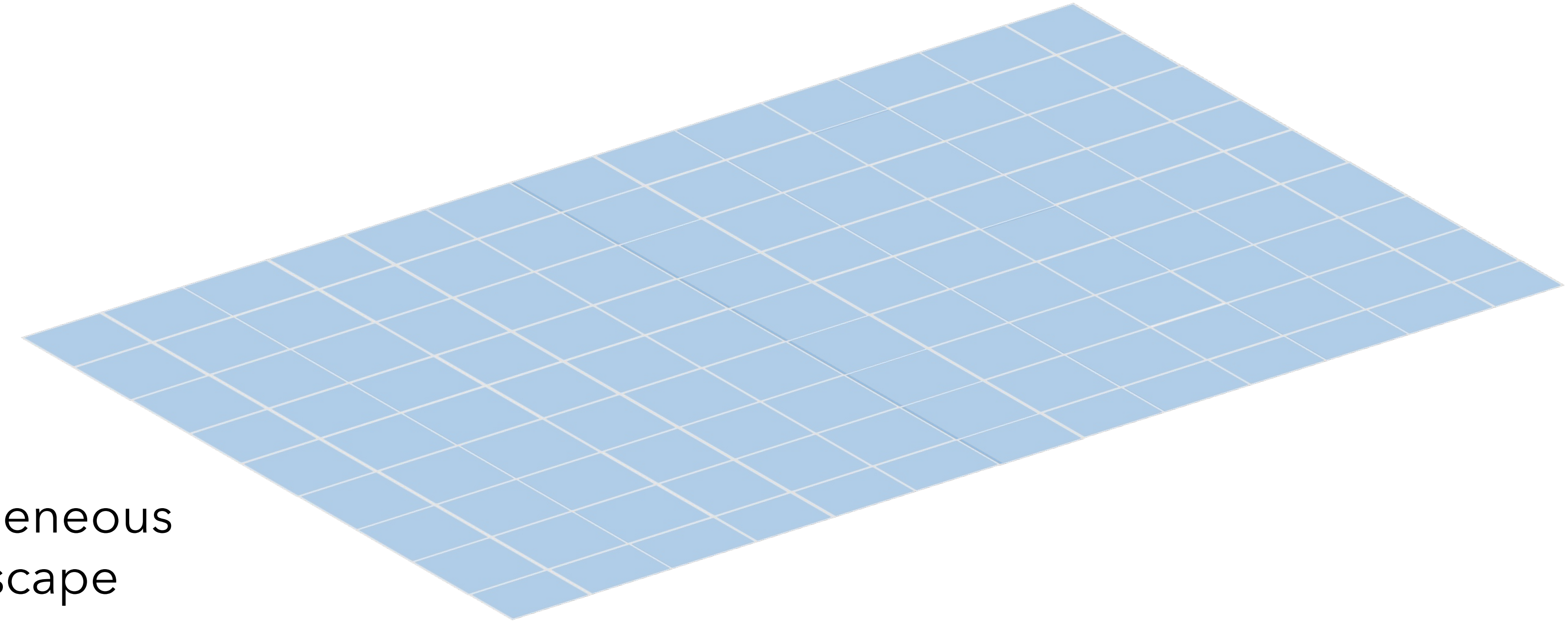

Homogeneous
landscape

2. Example: RED-BIO project

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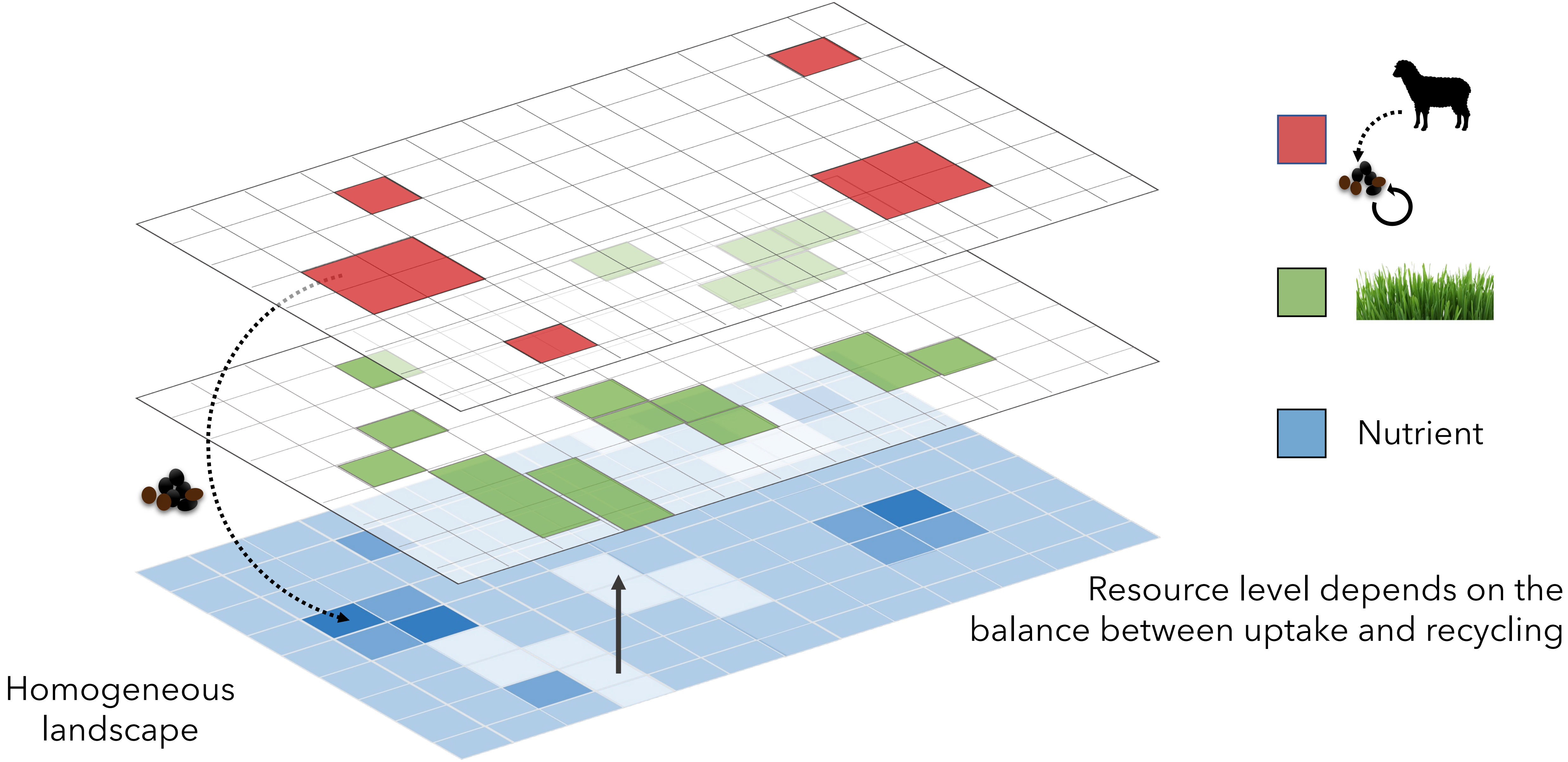

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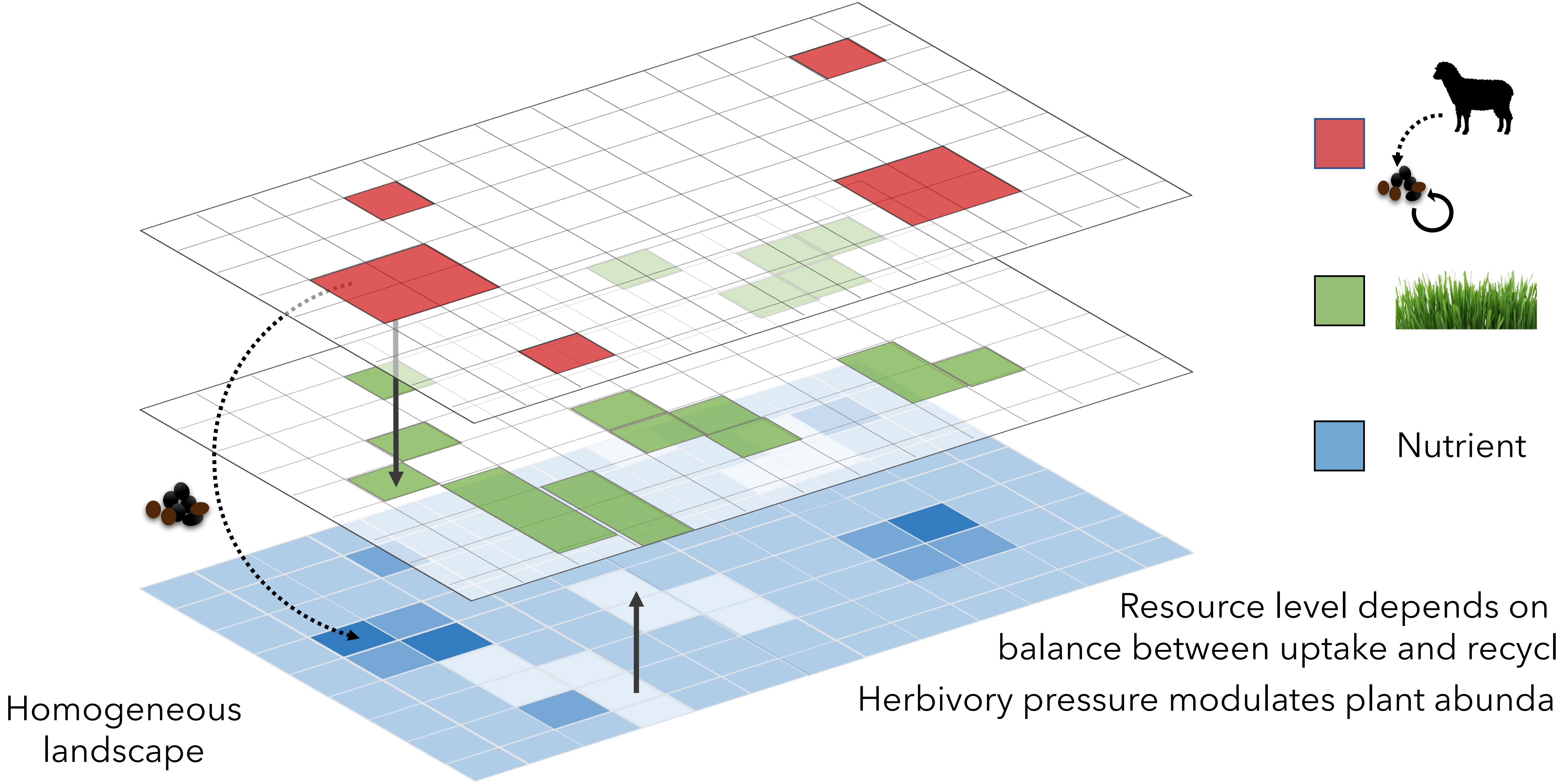

Resource level depends on the balance between uptake and recycling

Herbivory pressure modulates plant abundance

2. Example: RED-BIO project

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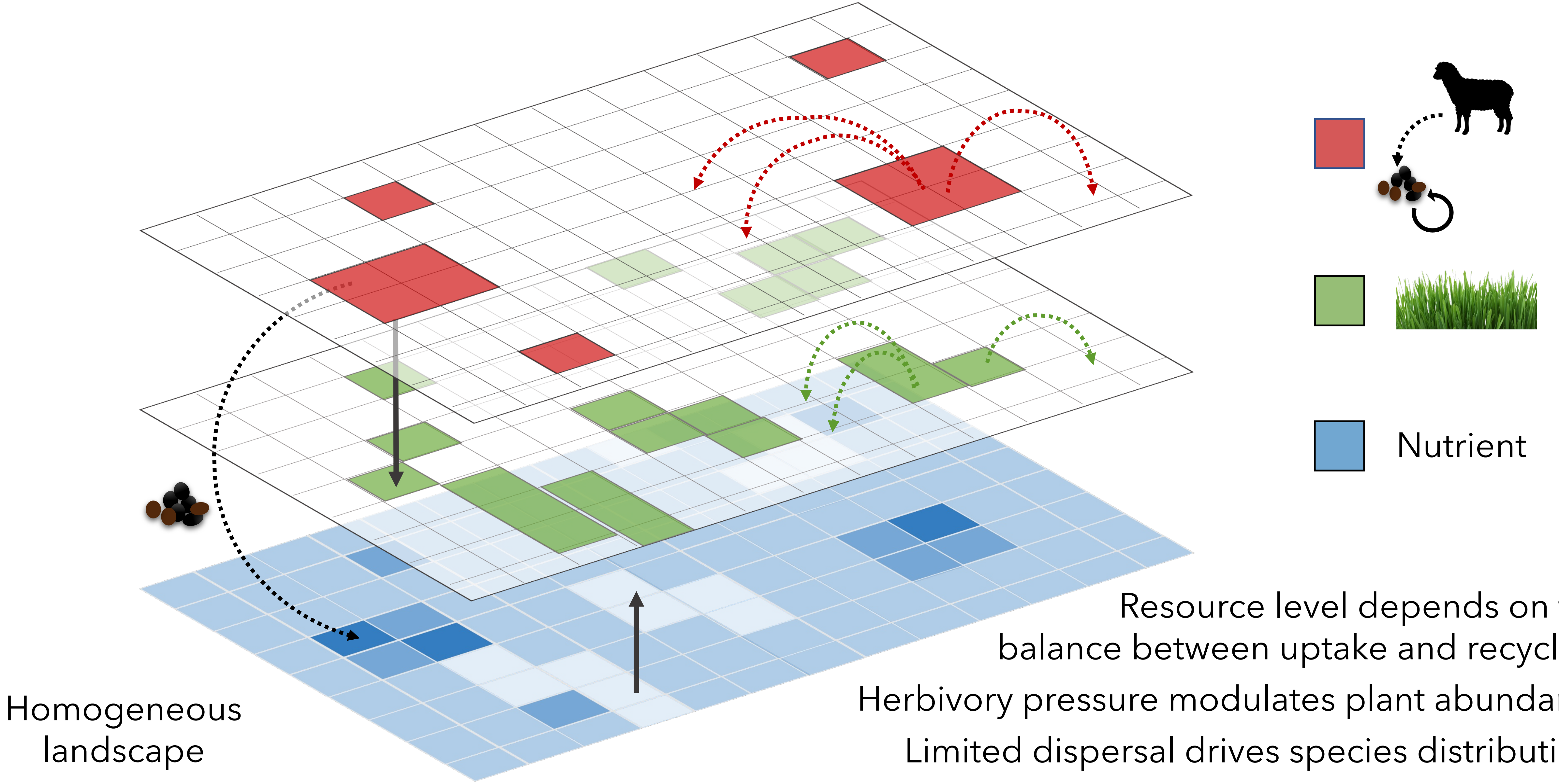


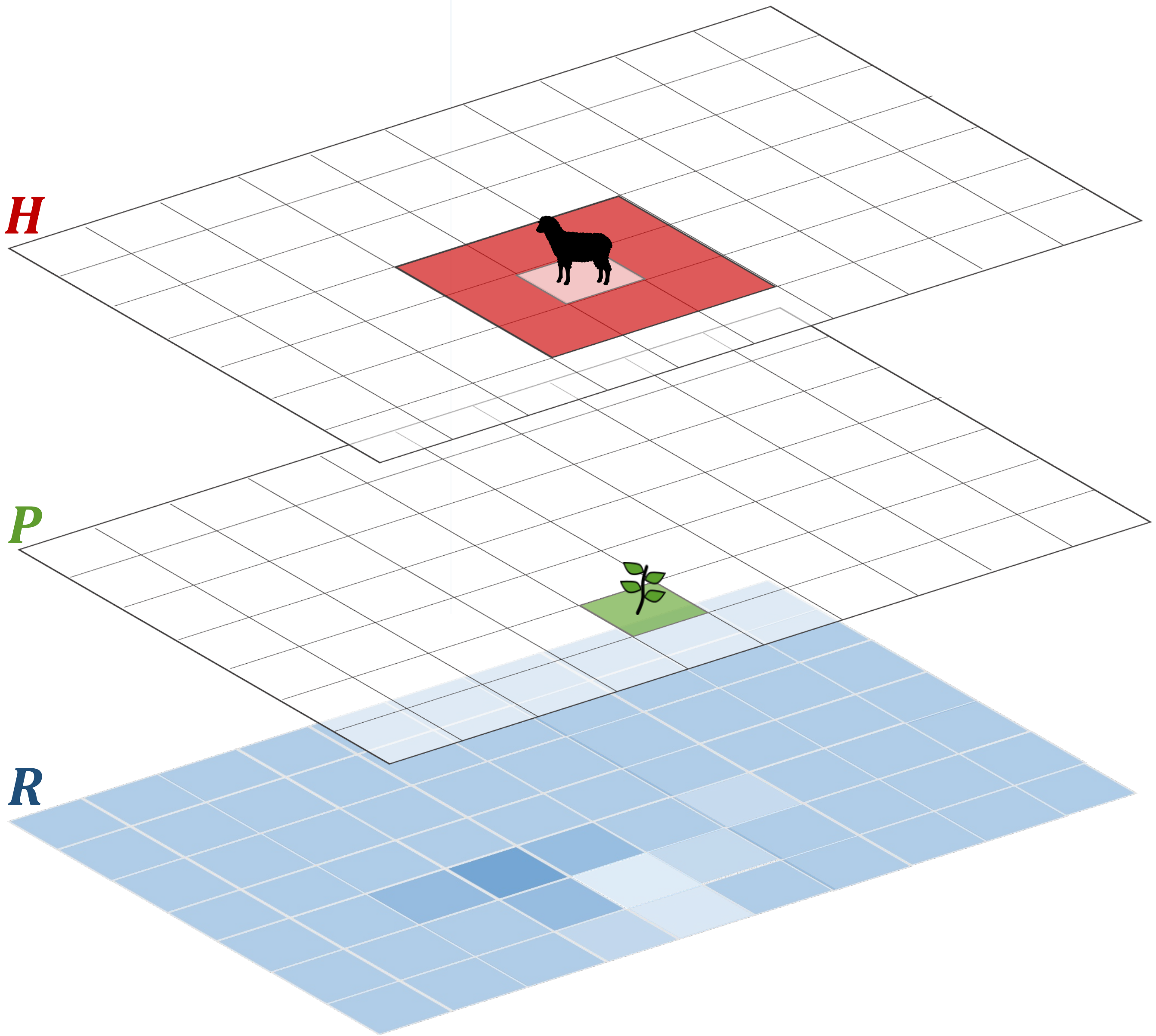
Resource level depends on the balance between uptake and recycling

Herbivory pressure modulates plant abundance

Limited dispersal drives species distribution

2. Example: RED-BIO project

How can biotic interactions generate resource spatial heterogeneity?



What formalisms in terms of space, time, stochasticity ?

Space explicit: 100 x 100 lattice
R, P, H layers, 1 cell = plant population
foraging range (sets the scale)

Occupancy model
⇒ No demography (larger time scale)
⇒ Population presence (at equilibrium)
⇒ Stochastic extinction-colonization
⇒ Nutrient level

Agent-Based model to handle easily stochastic processes in space

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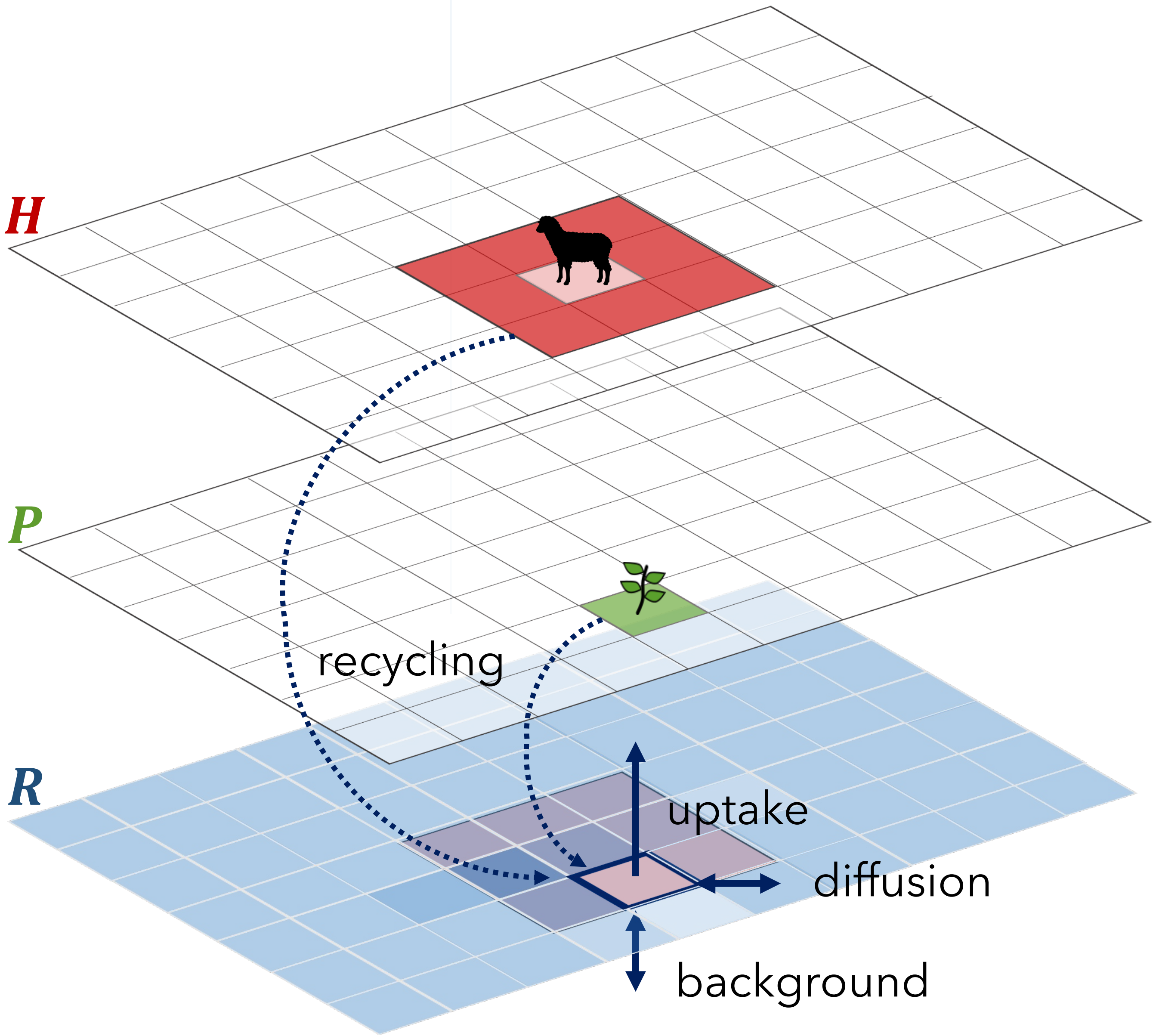

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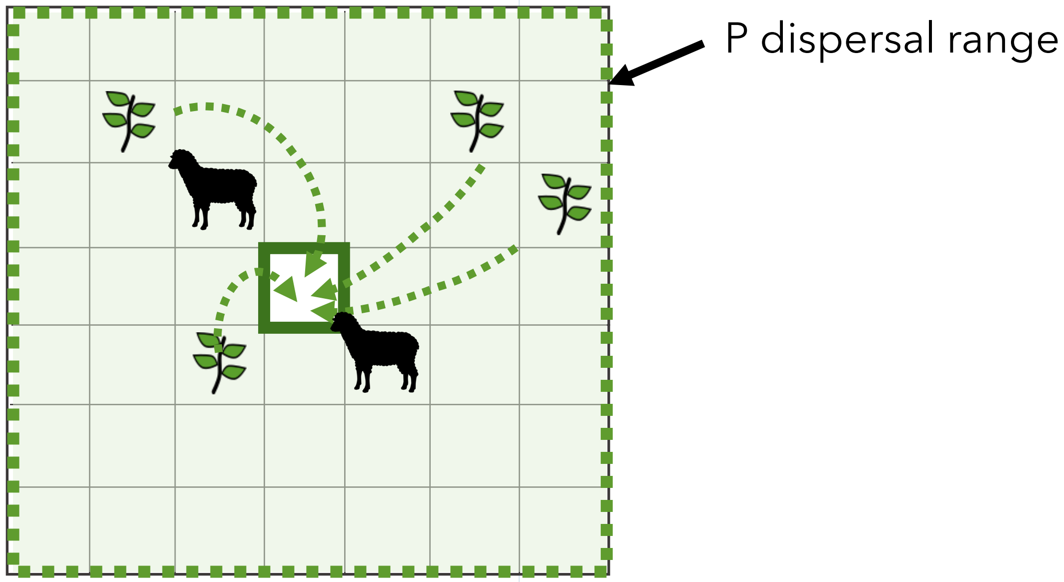
Agent-Based model to handle easily stochastic processes in space => rules

How to formulate processes?
⇒ Nutrient dynamics

2. Example: RED-BIO project



How can biotic interactions
generate resource spatial heterogeneity?

How to formulate processes?

⇒ Colonization extinction dynamics

Colonization of an empty cell depends on

- basal colonization rate (offspring prod.)
- proportion of colonizers

2. Example: RED-BIO project

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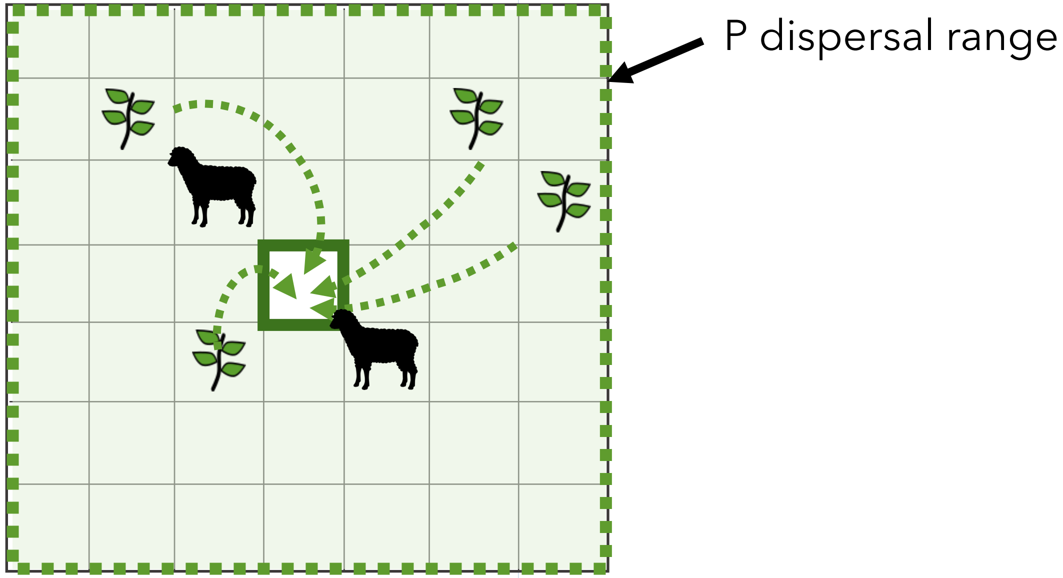

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$$c_p = \bar{P}_{disp}.c_{P_0}$$

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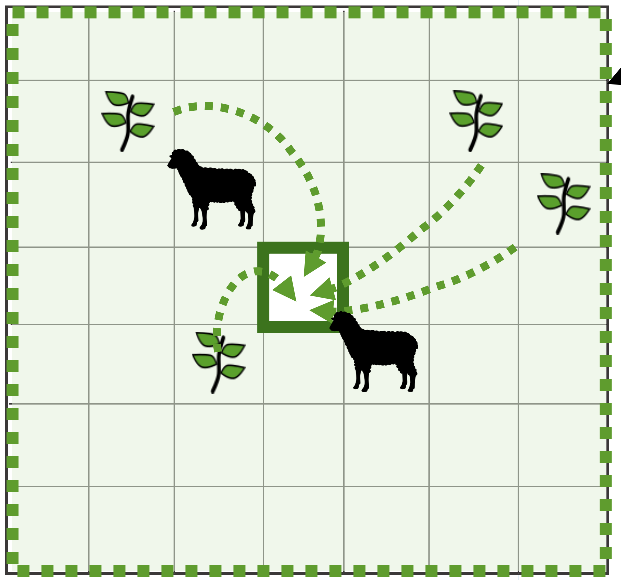

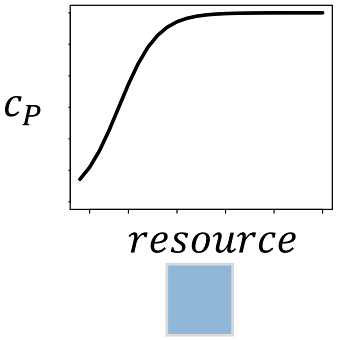

How to formulate processes?

⇒ Colonization extinction dynamics

Colonization of an empty cell depends on

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2. Example: RED-BIO project

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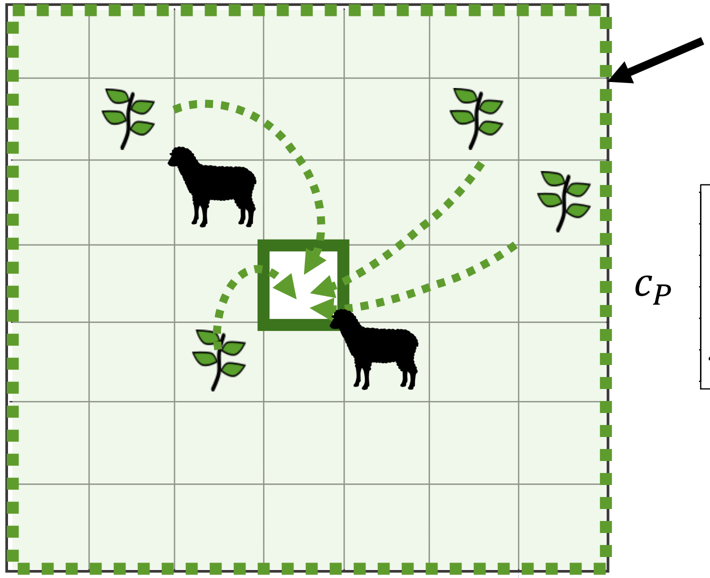

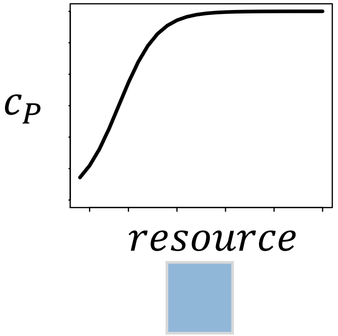

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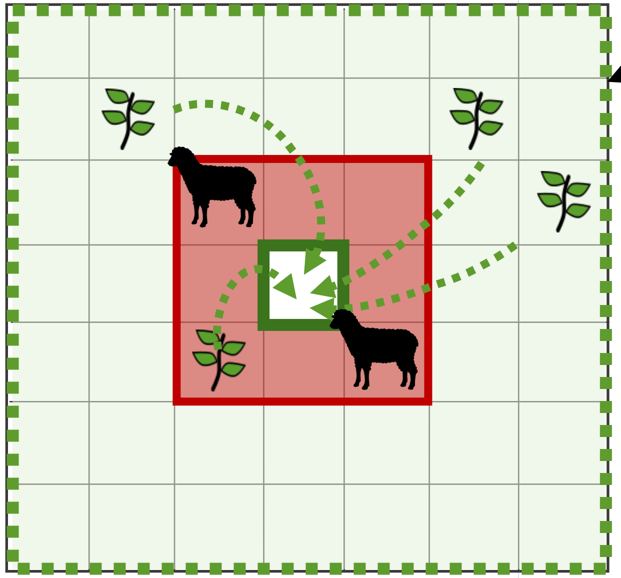
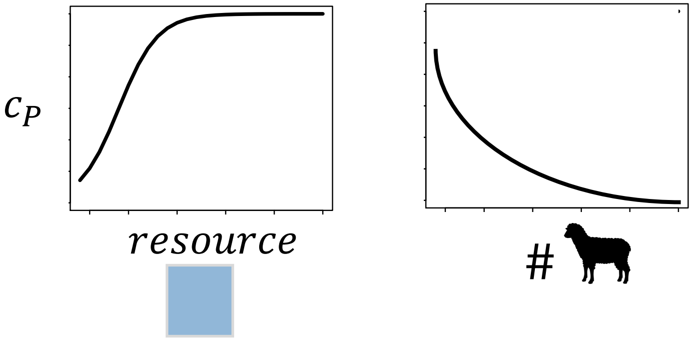
2. Example: RED-BIO project

How can biotic interactions generate resource spatial heterogeneity?





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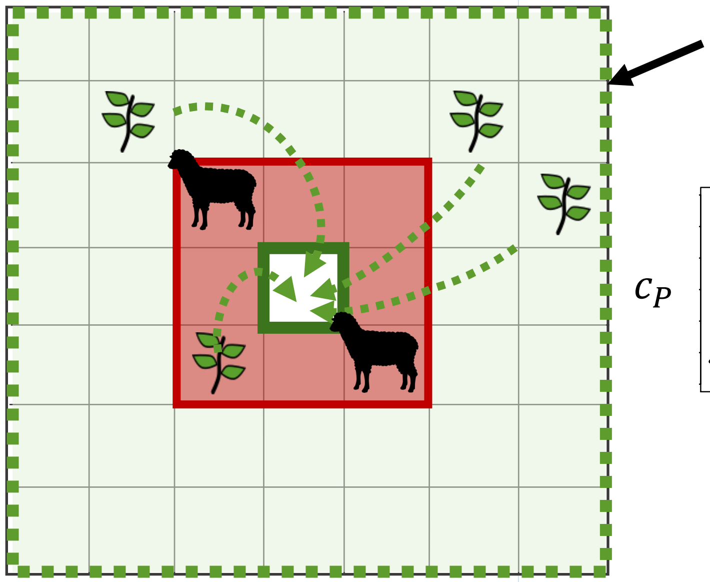

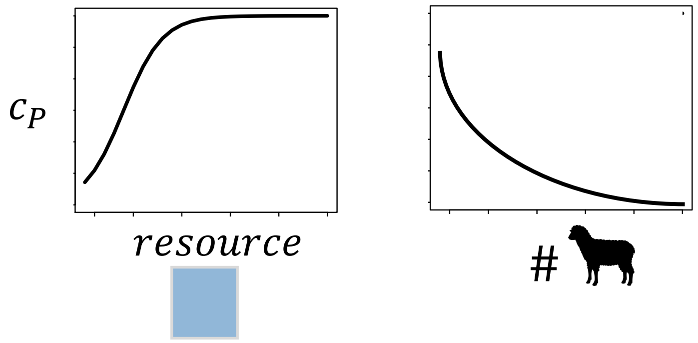

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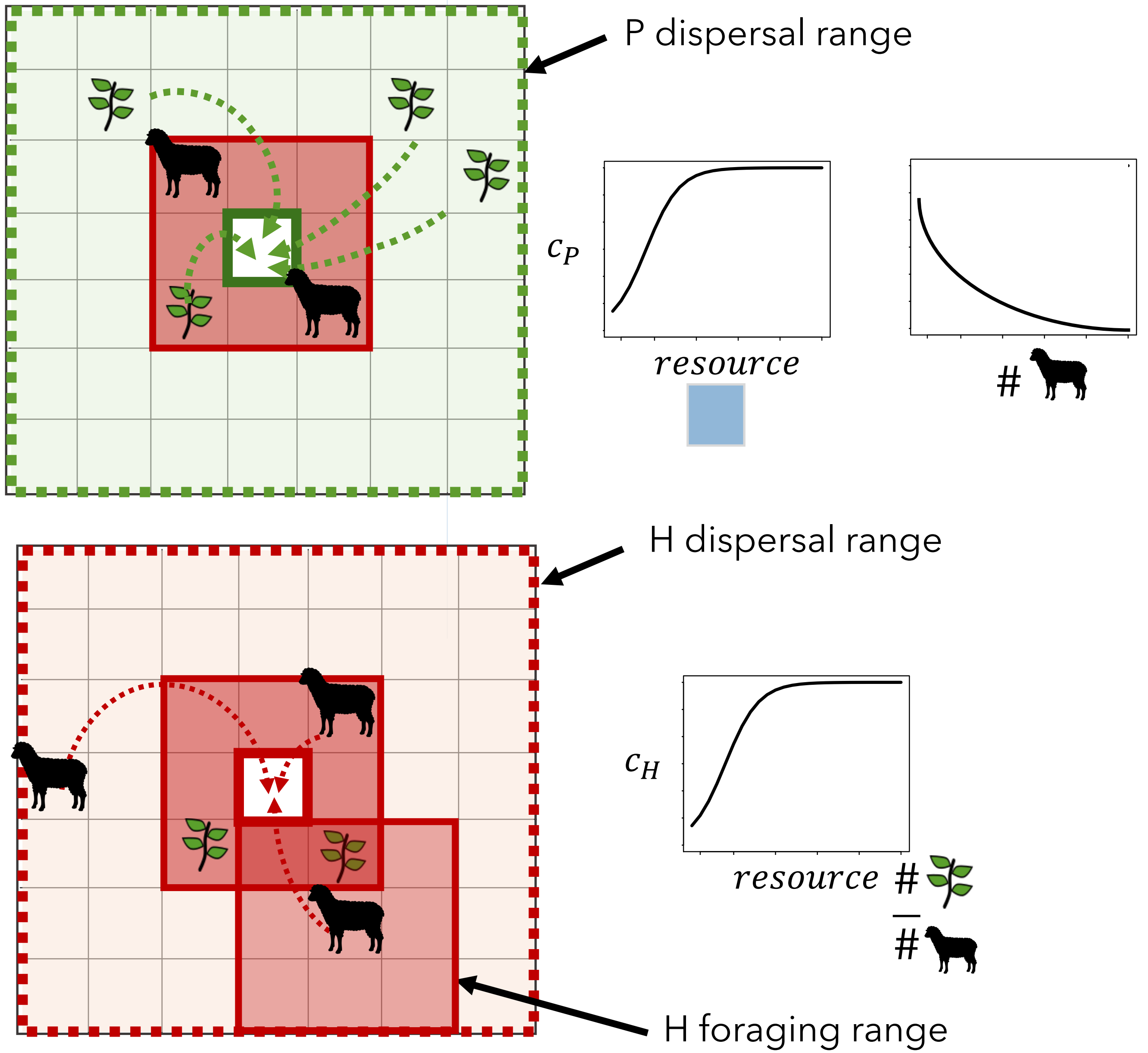
2. Example: RED-BIO project

How can biotic interactions generate resource spatial heterogeneity?



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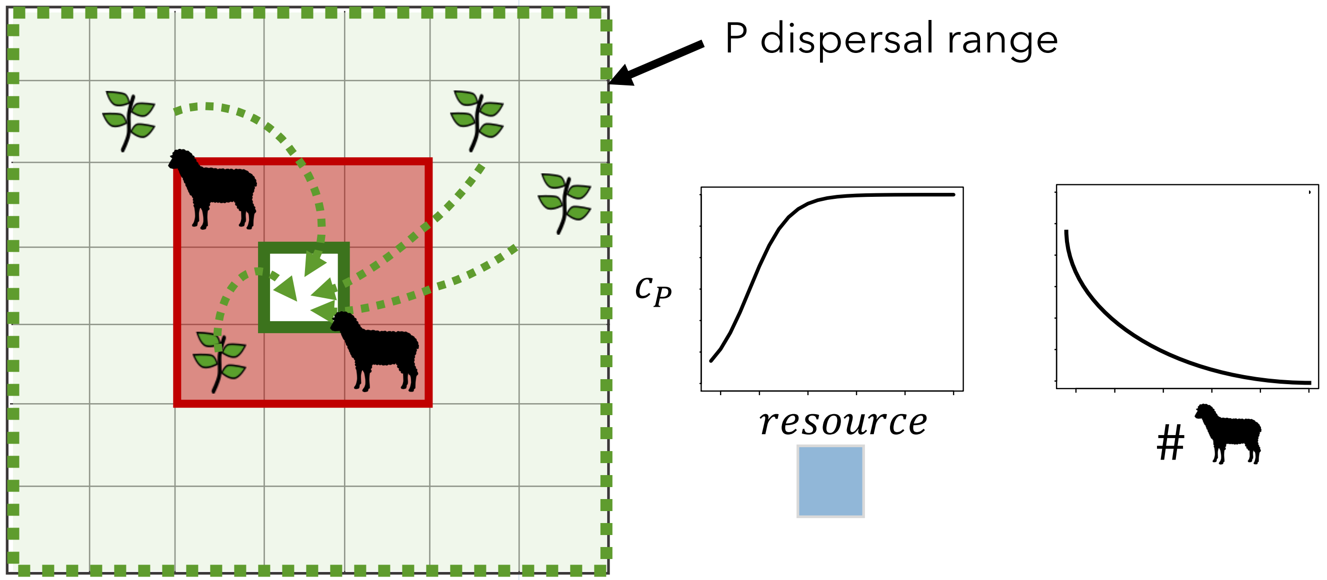

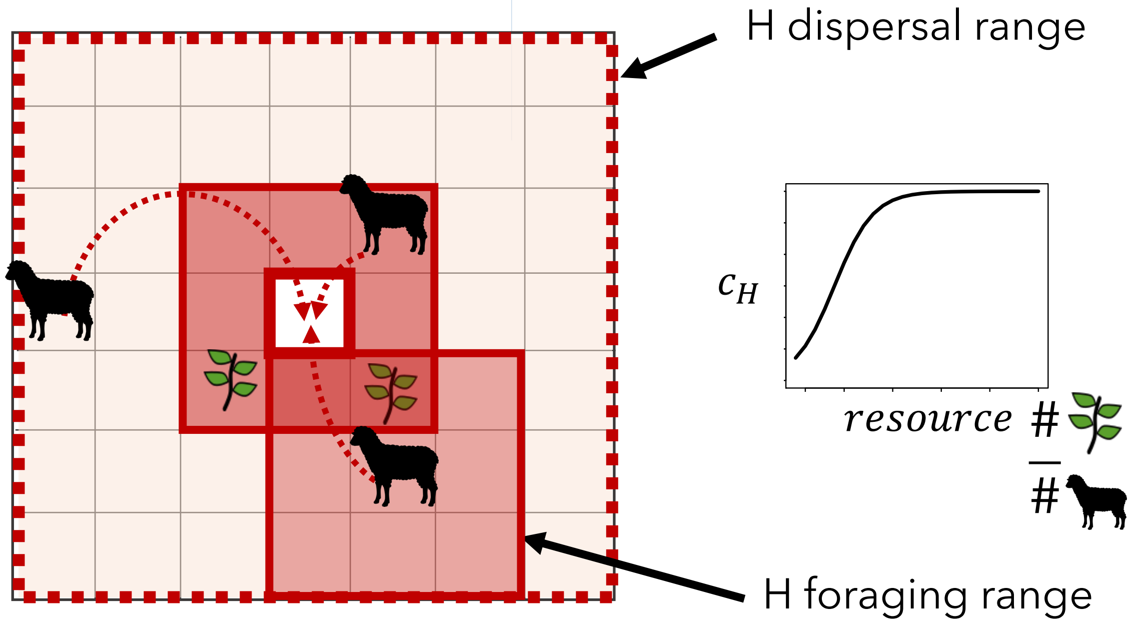

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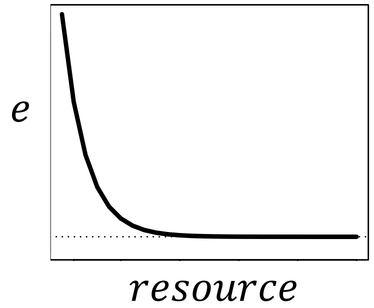

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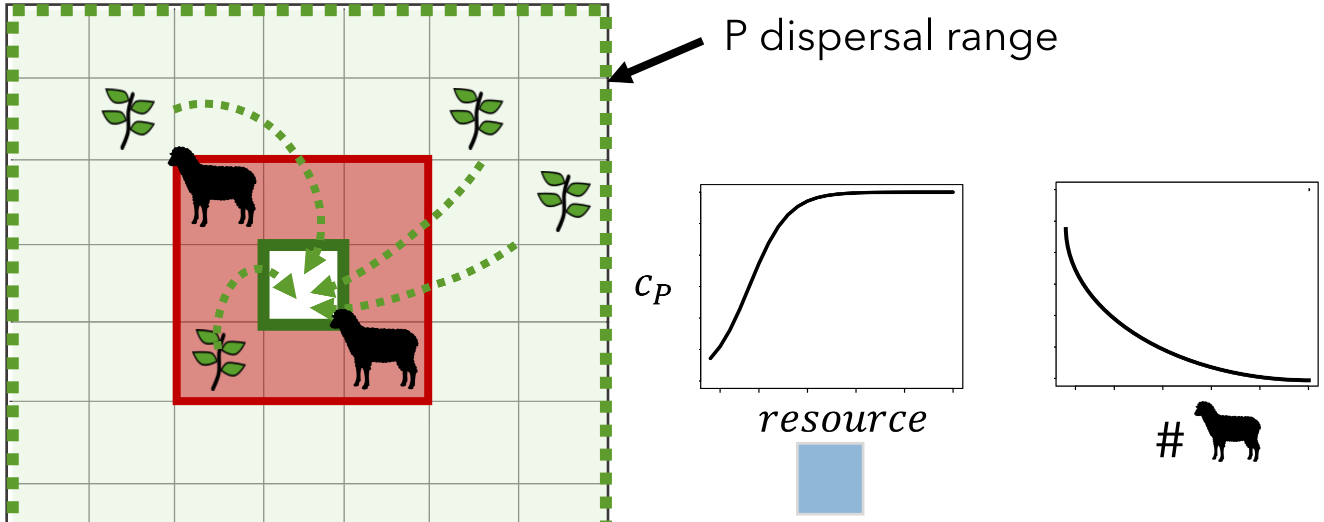

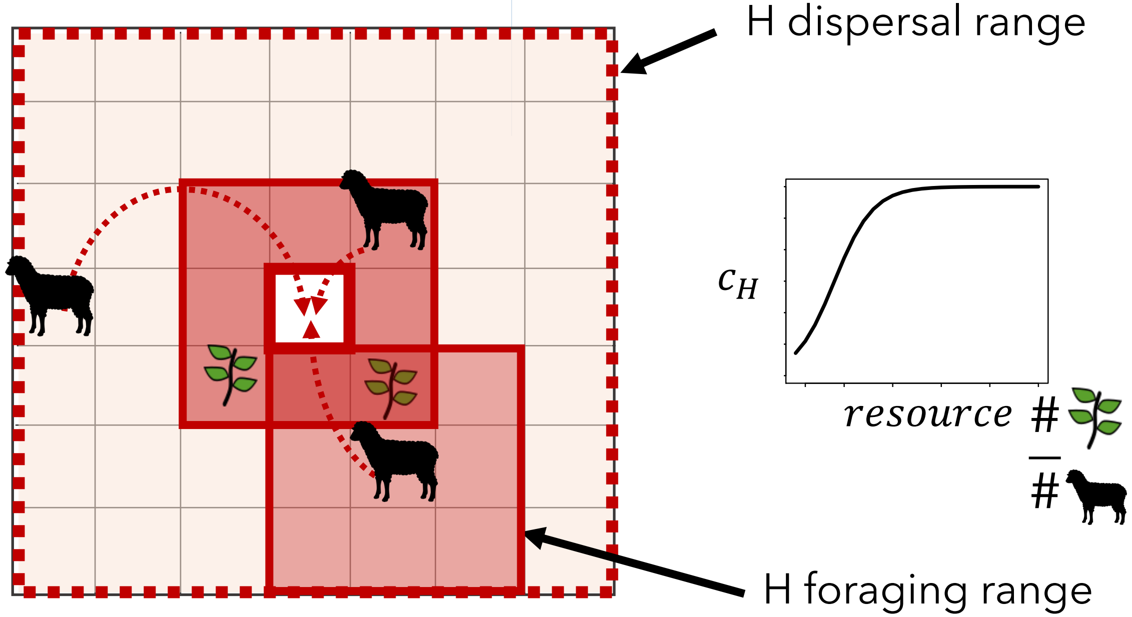

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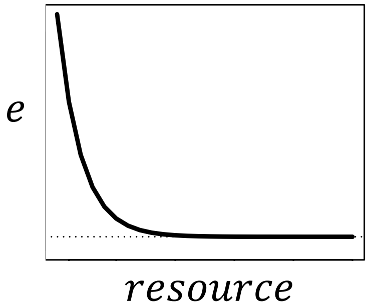
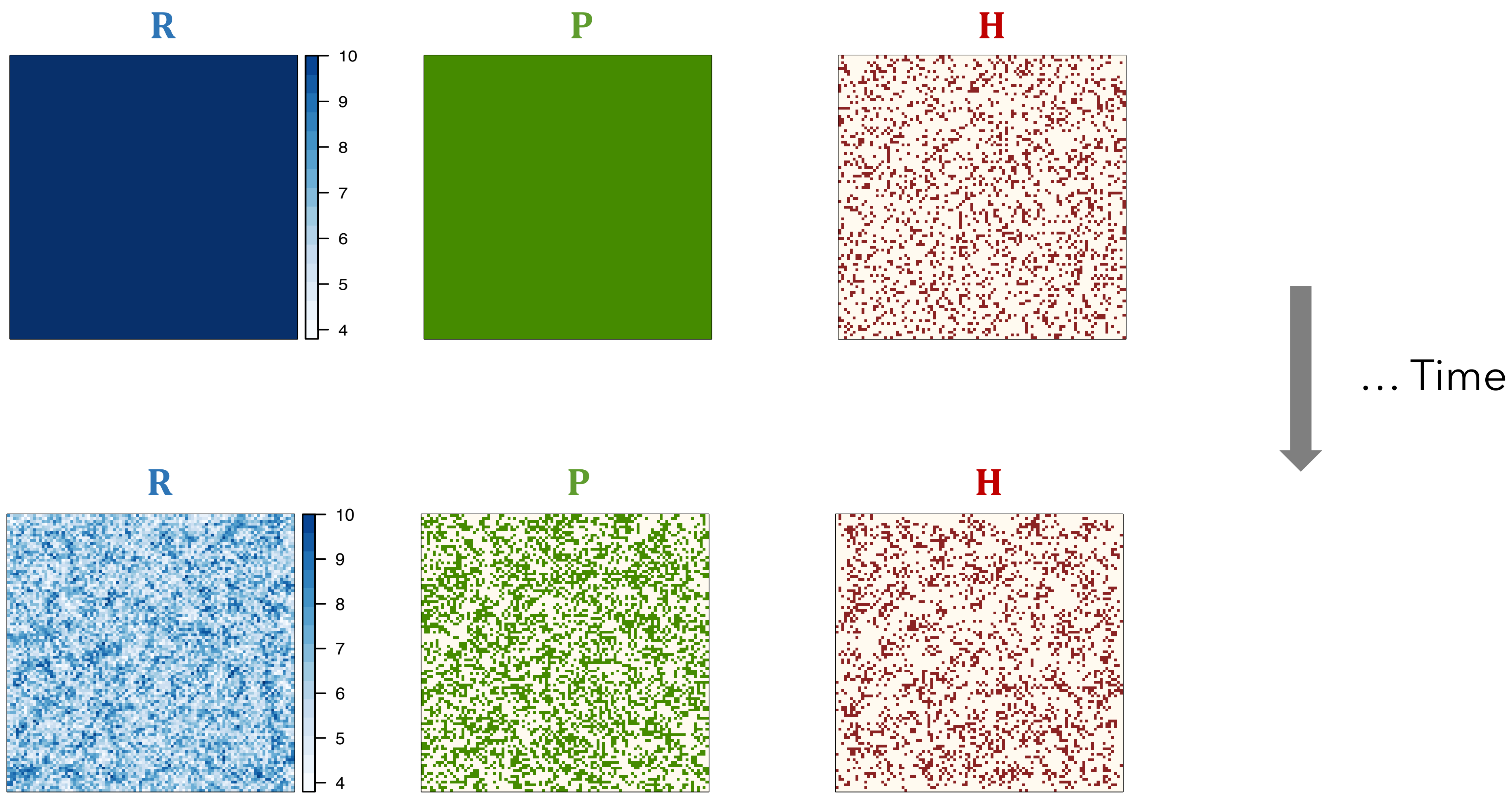


$$e_P = e_{P_0} + \epsilon_P e^{-\beta(N_i - N^*)}$$

2. Example: RED-BIO project

How can biotic interactions generate resource spatial heterogeneity?

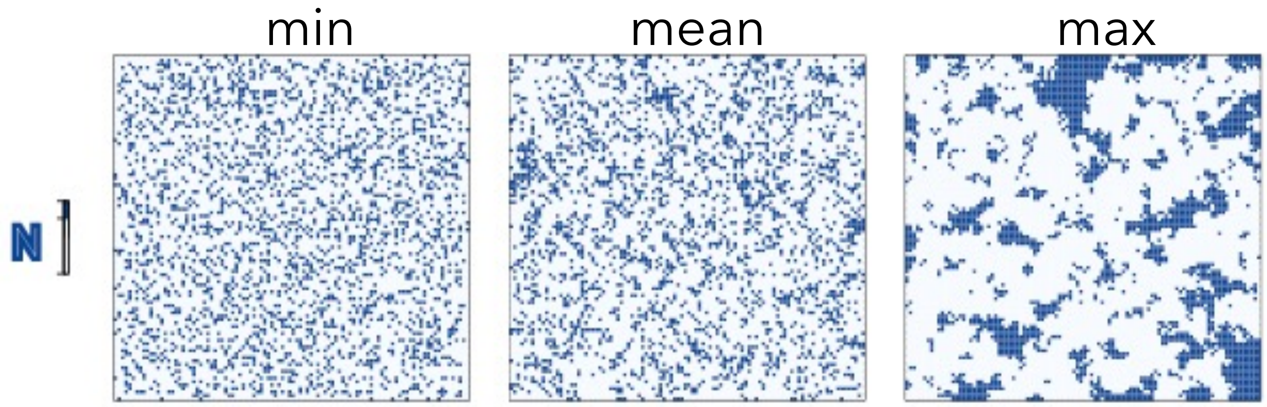


Analyse R mean level, P and H occupancies and spatial clustering of each layer

2. Example: RED-BIO project

How can biotic interactions generate resource spatial heterogeneity?

Resource clustering range:



Main results

- Plant dispersal range was the main driver
- Large herbivore foraging ranges increases nutrient clustering by making them persist
- Herbivore affects nutrients mainly by plant control but recycling increases H occupancy

What did we learn from what we observed?
- Mechanisms: aggregation + differential effect on nutrient cycling.
- Population persistence (productivity and large foraging range) is crucial.

How generalizable is it?
- Any consumer-resource system with consumers affecting resource colonization success and competition only through exploitation.
- Within the parameter range explored

What did we learn from what we did not observe?
- For nutrient patches to persist, other mechanims are needed. (null model thinking)

(more on Gounand et al. 2026 bioRxiv)

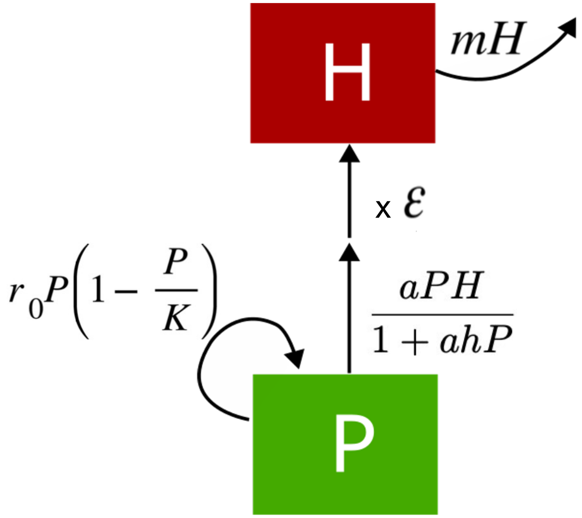
3. Identify assumptions in theoretical models

Rosenzweig-MacArthur model (1963)

$$\frac{dP}{dt} = \underbrace{r_0 P(1 - \frac{P}{K})}_{\text{growth}} - \underbrace{\frac{aPH}{1 + ahP}}_{\text{predation}}$$

$$\frac{dH}{dt} = \underbrace{\varepsilon \frac{aPH}{1 + ahP}}_{\text{consumption}} \underbrace{- mH}_{\text{mortality}}$$

r_0 growth rate
K carrying capacity
a attack rate
h handling time
ε conversion efficiency
m mortality rate



General assumptions from formalism

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

Assumptions from mathematical formulations

- K: Resources for producers are limited
- No recycling feedback => resource dynamics faster than demography
- Mass action law: encounter rates are proportional to densities
- Type II: H consumption saturates as time is needed to manipulate food
- Only a part of herbivore consumption is converted into new biomass
- Herbivores dies without producers (metabolic needs) (and plants?)

How to analyse a theoretical model?

Content

1. Analytical study
   - Equilibria
   - Local stability analysis (Jacobian matrix)

2. Numerical analysis & simulation strategy
   - Numerical integration
   - Bifurcation diagrams
   - Parameter exploration and robustness of conclusions

Analytical study

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)

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

Equilibria (we know long-term dynamics)

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

No

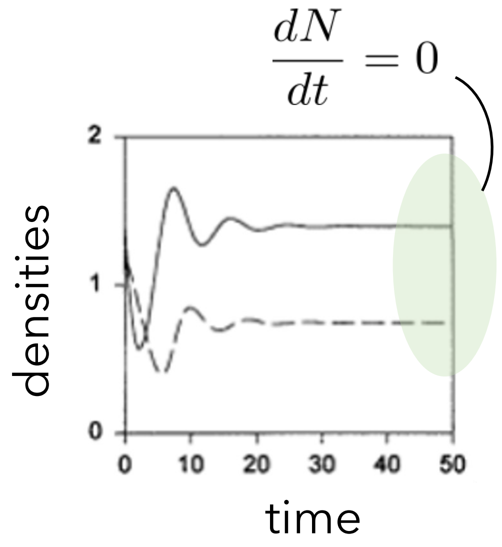
(results are specific to parameter values)

Simulations (many runs to explore parameter space)

Numerical integration (ODE)

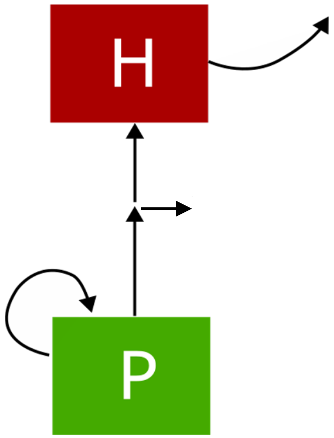
Coding algorithm (ABM)

Simplifications



Numerical analysis

1. Analytical study (1) Equilibria



The Rosenzweig-MacArthur model (1963)

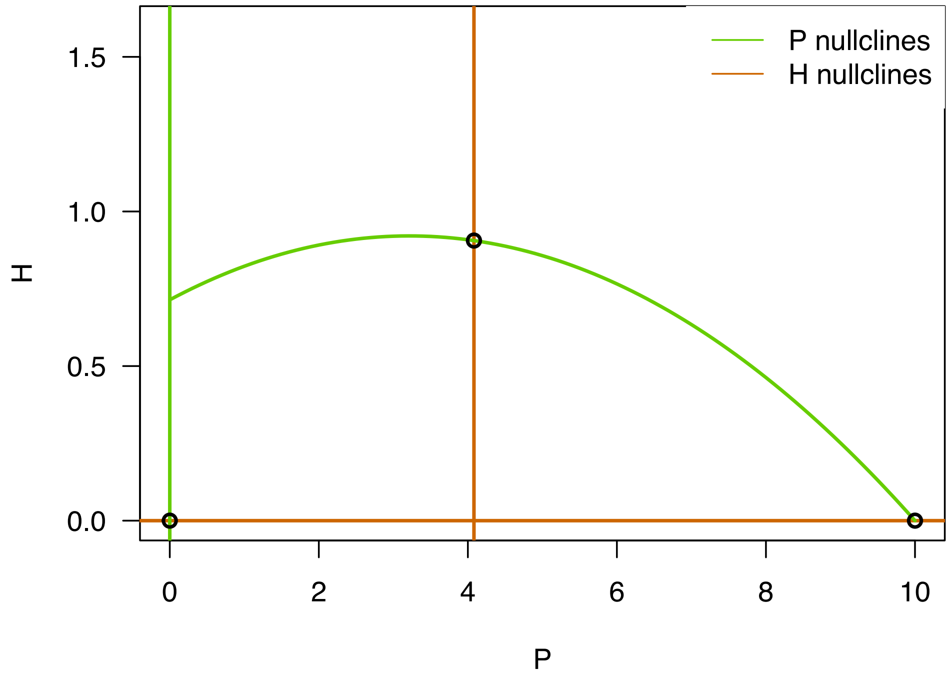
$$\frac{dP}{dt} = r_0 P(1 - \frac{P}{K}) - \frac{aPH}{1 + ahP}$$

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

- First Step : Determine the Equilibria, solve: $\begin{cases} \frac{dP}{dt} = 0 \\ \frac{dH}{dt} = 0 \end{cases}$
- 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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$$\left\{ P^* = 0,\ H^* = 0 \right\}$$

$$\left\{ P^* = K,\ H^* = 0 \right\}$$

When tractable, expresses P^* and H^* with parameters

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

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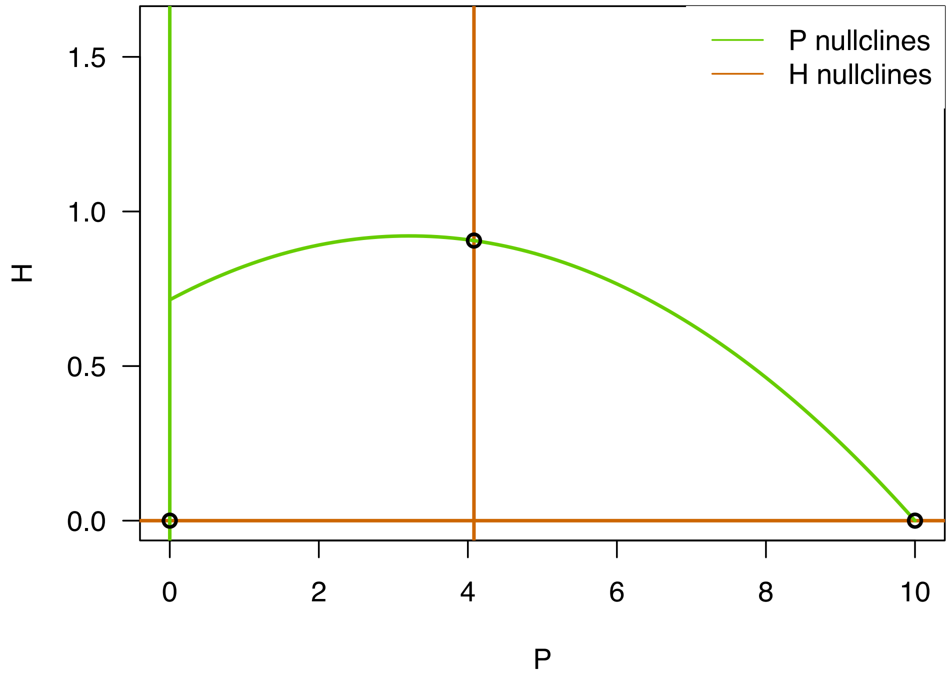
- Symbolic calculus (Maxima, Mathematica, Matlab)
- General expression



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

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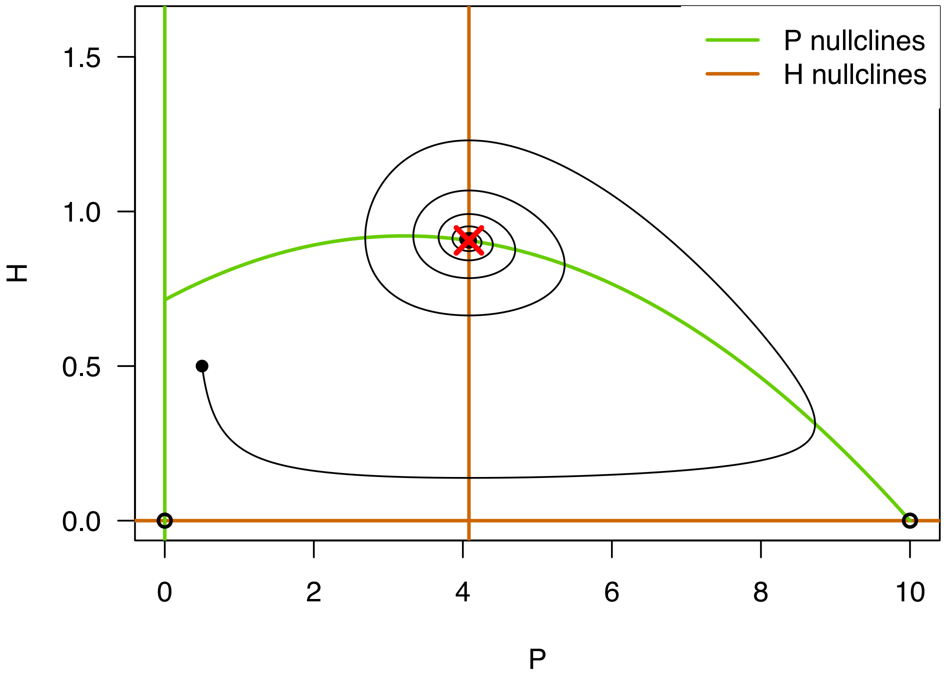

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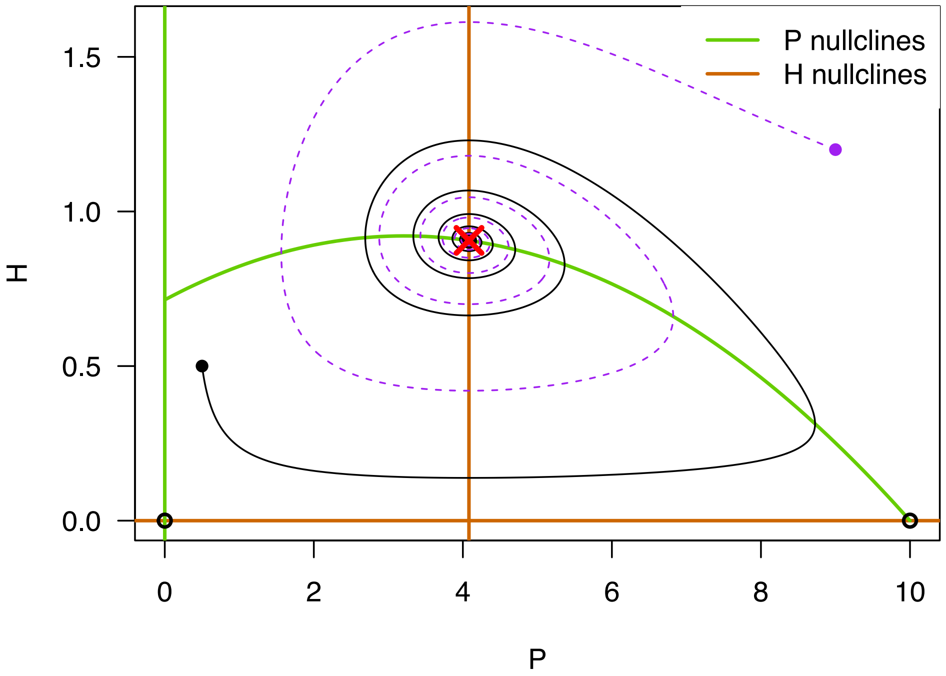
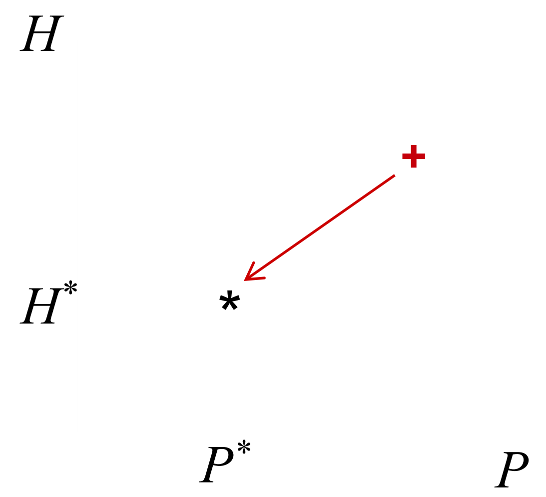


- **Feasibility criteria**
- **Interpretation on parameters**
- **doesn't depend on initial densities**

1. Analytical study (2) Local stability analysis

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

$$J = \begin{bmatrix} \dfrac{\partial \frac{dP}{dt}}{\partial P} & \dfrac{\partial \frac{dP}{dt}}{\partial H} \\[2ex] \dfrac{\partial \frac{dH}{dt}}{\partial P} & \dfrac{\partial \frac{dH}{dt}}{\partial H} \end{bmatrix}_{P^*,\, H^*}$$



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

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

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

1. Analytical study (2) Local stability analysis

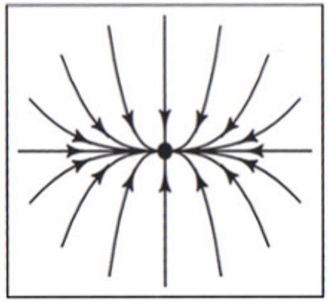
For a 2-equation system in continuous time

Eigenvalues of J also give information about trajectory type

Monotonous trajectories

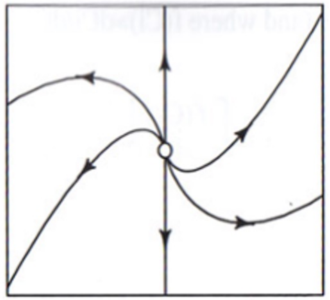
eigenvalues are real

Stable node



$-$	$-$

Unstable node

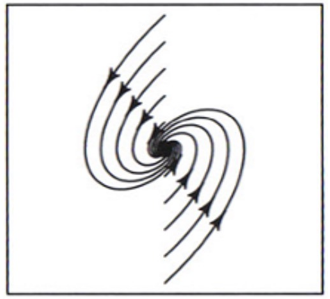


$+$	$+$

Oscillatory trajectories

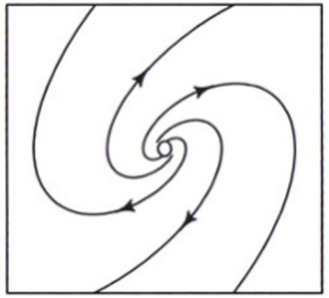
eigenvalues are complex

Stable spiral



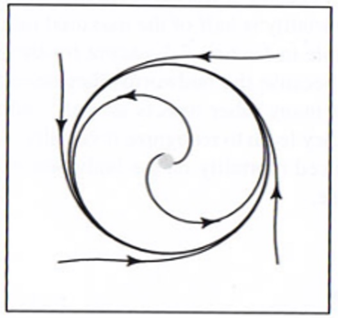
$-a \pm ib$	$-a \pm ib$

Unstable spiral



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

Limit cycle

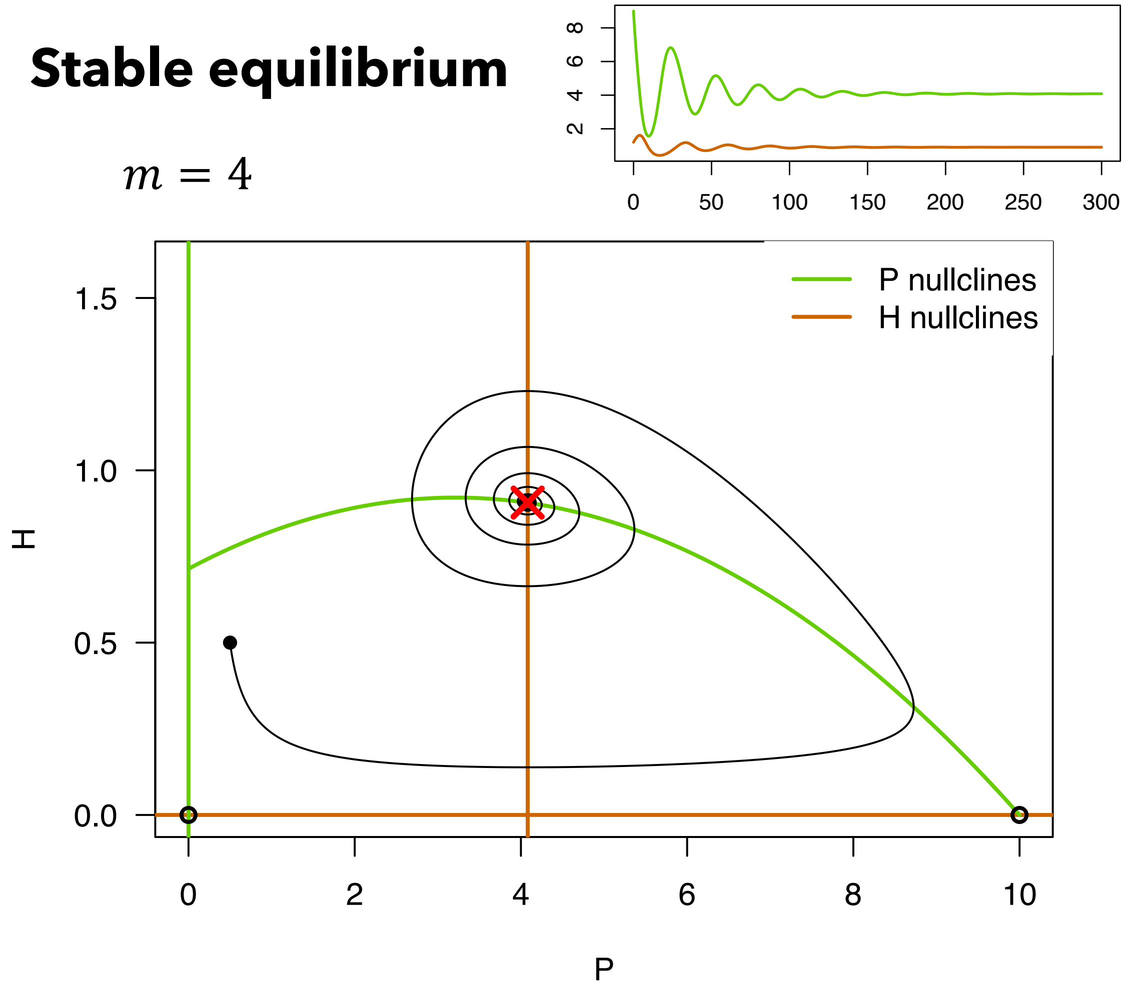


$+a \pm ib$	$+a \pm ib$

1. Analytical study (2) Local stability analysis

Stable equilibrium

$m = 4$



(1) $\begin{cases} P^* = 0,\ H^* = 0 \end{cases}$ $\quad \lambda_1 = 0.5 \quad \lambda_2 = -0.4$

(2) $\begin{cases} P^* = K,\ H^* = 0 \end{cases}$ $\quad \lambda_1 = -0.5 \quad \lambda_2 = 0.153$

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

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

1. Analytical study (2) Local stability analysis

Stable equilibrium

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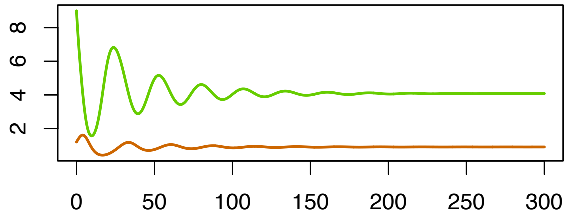
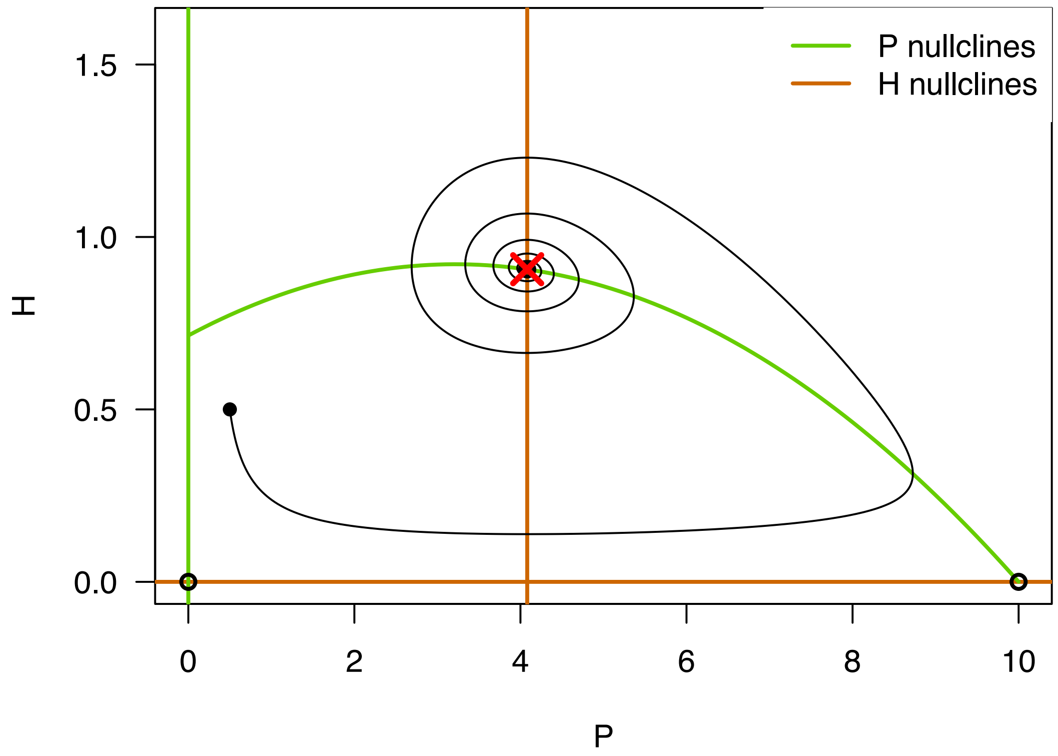
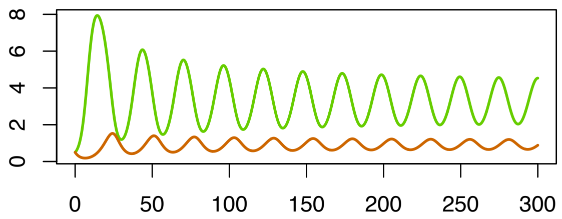


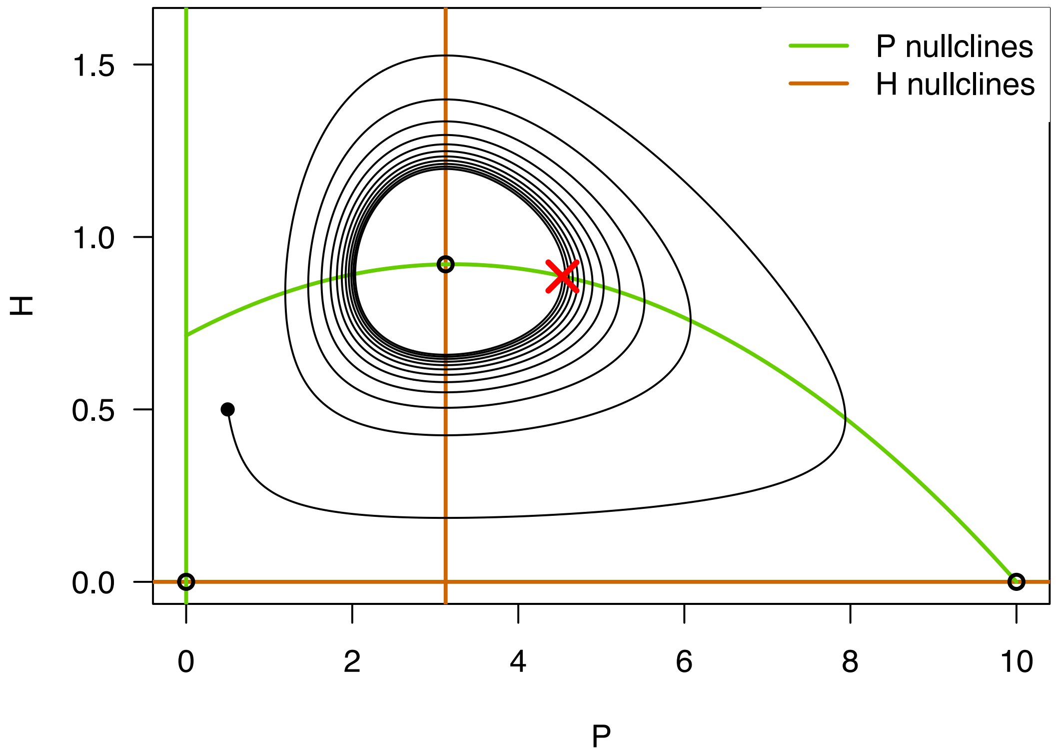


$$\lambda_1 = -0.023 + i0.234$$
$$\lambda_2 = -0.023 - i0.234$$

Limit cycle

$m = 3.5$





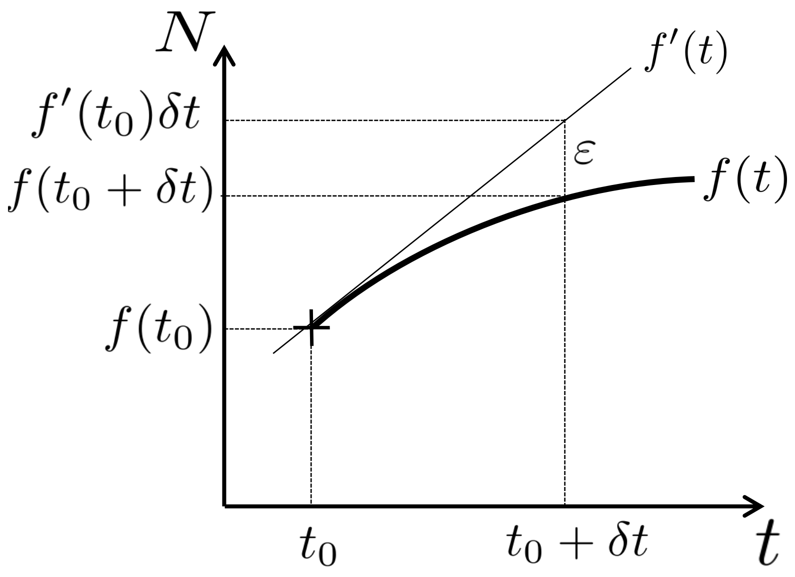
$$\lambda_1 = +0.002 + i0.253$$
$$\lambda_2 = +0.002 - i0.253$$

2. Numerical analysis

1. Numerical integration
2. Bifurcation diagrams
3. Parameter exploration & robustness of conclusions

2. Numerical analysis (1) Numerical integration

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



- 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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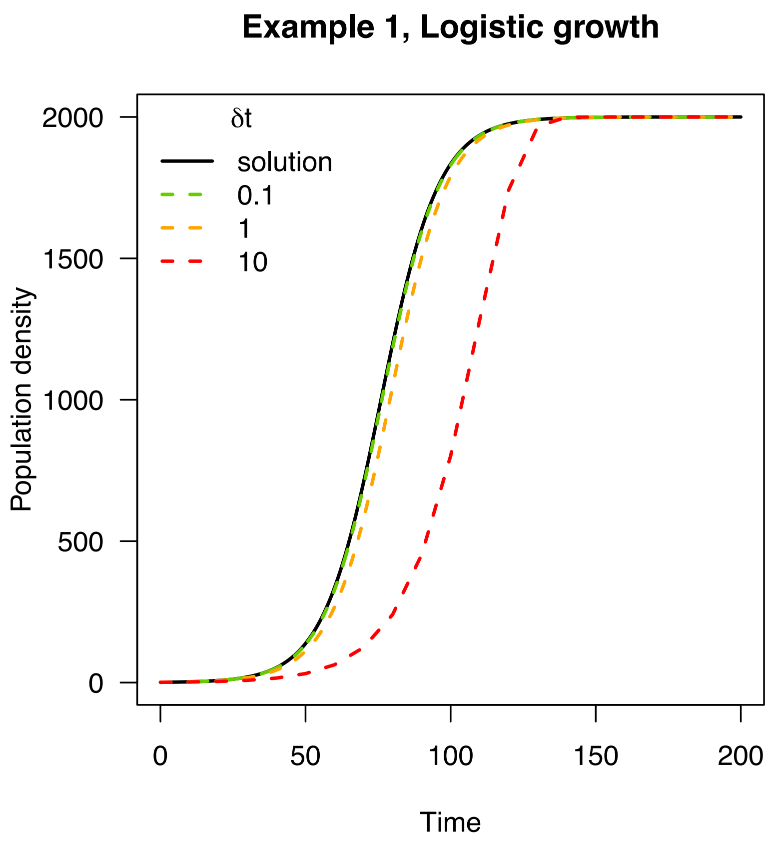

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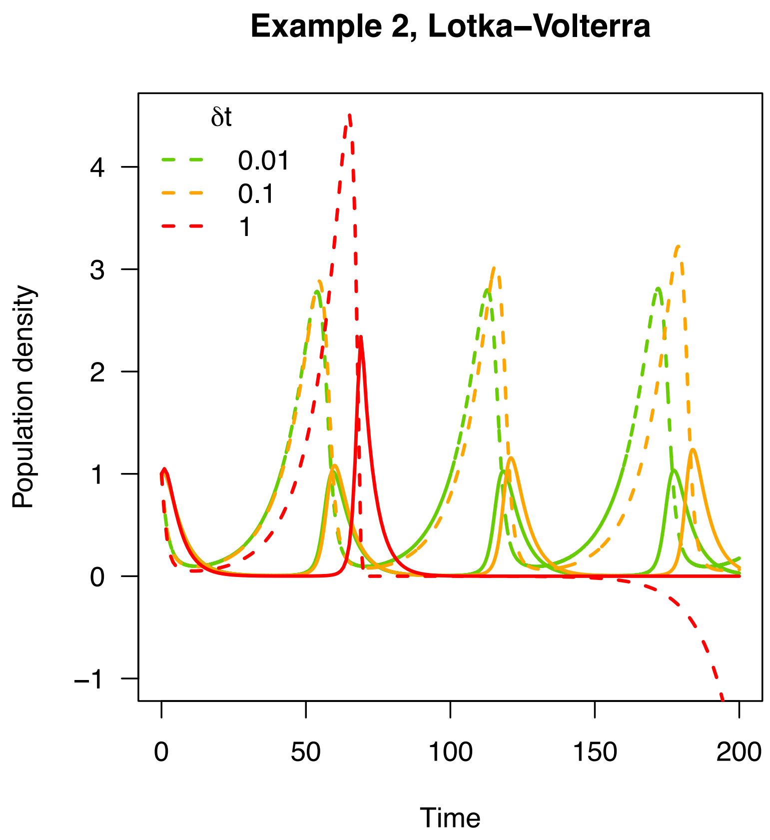

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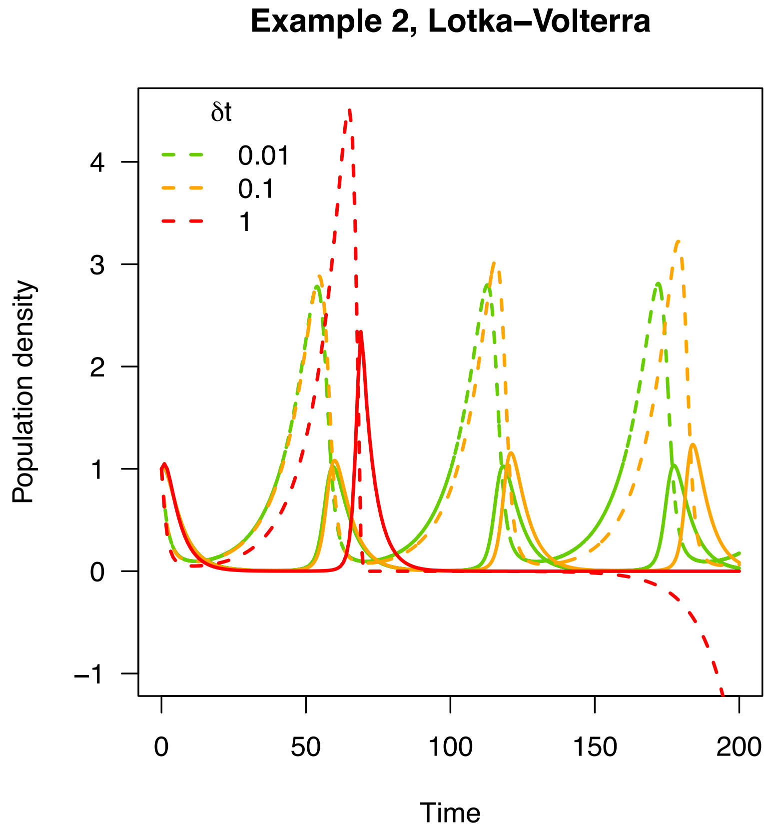

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- These algorithms are implemented into solvers. Some have adaptive time steps with error tolerance.

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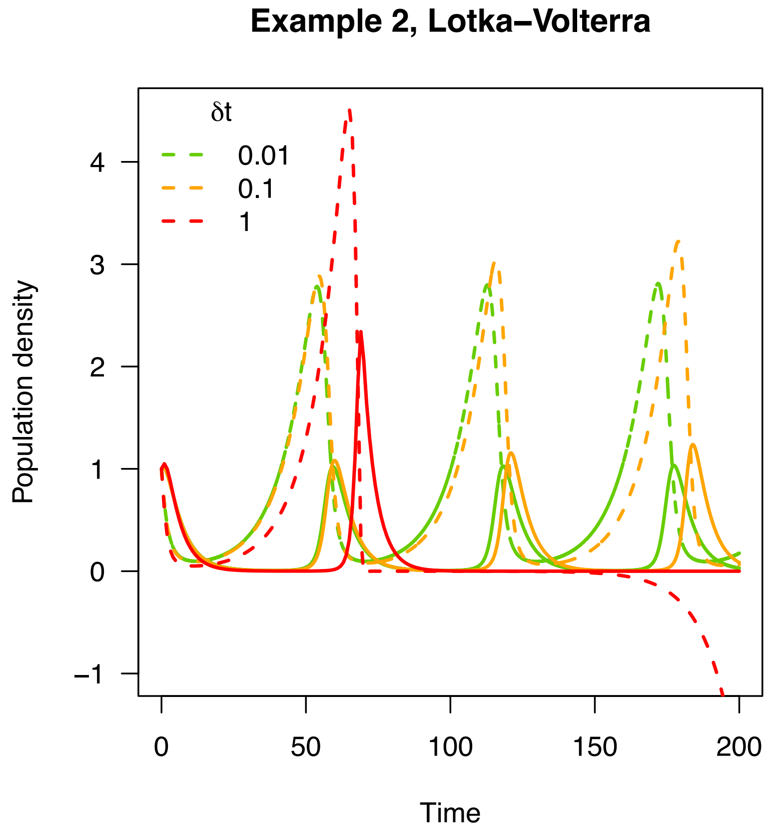

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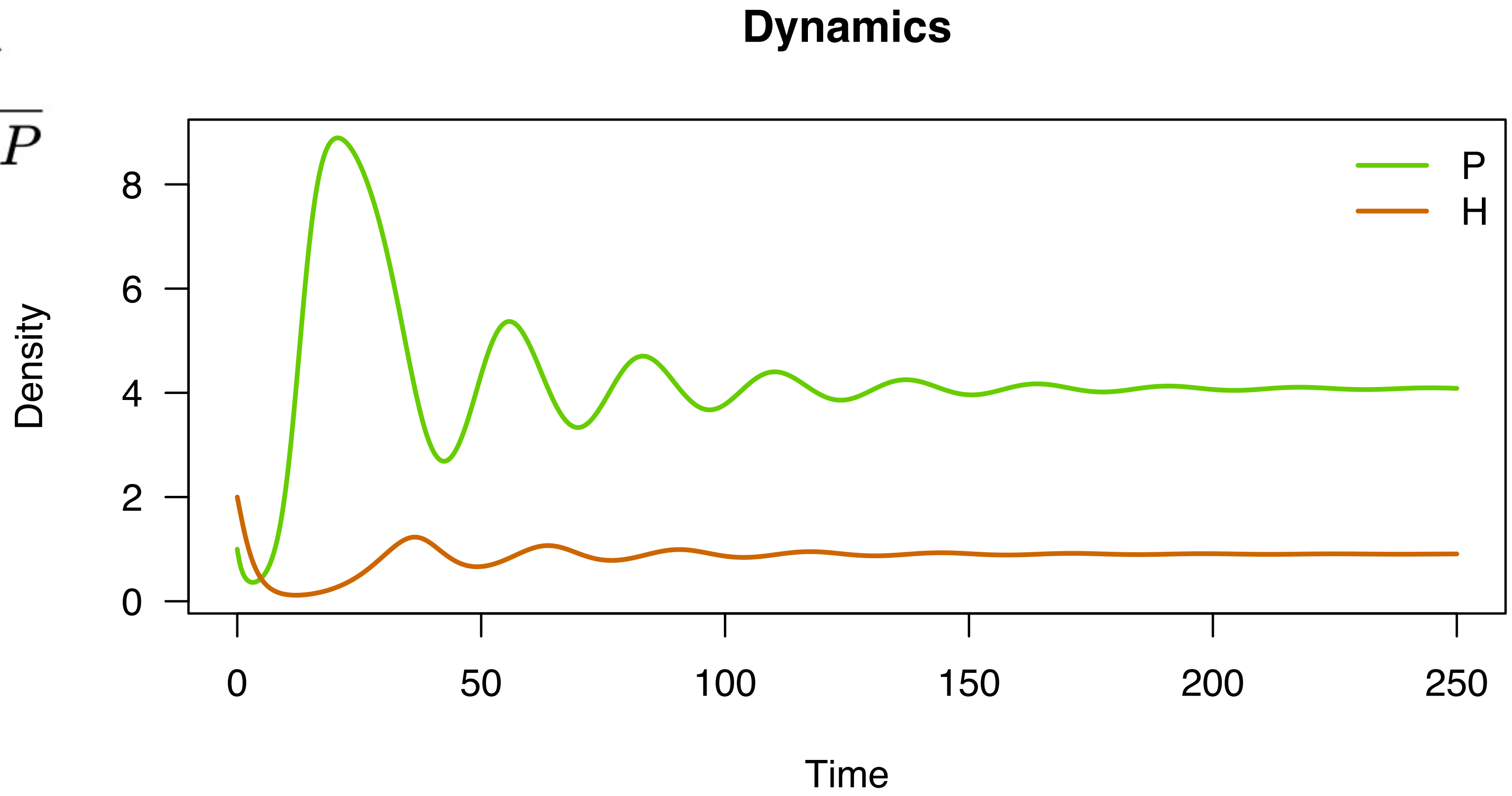
2. Numerical analysis (1) Numerical integration

Rosenzweig-MacArthur model (1963)

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



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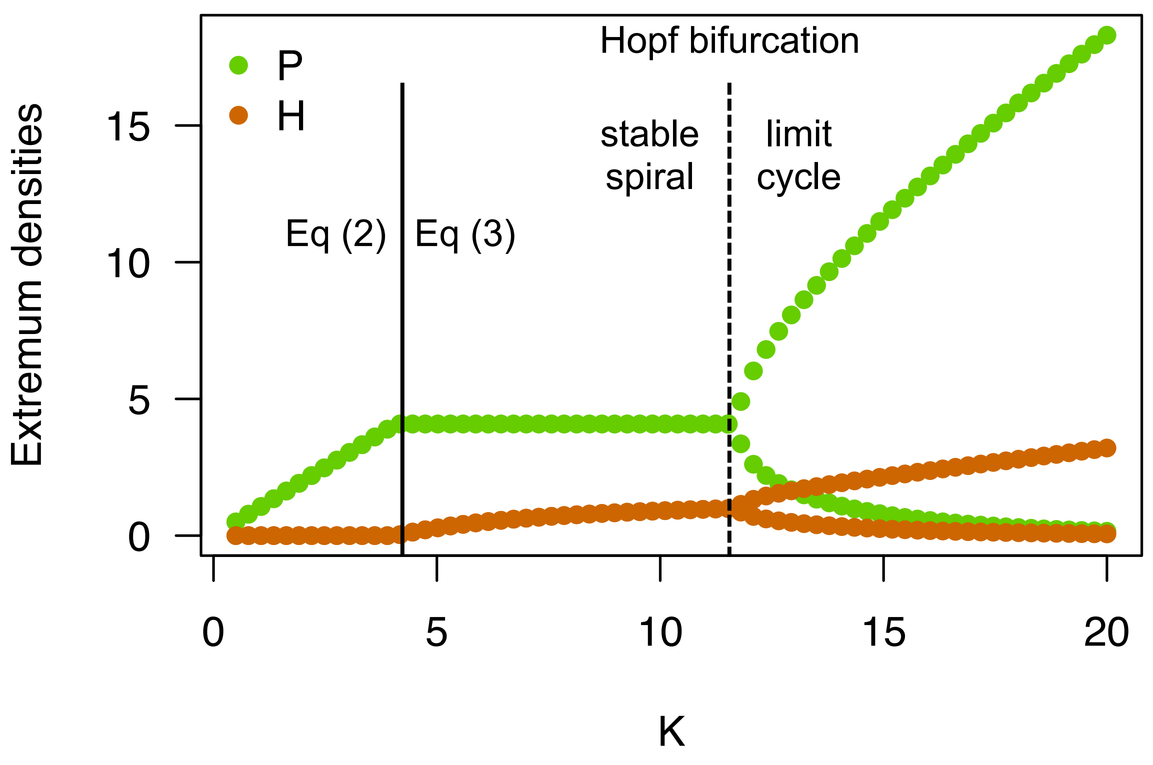
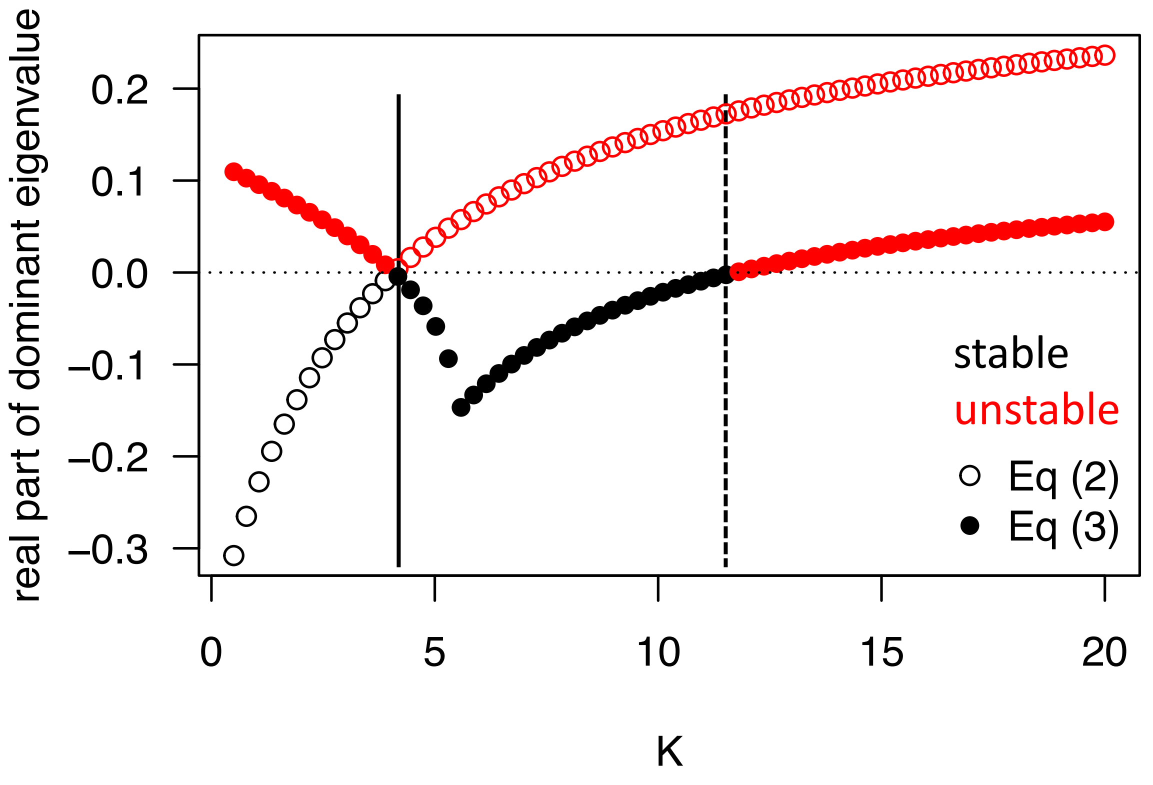
2. Numerical analysis (2) Bifurcation diagrams

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

Variables



Stability



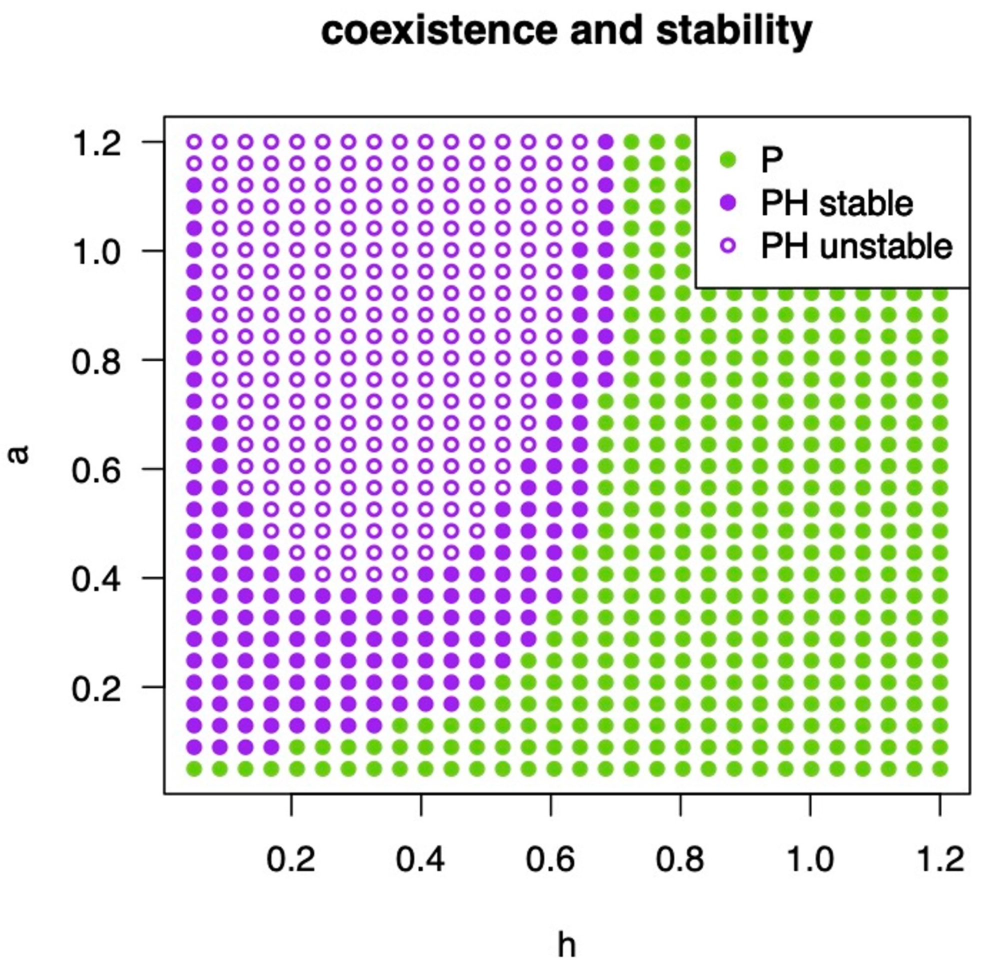
Increasing K allows H to install but then destabilizes the system

2. Numerical analysis **(3) parameter exploration & robustness of conclusions**

- 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

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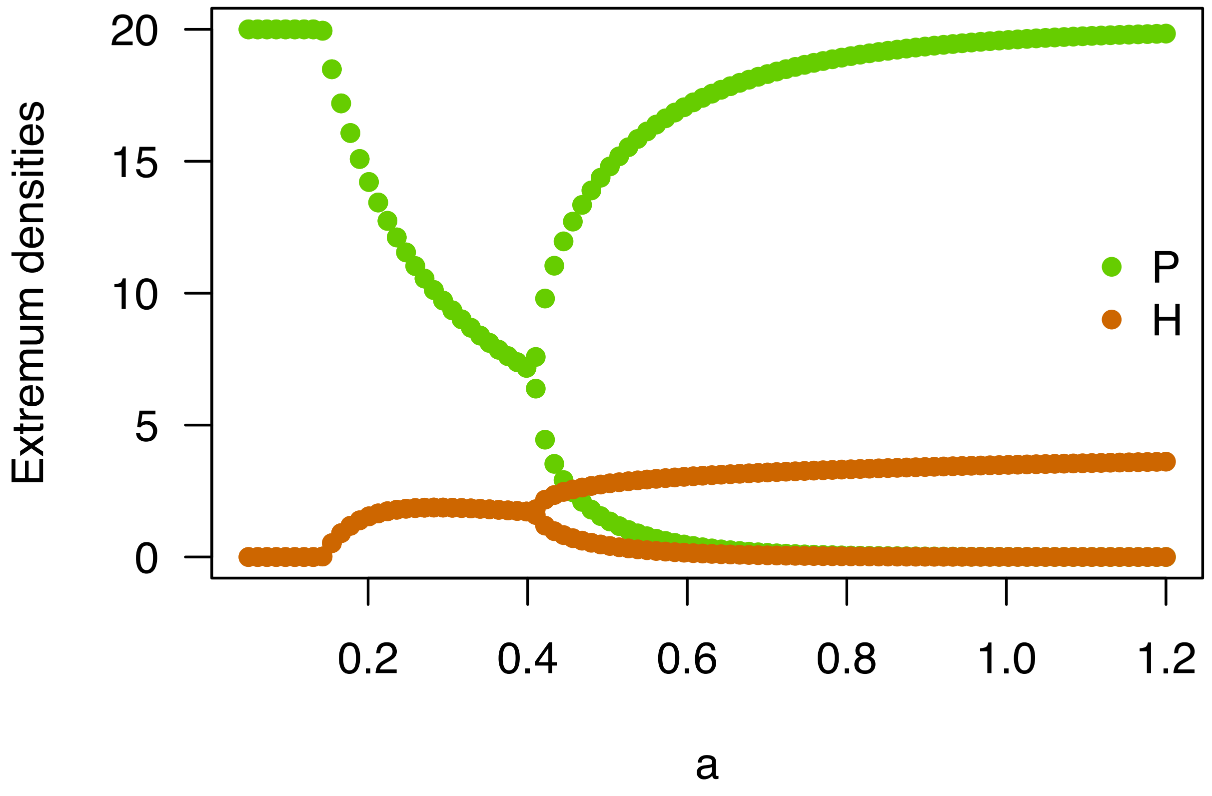
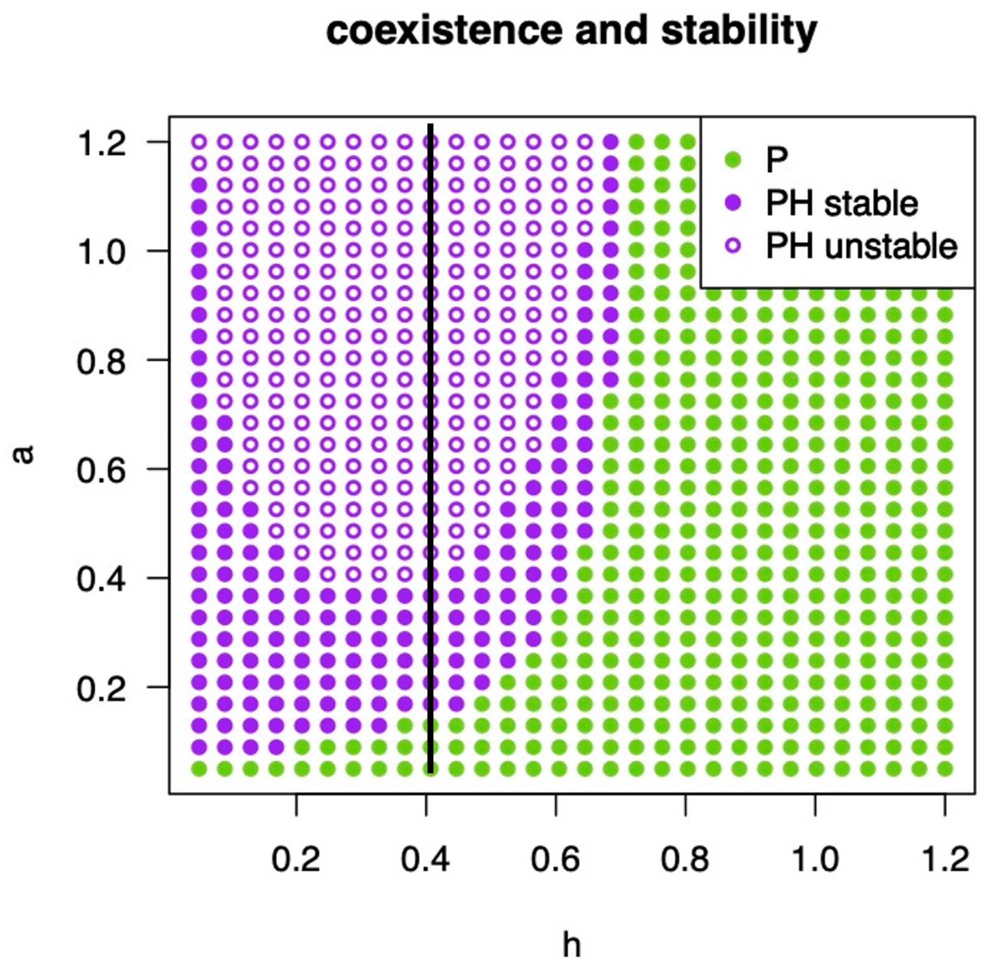


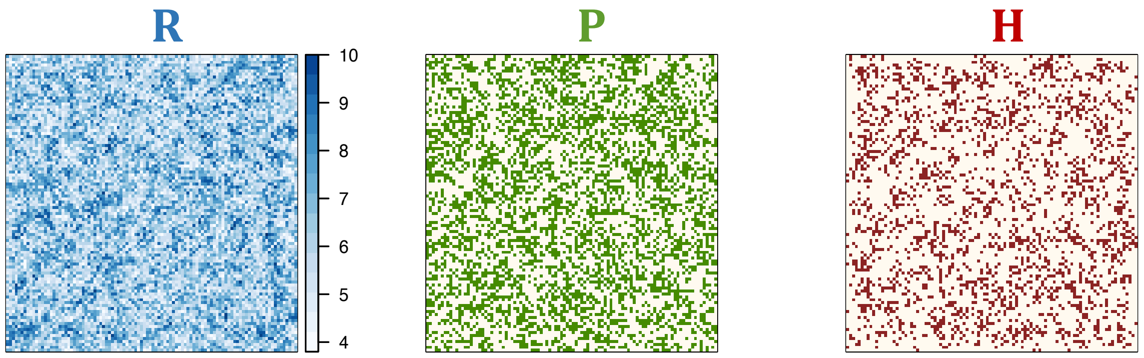


2. Numerical analysis **(3) parameter exploration & robustness of conclusions**

Example for a more complex model: **Simulation design for Red-Bio project**

Plant dispersal range
Herbivore dispersal range
Herbivore foraging range

3 levels



Recycling levels : ø low, high, (both species = or ≠)

With and without H

Colonization- extinction basal rates, c_0, e_0: slow / fast / frequent / rare

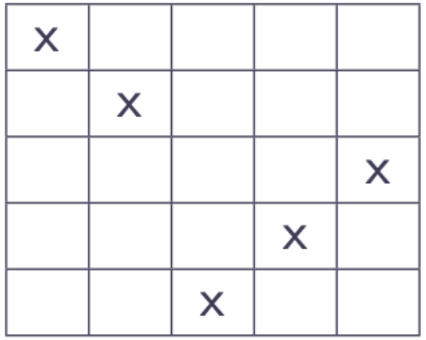
Full factorial x 25 replicates

Compare the results like for an experiment

Further robustness check
Parameter herbivory pressure
effect of nutrient diffusion, etc.

2. Numerical analysis **(3) parameter exploration & 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.*
Campolongo et al. (2011). From screening to quantitative sensitivity analysis. a unified approach. *Computer Physics Communications*, 182(4):978–988.

❖ Some useful references

Breckling, B., Jopp, F., & Reuter, H. (2011). Historical background of ecological modelling and its importance for modern ecology. In Modelling Complex Ecological Dynamics: An Introduction into Ecological Modelling for Students, Teachers & Scientists (pp. 29-40). Berlin, Heidelberg: Springer Berlin Heidelberg.

Caswell, H. (1988). Theory and models in ecology: a different perspective. Ecological modelling, 43(1-2), 33-44.

Grainger, T. N., Senthilnathan, A., Ke, P. J., Barbour, M. A., Jones, N. T., DeLong, J. P., ... & Germain, R. M. (2022). An empiricist's guide to using ecological theory. The American Naturalist, 199(1), 1-20.

Levins, R. (1966). The strategy of model building in population biology. American scientist, 54(4), 421-431.

Otto, S. P., & Day, T. (2007). A biologist's guide to mathematical modeling in ecology and evolution. Princeton University Press

Servedio, M. R., Brandvain, Y., Dhole, S., Fitzpatrick, C. L., Goldberg, E. E., Stern, C. A., ... & Yeh, D. J. (2014). Not just a theory—the utility of mathematical models in evolutionary biology. PLoS biology, 12(12), e1002017.

❖ Other quoted references

De Mazancourt, C., Loreau, M., & Abbadie, L. (1998). Grazing optimization and nutrient cycling: when do herbivores enhance plant production?. Ecology, 79(7), 2242-2252.

Fisher, R. A. (1937). The wave of advance of advantageous genes. Annals of eugenics, 7(4), 355-369.

Gounand I., Loeuille N., Charberet S., Fronhofer E. A., Harvey E., Kéfi S., Leroux S.L., Little C.J., McLeod A., Saade C., and Massol F. (2026) Nutrient heterogeneity emerges from dynamical abiotic-biotic feedback in a spatially explicit plant-herbivore occupancy model. bioRxiv: https://www.biorxiv.org/lookup/doi/10.64898/2026.03.03.709064

Kéfi, S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A., & De Ruiter, P. C. (2007). Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature, 449(7159), 213-217.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the ESA, 15(3), 237-240.

Rosenzweig, M. L., & MacArthur, R. H. (1963). Graphical representation and stability conditions of predator-prey interaction. The American Naturalist, XCVII(895), 209–223.