Introduction to deterministic models in ecology and evolution

Frédéric Hamelin

1. Introduction to dynamical systems in ecology
2. Introduction to **resilience** in ecological systems
3. Introduction to evolutionary invasion analysis

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Introduction to **resilience** in ecological systems

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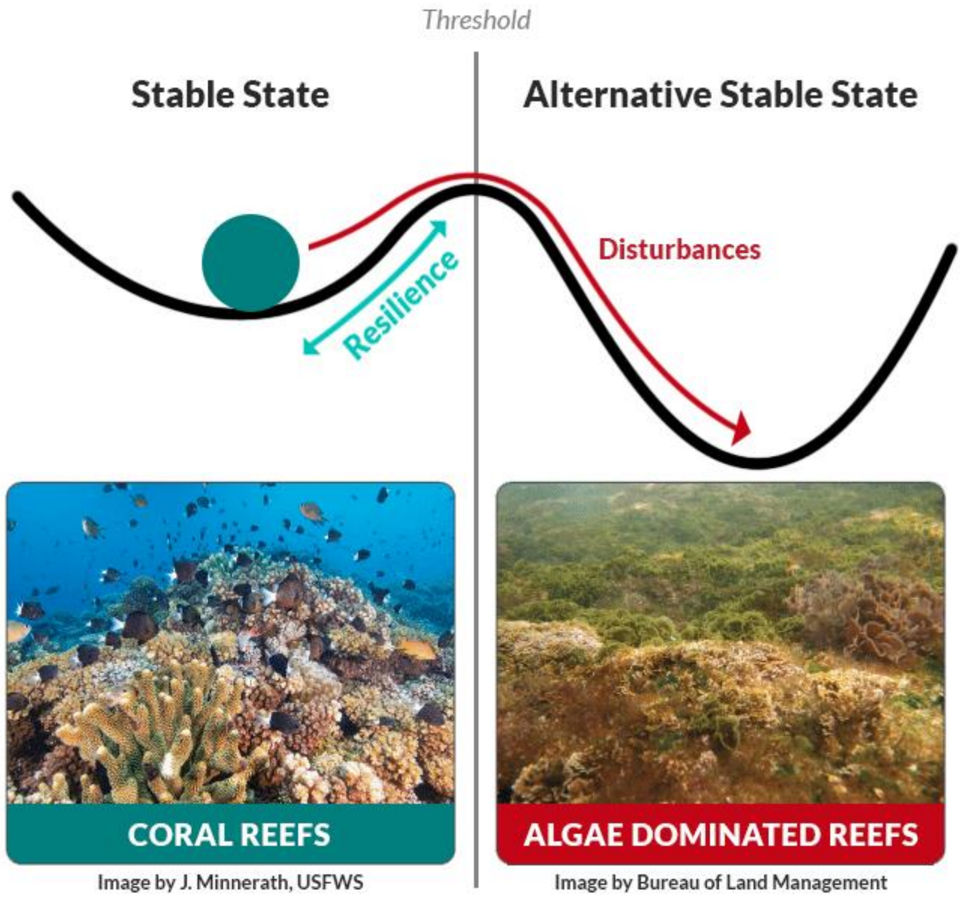
Outline

- Ecological resilience
- Abrupt regime shifts:
    1. Facts
    2. Theory
        - Exploited population dynamics
            - Overfishing
            - Overgrazing
        - Shifts due to pollution or loss of biodiversity
            - Shallow lakes eutrophication
            - Coral reef degradation
        - Recurring outbreaks of insect pests
- Tipping points and early warning signals

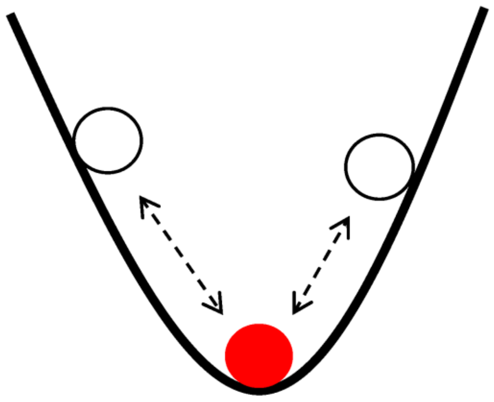


Resilience

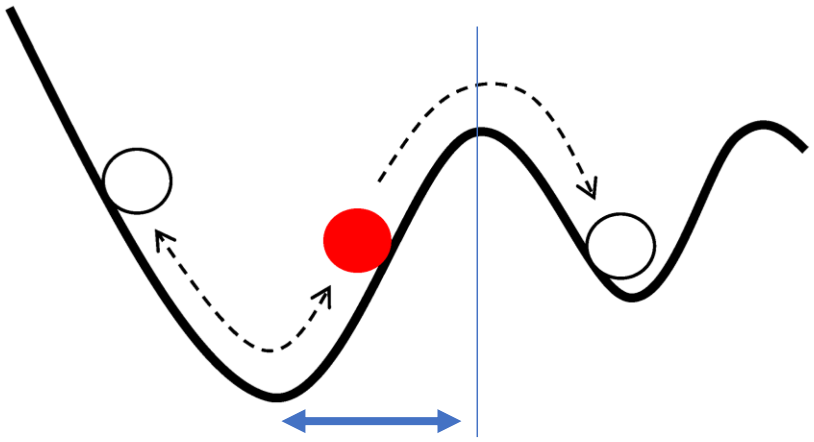
- **Engineering**: the amount of stress a material can withstand before breaking
- **Psychology**: the ability to bounce back after negative emotional experiences
- **Development**: the ability of a person, household, or other aggregate unit to avoid poverty in the face of various stressors and shocks
- **Ecology**: the ability of ecosystems to absorb change and disturbance
- **Socio-ecology**: the ability to adapt or transform in the face of change

Resilience in ecology

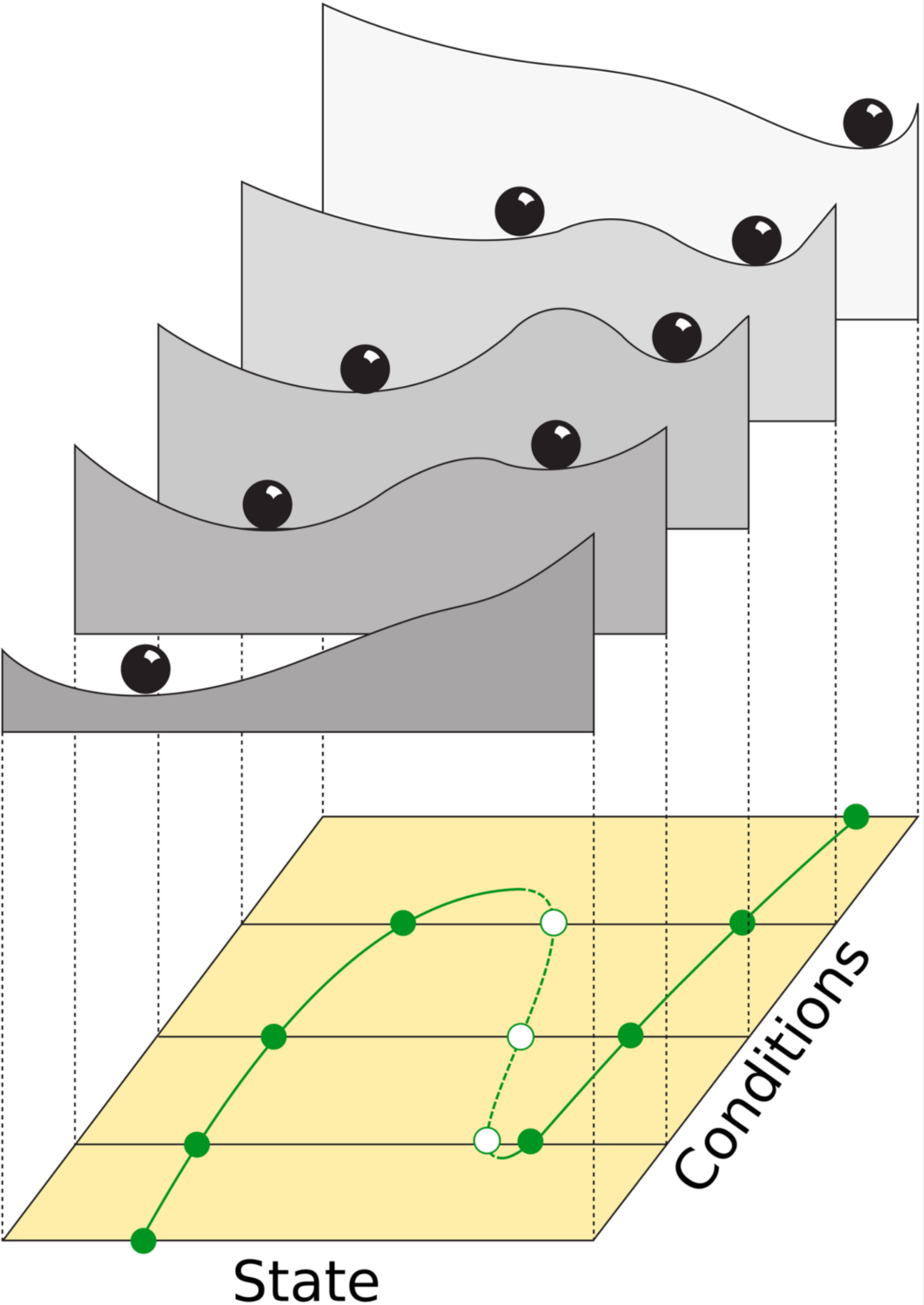
- Intuitively: the ability of a system to cope with disturbances, bounce back, and maintain its state and functionality
- 2 concurrent definitions:
  - **Engineering resilience**: the speed at which a system returns to a reference state after a disturbance
  - **Ecological resilience**: the magnitude of disturbance that can be absorbed before a system tips into another state



Engineering resilience



Ecological resilience



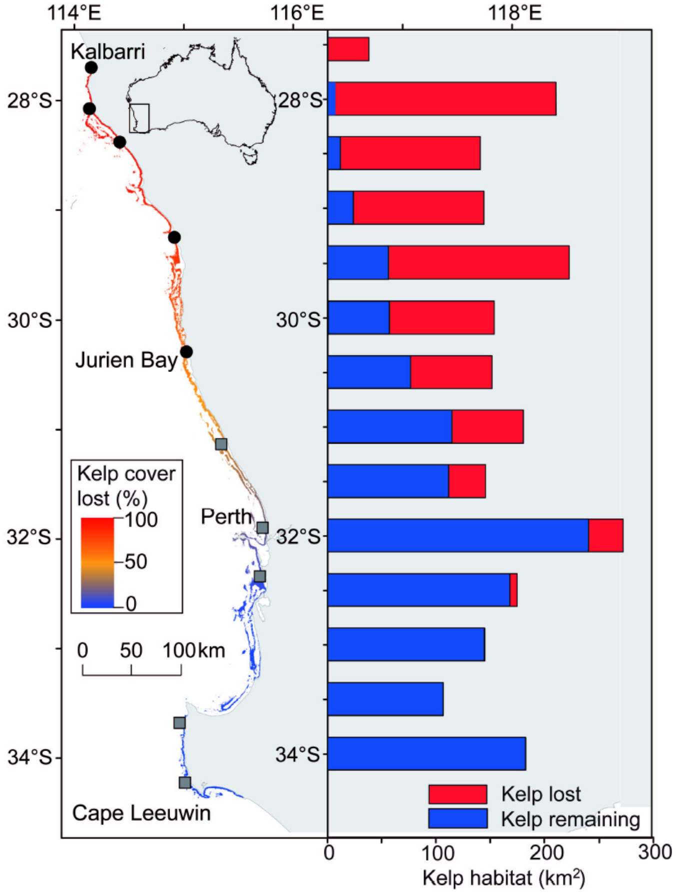
Stability, tipping point, theory

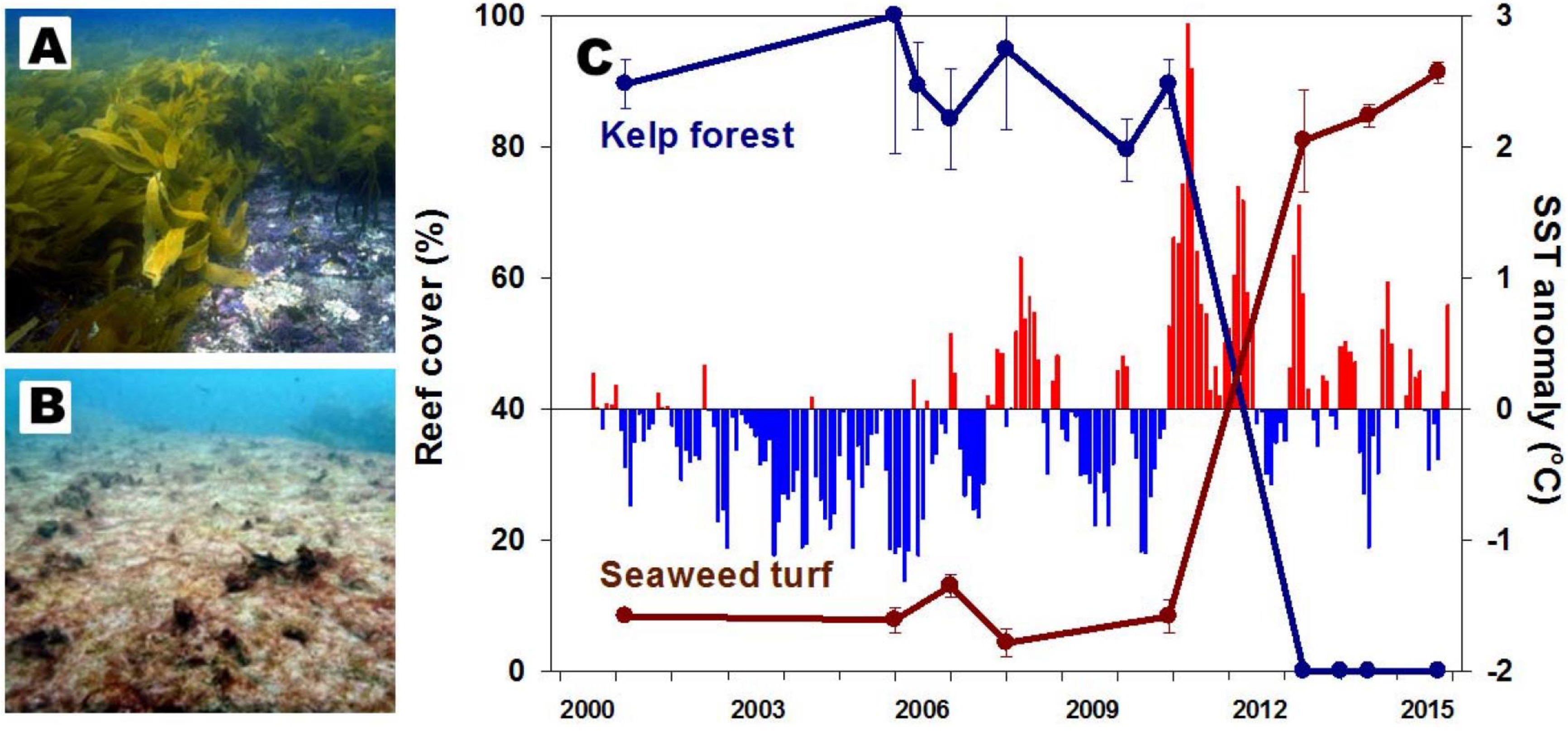
Examples?

Rodríguez-Sánchez et al (2020). Climbing Escher's stairs: A way to approximate stability landscapes in multidimensional systems. *PLoS Computational Biology*

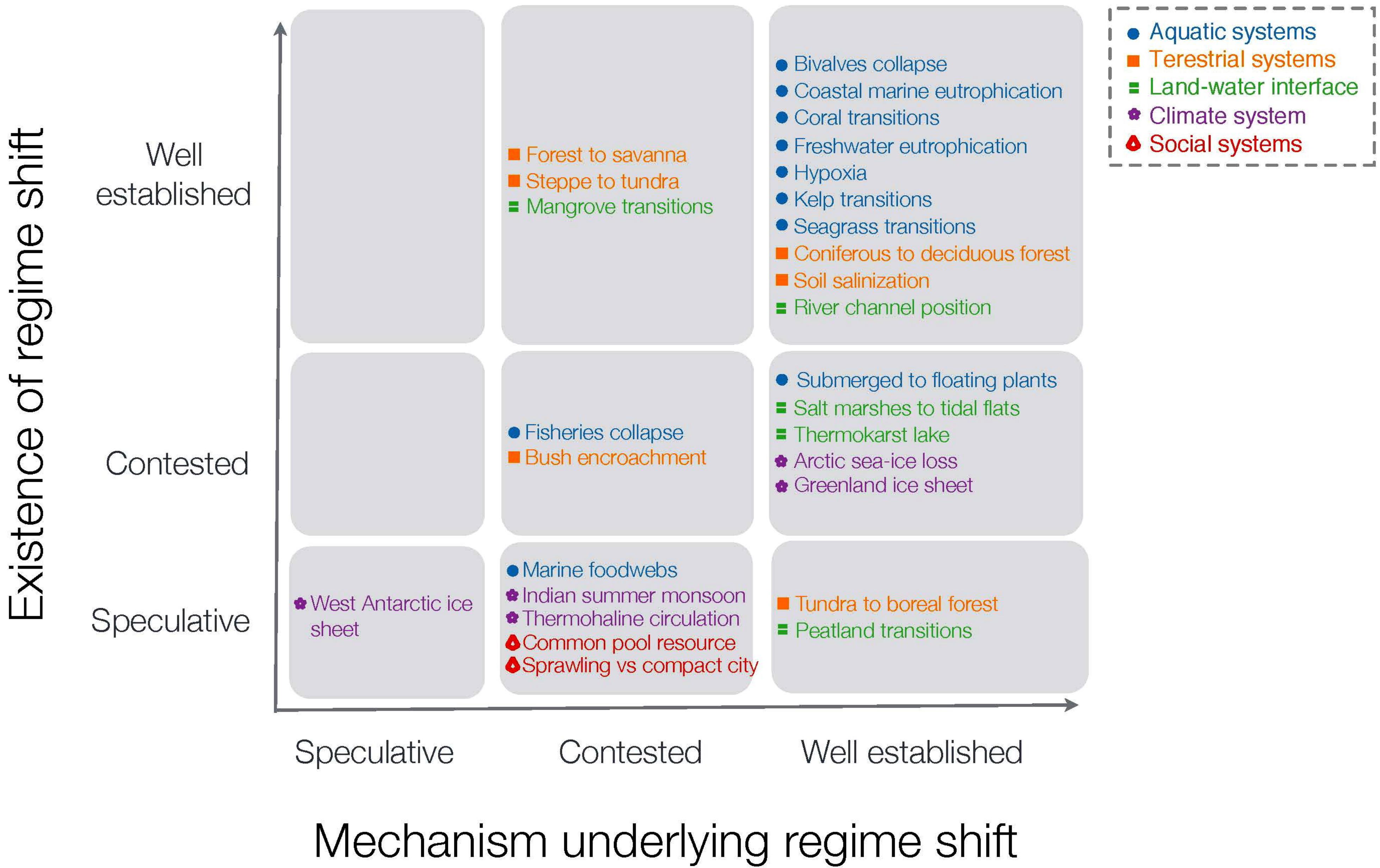
Abrupt regime shifts: the facts

Wernberg et al (2016) **Climate-driven regime shift** of a temperate marine ecosystem. *Science*

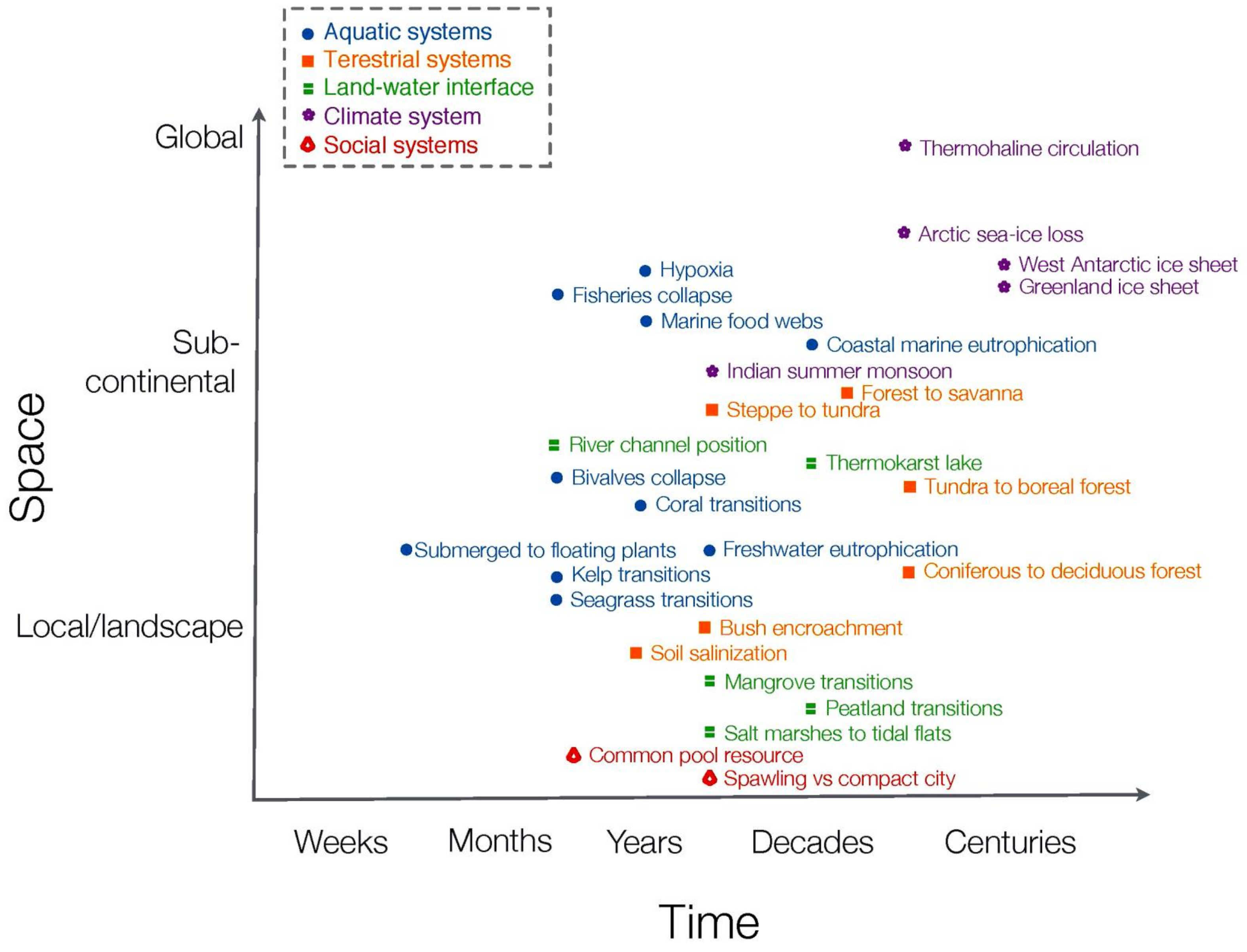




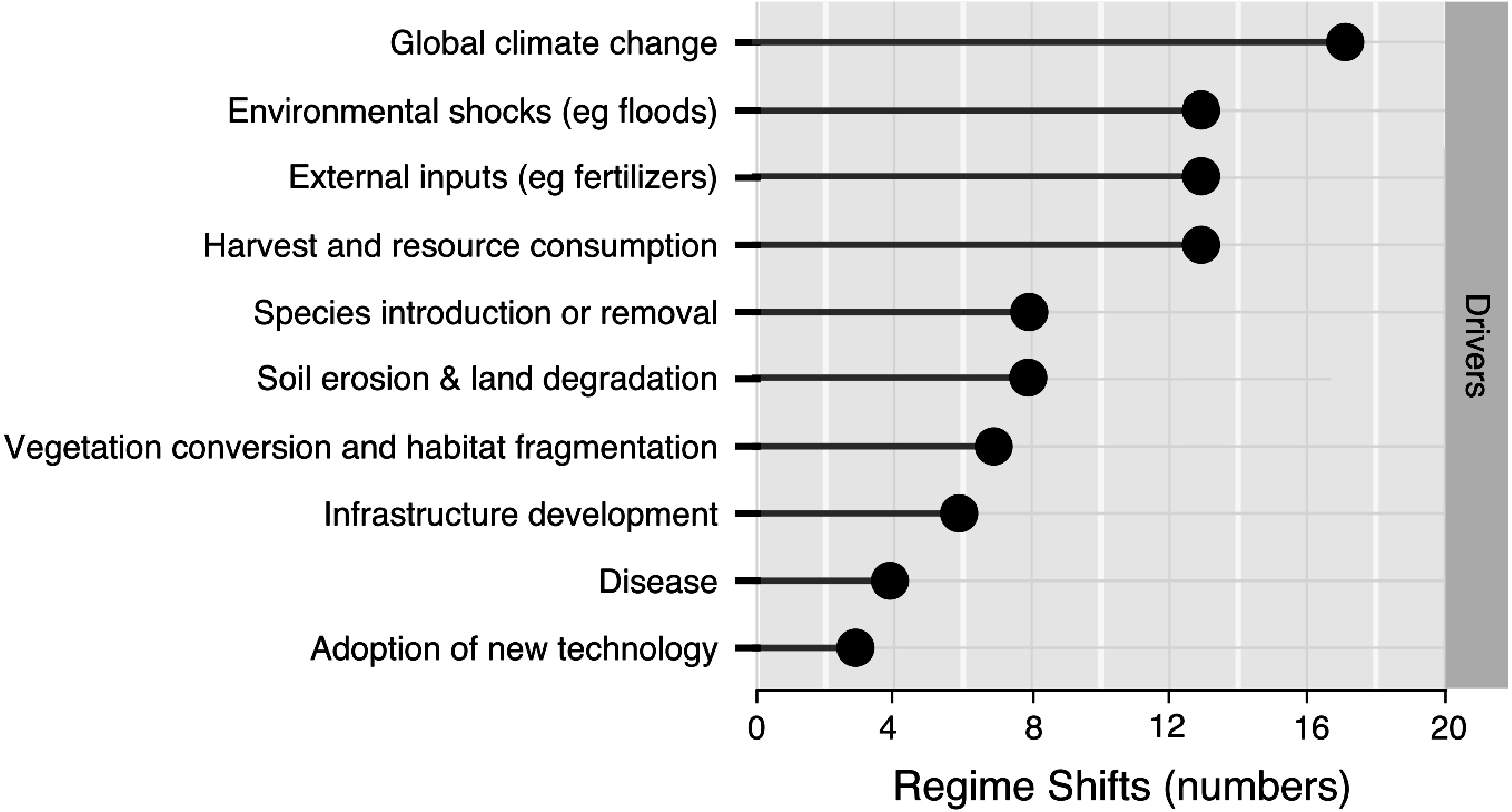
Biggs et al (2018) The regime shifts database. *Ecology and Society*



Biggs et al (2018) The regime shifts database. *Ecology and Society*



Biggs et al (2018) The regime shifts database. *Ecology and Society*



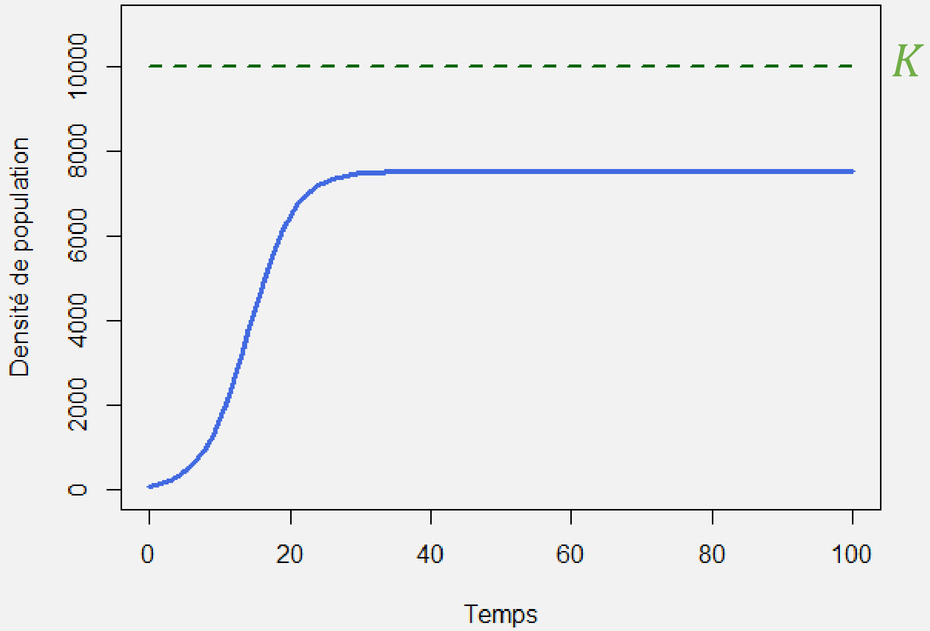
Abrupt regime shifts: theory

Exploited population dynamics

Exploitation of a fish population

- Population density: N
- Intrinsic growth rate: r
- Carrying capacity: K
- Catchability: c
- Fishing effort: e

$$\underbrace{\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)}_{\text{logistic growth}} - \underbrace{ceN}_{\text{catches}}$$



Kot (2001) *Elements of mathematical ecology*. Cambridge University Press.

Equilibria

- Species absent: $N = 0$
- Species present:

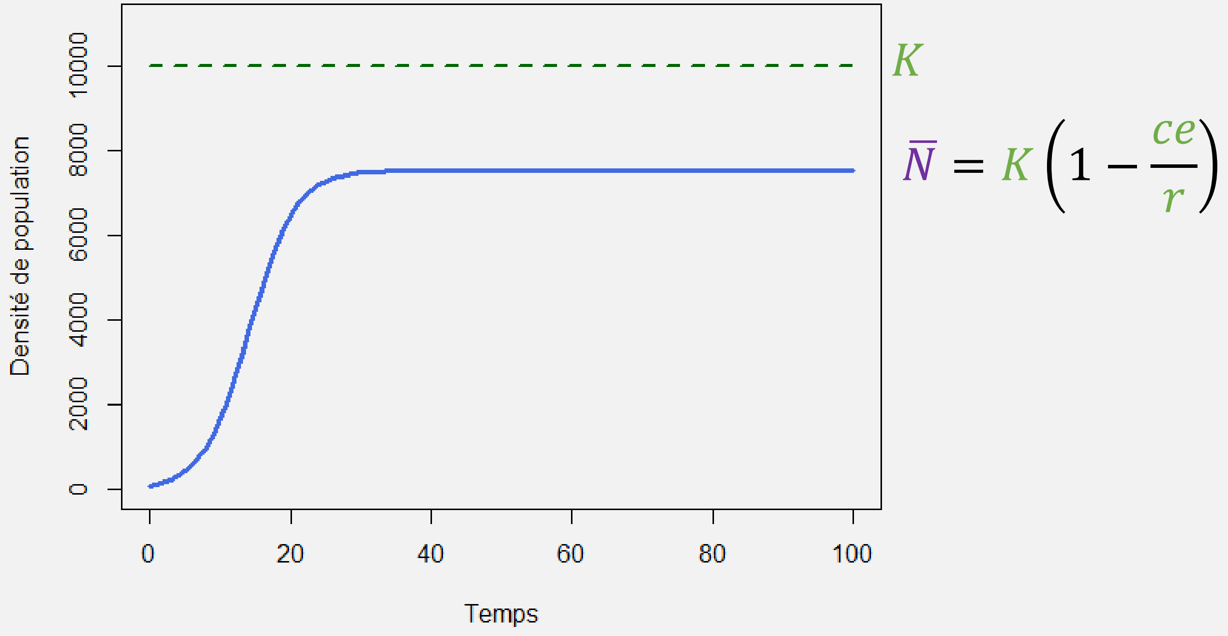
$$\bar{N} = K\left(1 - \frac{ce}{r}\right)$$

- Species persistence iff:

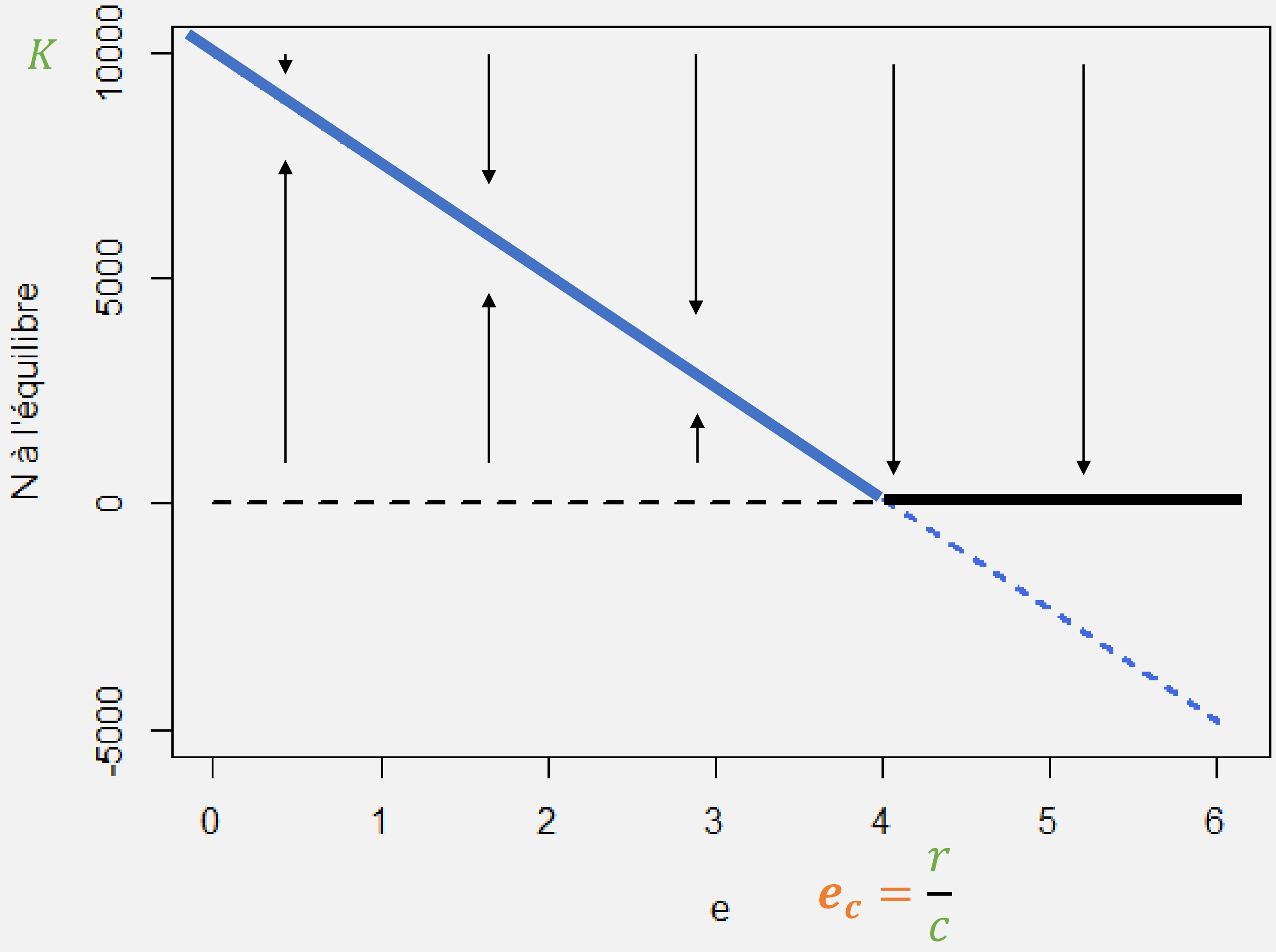
$$e < \frac{r}{c}$$

- Fishing effort must be limited, otherwise overfishing and extinction

$$\underbrace{\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)}_{\text{logistic growth}} - \underbrace{ceN}_{\text{catches}}$$



Bifurcation diagram



Critical fishing effort beyond which the population goes extinct (due to overfishing)

Continuous bifurcation (“soft” and “reversible” extinction)

Sustainable yield

- Yield at equilibrium

(catches per unit time):

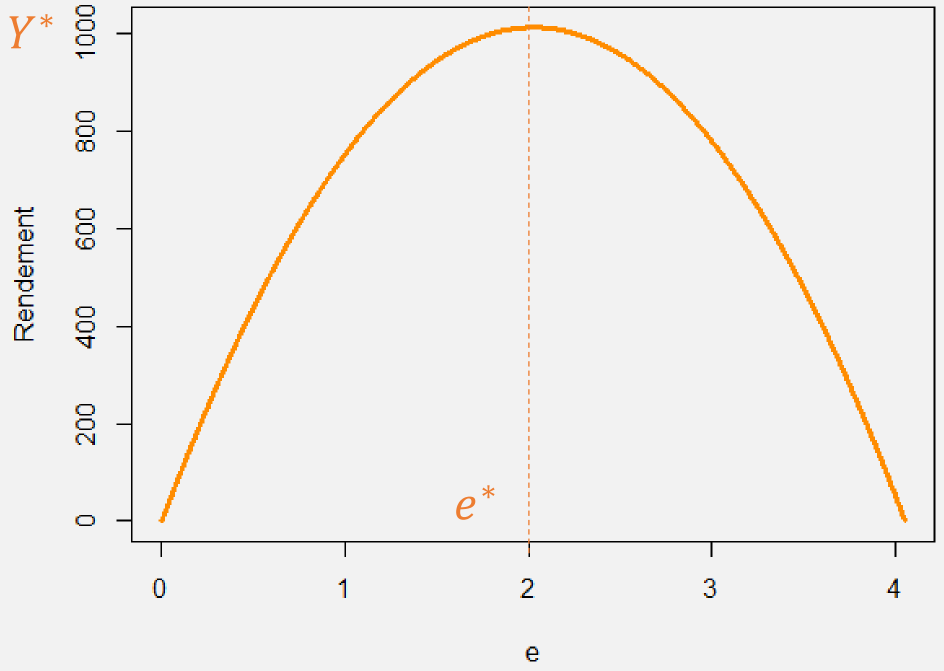
$$Y(e) = ce\bar{N} = ceK\left(1 - \frac{ce}{r}\right)$$

- Maximum sustainable yield s.t.:

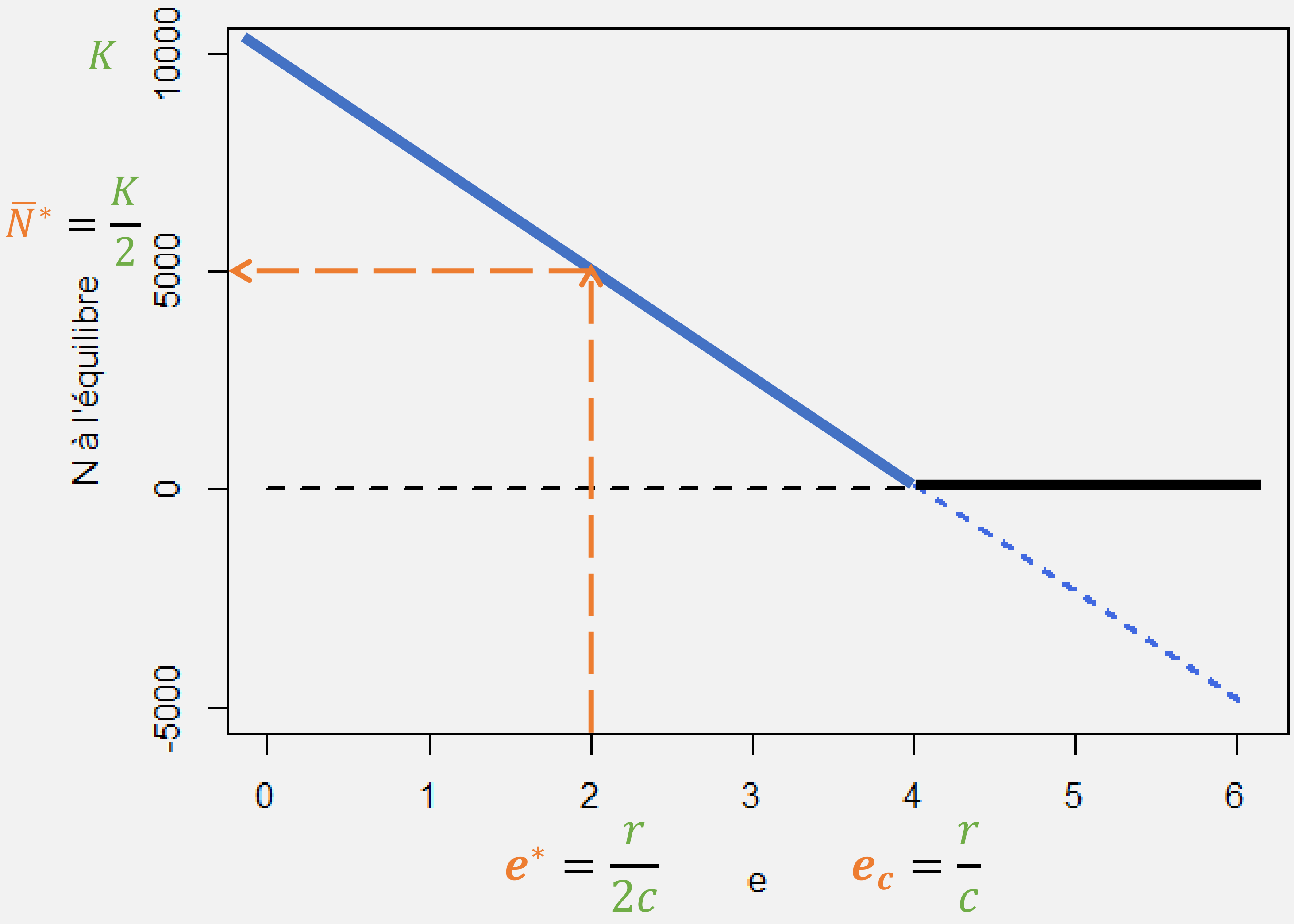
$$Y'(e^*) = cK\left(1 - 2\frac{ce^*}{r}\right) = 0$$

- Hence, $e^* = \frac{r}{2c}$, $Y^* = \frac{rK}{4}$ et $\bar{N}^* = \frac{K}{2}$

$$\underbrace{\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)}_{\text{logistic growth}} - \underbrace{ceN}_{\text{catches}}$$

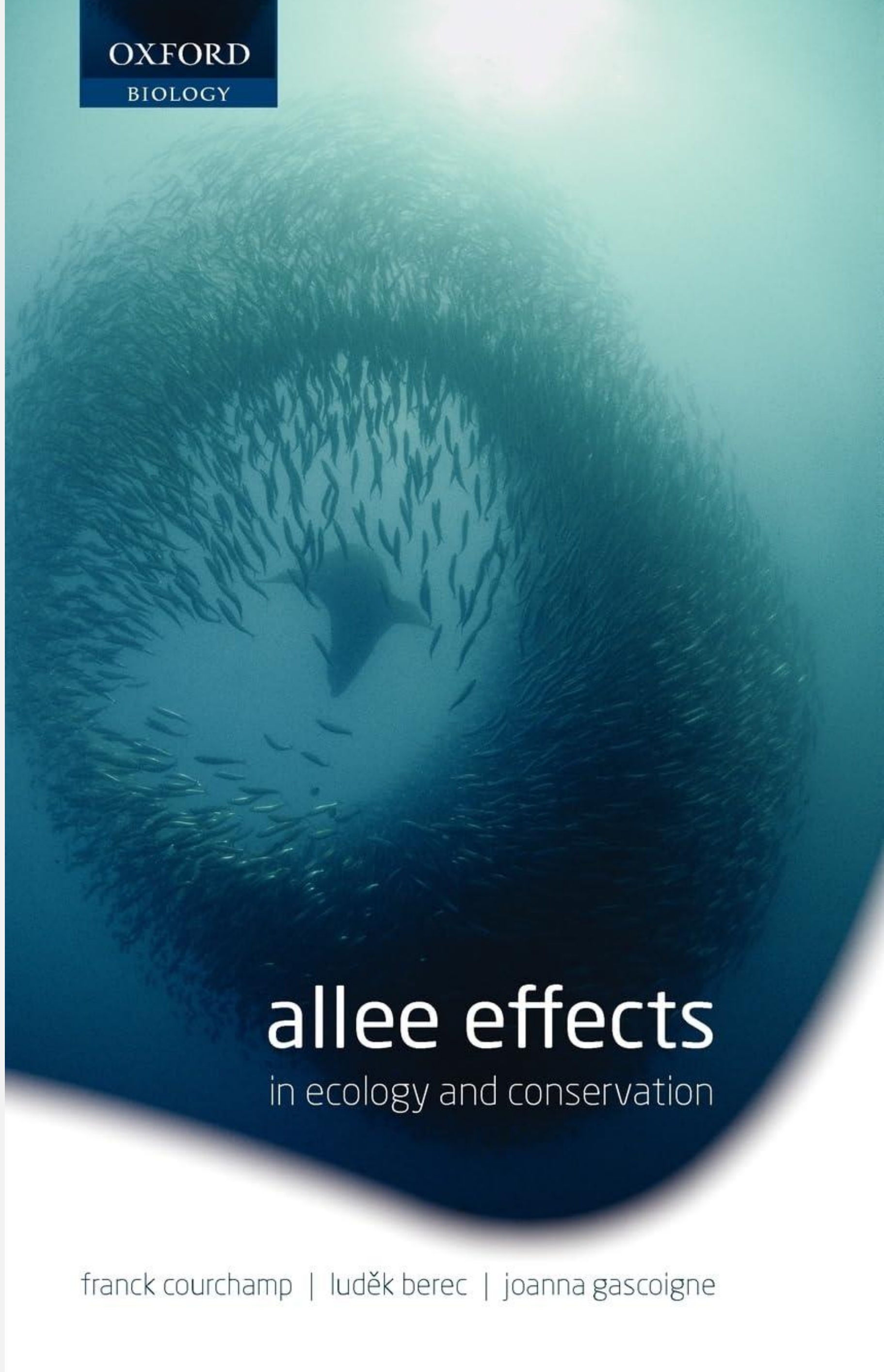


Sustainable yield



Optimal fishing effort allows half of the population to be conserved

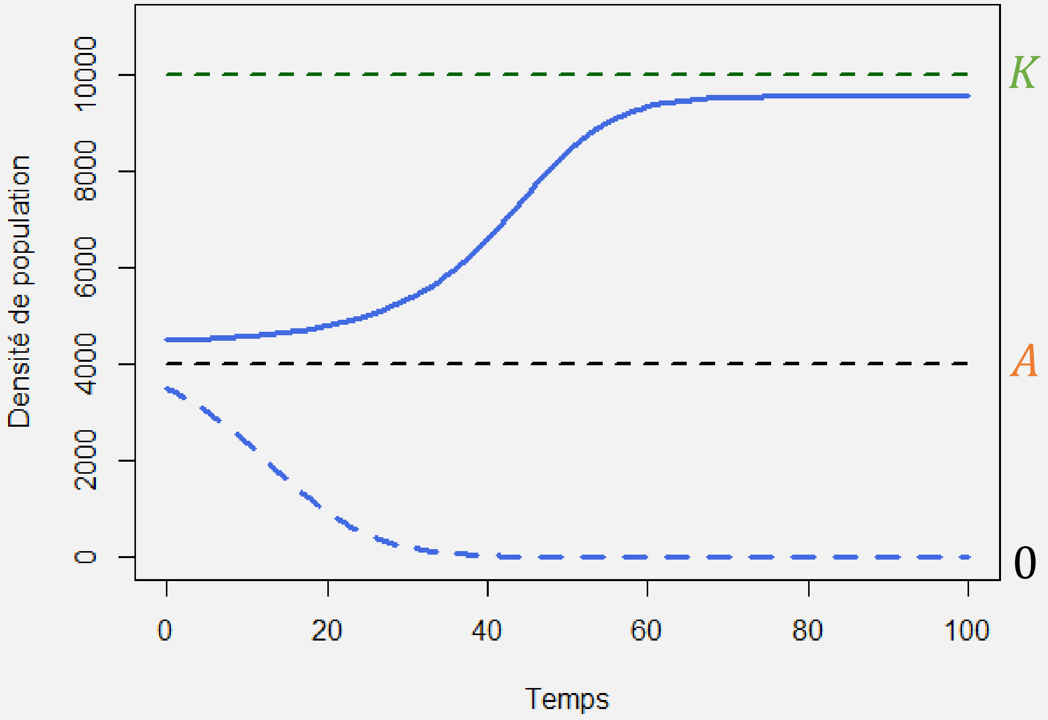
Introduction of an Allee effect



Fishing a population with strong Allee effect

- Population density: N
- Intrinsic growth rate: r
- Carrying capacity: K
- Catchability: c
- Fishing effort: e
- Allee threshold: A

$$\underbrace{\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right)}_{\text{logistic growth}}\underbrace{\left(\frac{N-A}{K}\right)}_{\text{Allee effect}} - \underbrace{ceN}_{\text{catches}}$$

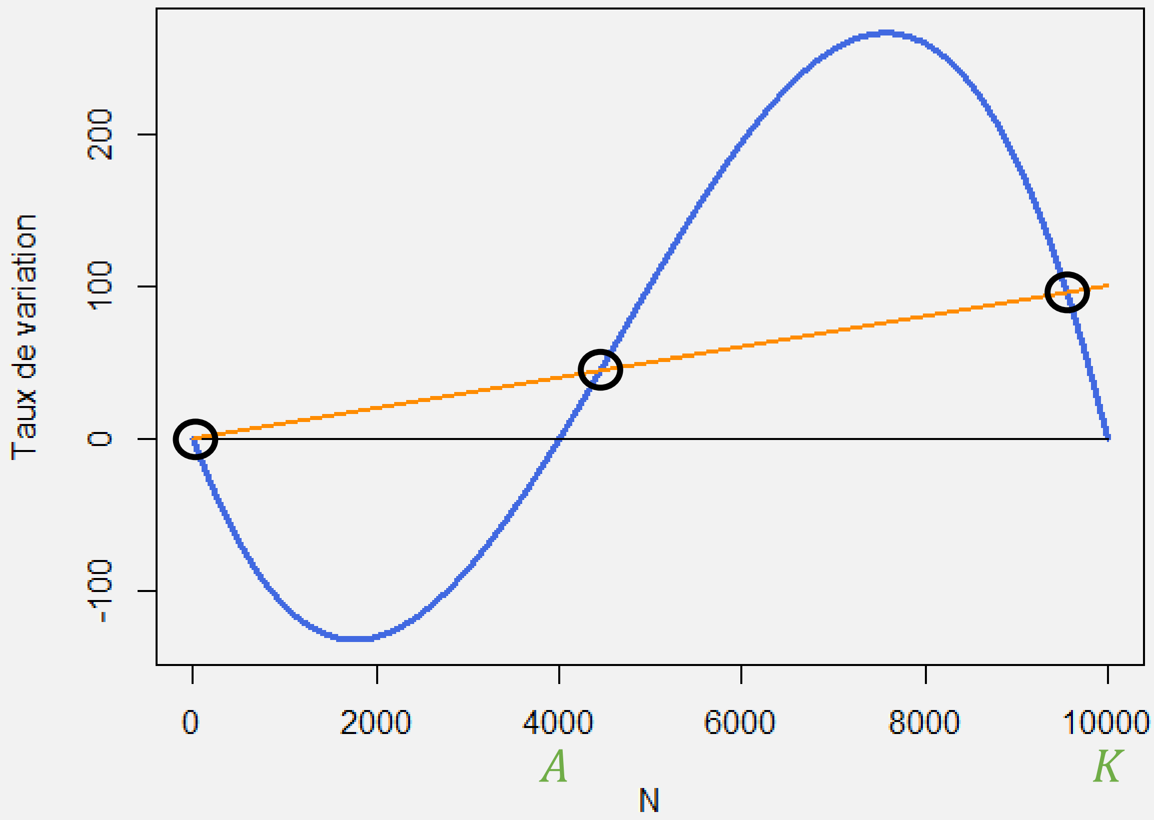


Equilibria

- Equilibrium: any $\bar{N}$ such that:

$$\underbrace{r\bar{N}\left(1-\frac{\bar{N}}{K}\right)}_{\text{logistic growth}}\underbrace{\left(\frac{\bar{N}-A}{K}\right)}_{\text{Allee effect}} = \underbrace{ce\bar{N}}_{\text{catches}}$$

$e = 0.1$



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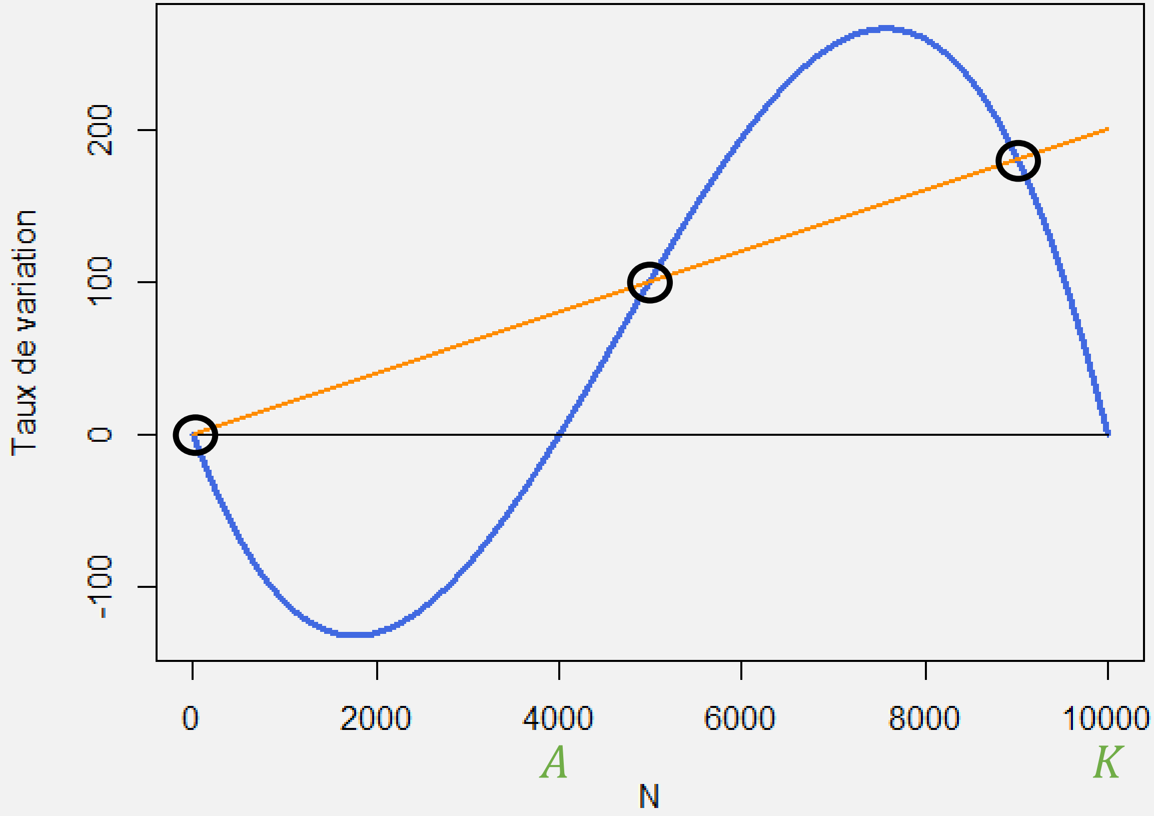
$e = 0.2$



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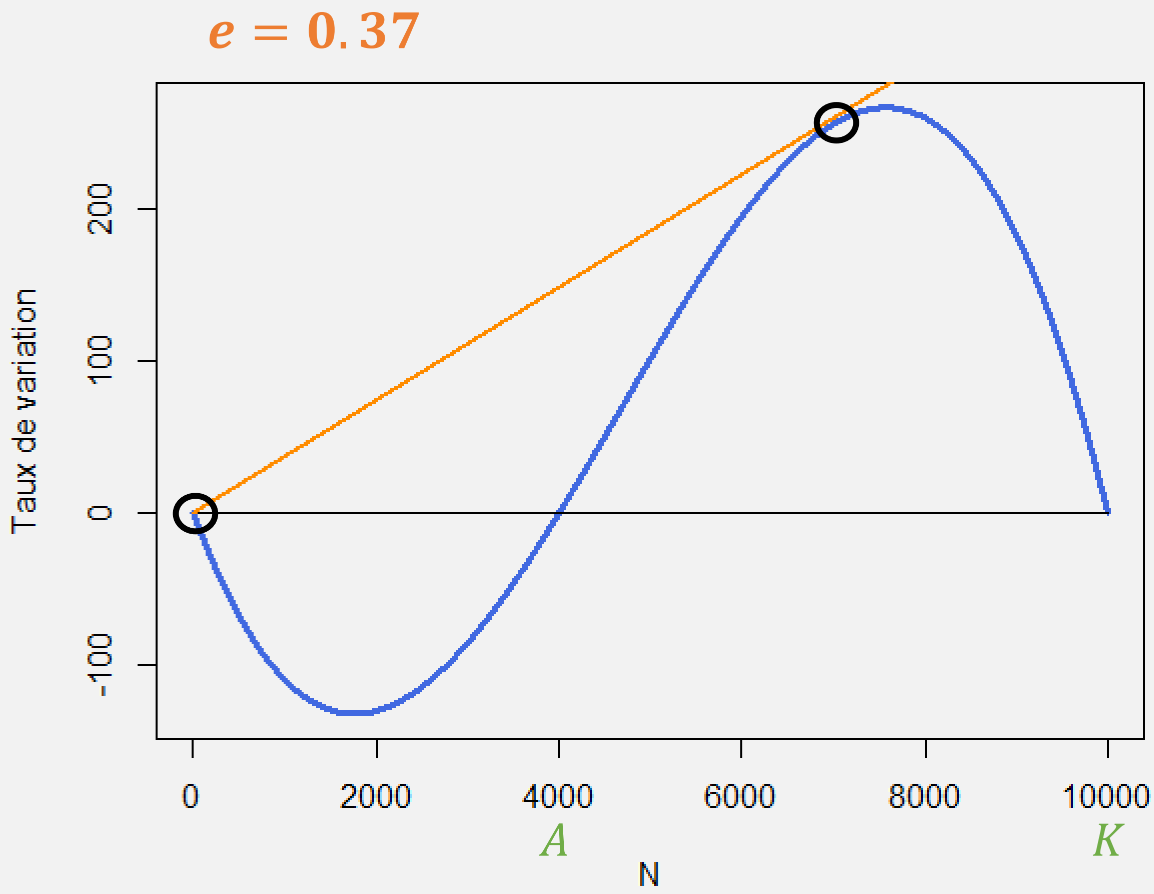
$$\underbrace{r\bar{N}\left(1-\frac{\bar{N}}{K}\right)}_{\text{logistic growth}}\underbrace{\left(\frac{\bar{N}-A}{K}\right)}_{\text{Allee effect}} = \underbrace{ce\bar{N}}_{\text{catches}}$$

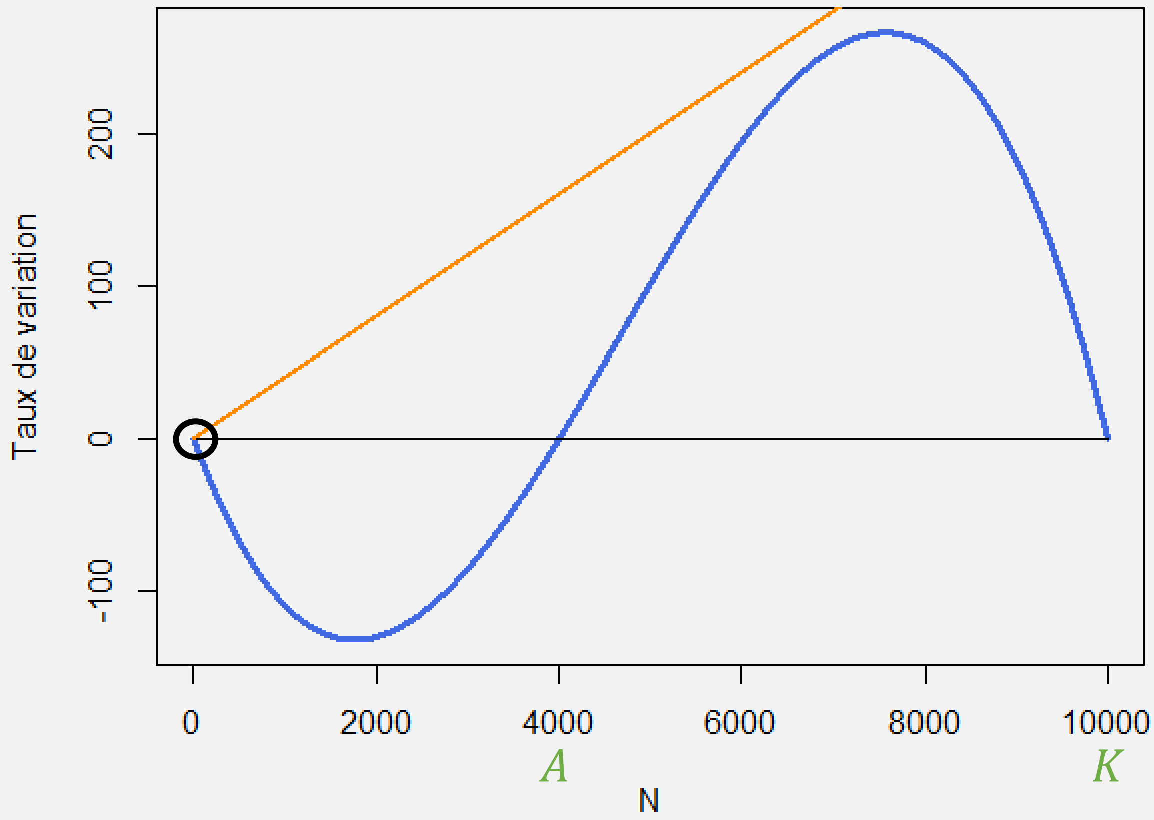


Equilibria

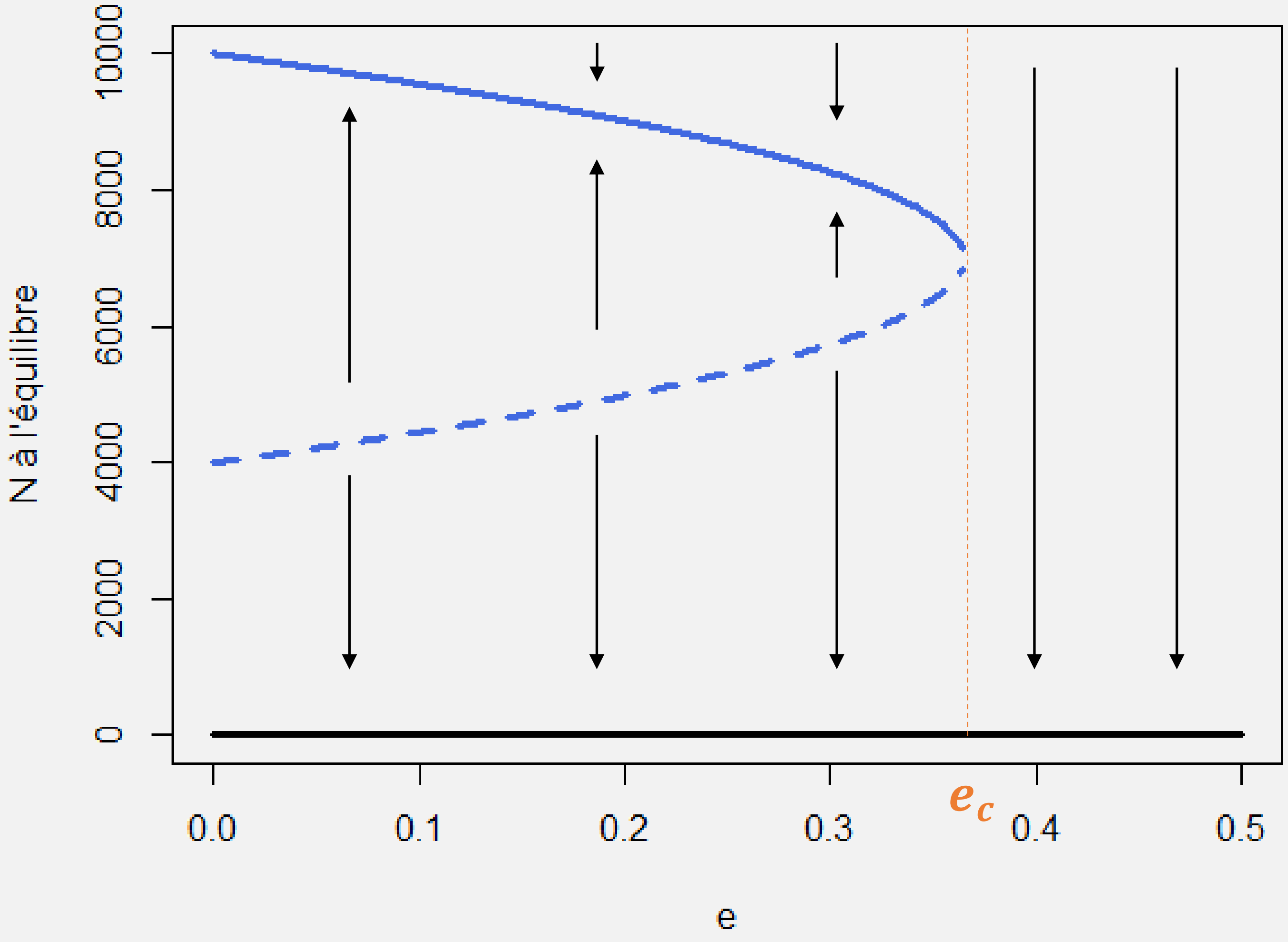
- Equilibrium: any $\bar{N}$ such that:

$$\underbrace{r\bar{N}\left(1-\frac{\bar{N}}{K}\right)}_{\text{logistic growth}}\underbrace{\left(\frac{\bar{N}-A}{K}\right)}_{\text{Allee effect}}=\underbrace{ce\bar{N}}_{\text{catches}}$$

$e = 0.4$



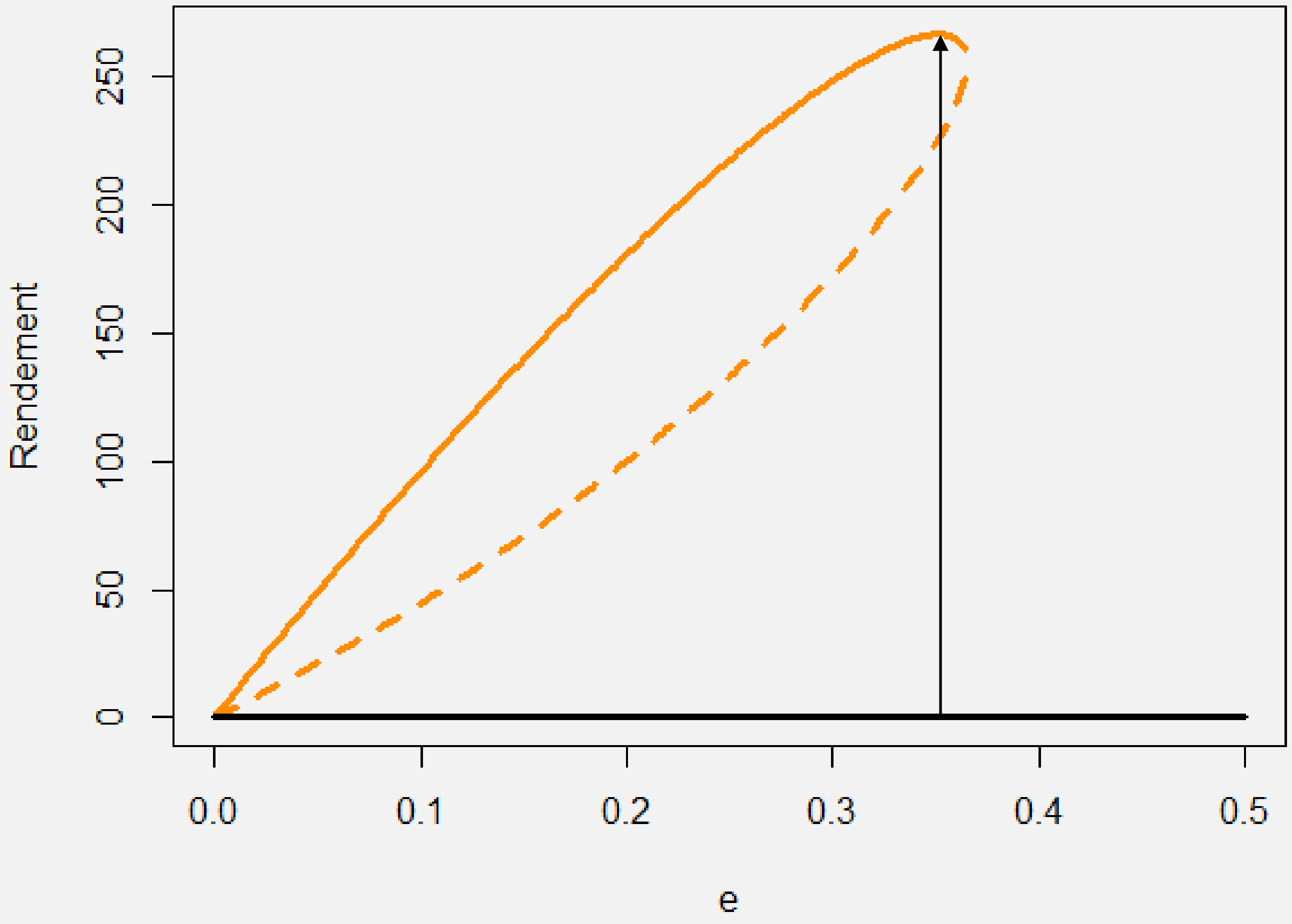
Catastrophic bifurcation



Critical fishing effort beyond which the population suddenly dies out (tipping point).

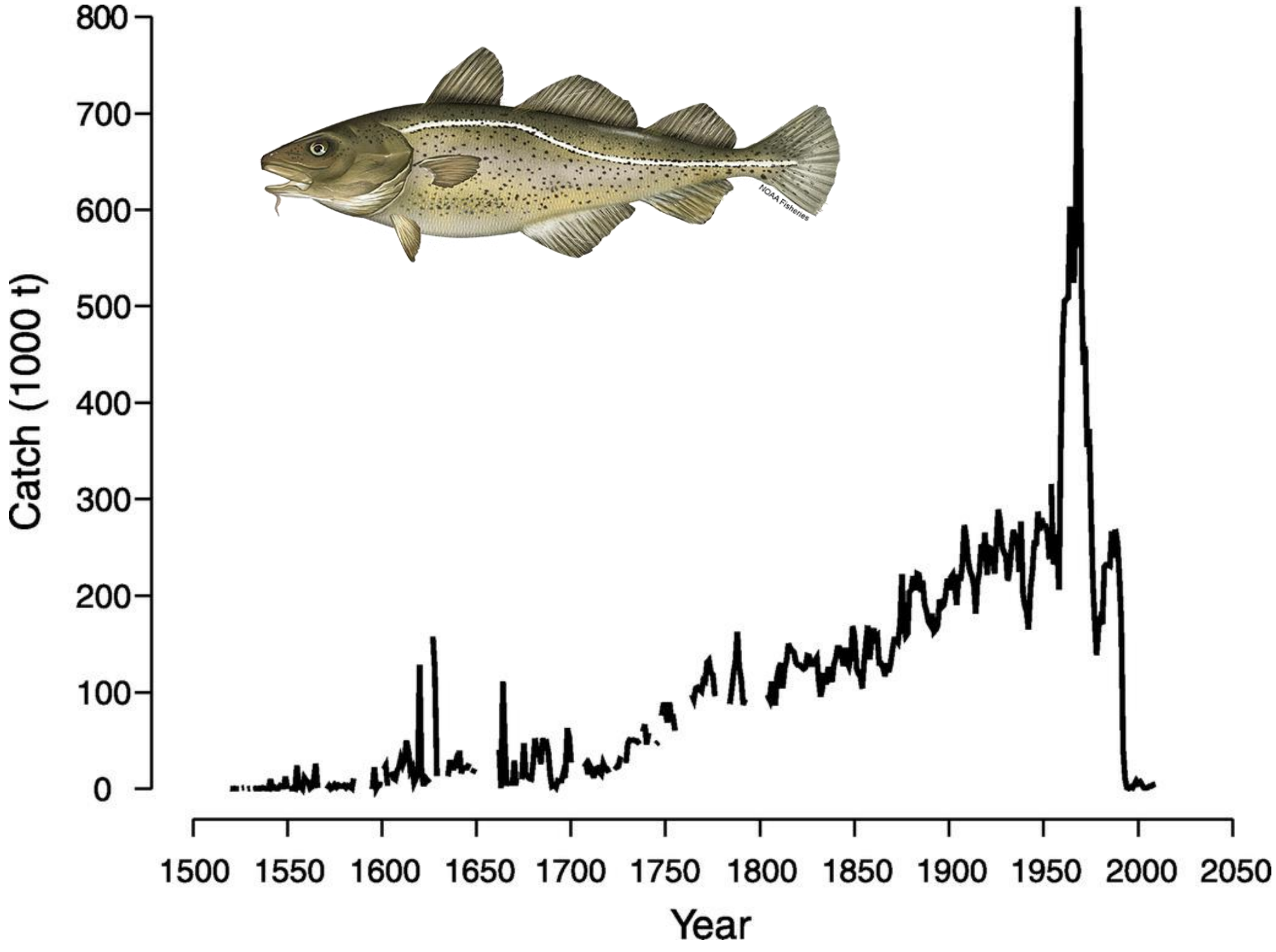
Discontinuous bifurcation (abrupt and irreversible extinction).

Yield curve



Optimal fishing effort is dangerously close to the tipping point!

Dynamics of North Atlantic cod



Apparent extinction due to fishing

Hutchings & Rangeley (2011) Correlates of recovery for Canadian Atlantic cod (*Gadus morhua*). *Canadian Journal of Zoology*.

Dynamics of grazed vegetation

- Plant density: N
- Grazer density: B (constant)
- Plants grazed per unit time:

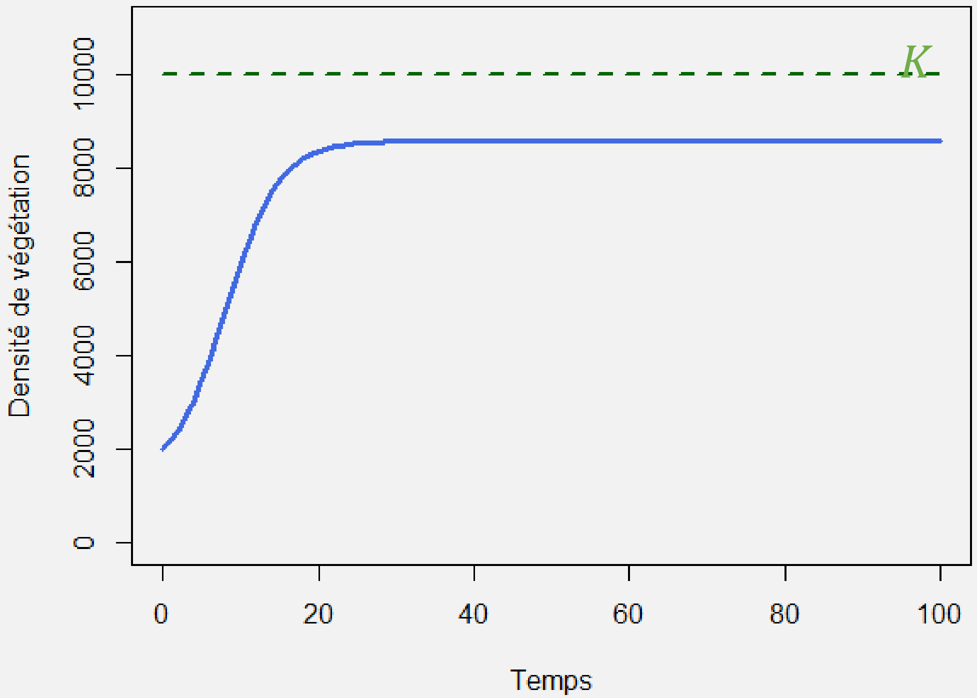
$$\frac{cBN}{a+N}$$

(Holling functional response)

- Model due to

Noy-Meir (1975) Stability of grazing systems: an application of predator-prey graphs. *Journal of Ecology*

$$\underbrace{\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right)}_{\text{logistic growth}} - \frac{cBN}{\underbrace{a+N}_{\text{grazing}}}$$

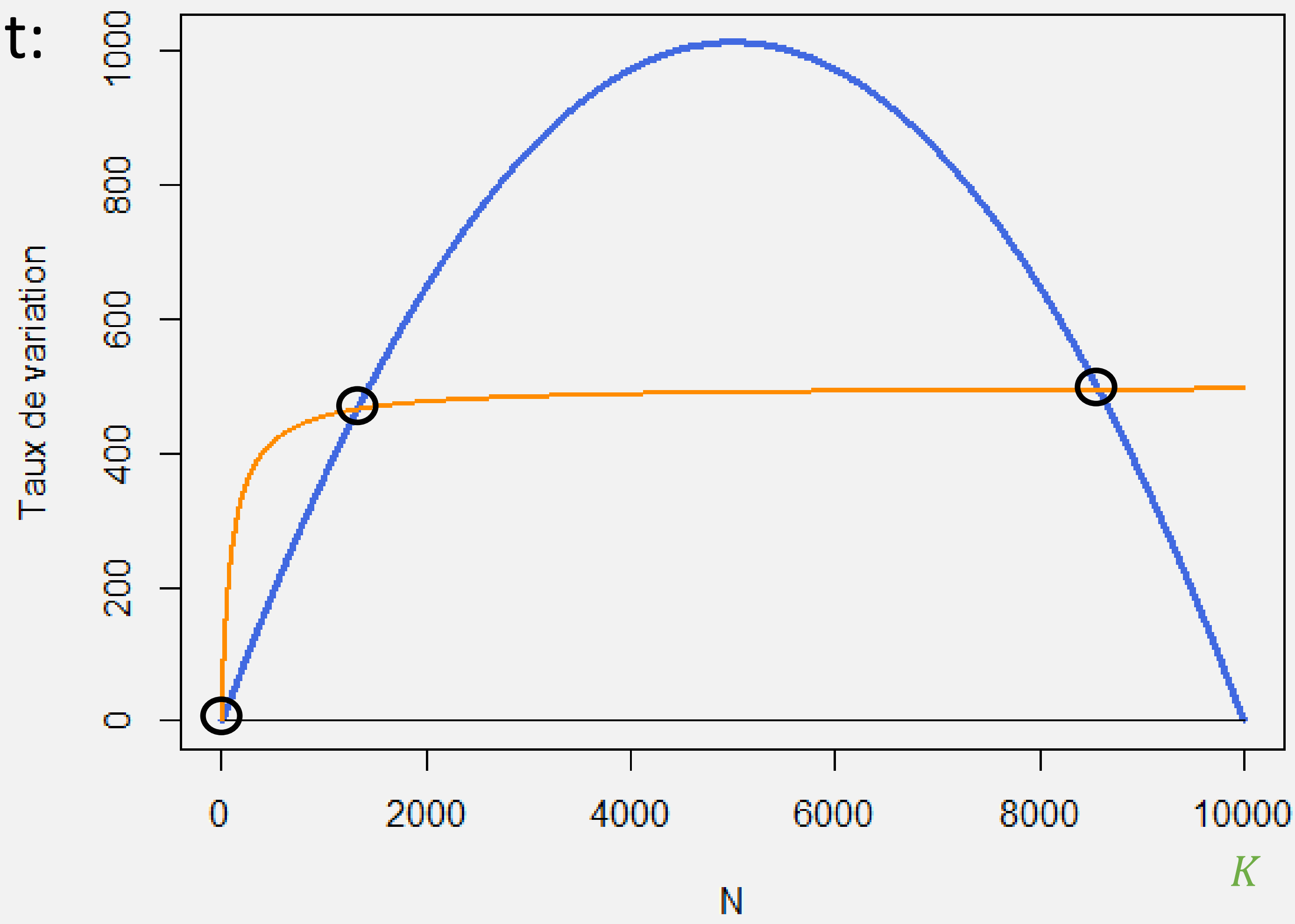


Equilibria

- Equilibium: any $\bar{N}$ such that:

$$\underbrace{r\bar{N}\left(1-\frac{\bar{N}}{K}\right)}_{\text{logistic growth}} = \frac{cB\bar{N}}{\underbrace{a+\bar{N}}_{\text{grazing}}}$$

$\boldsymbol{B = 10}$



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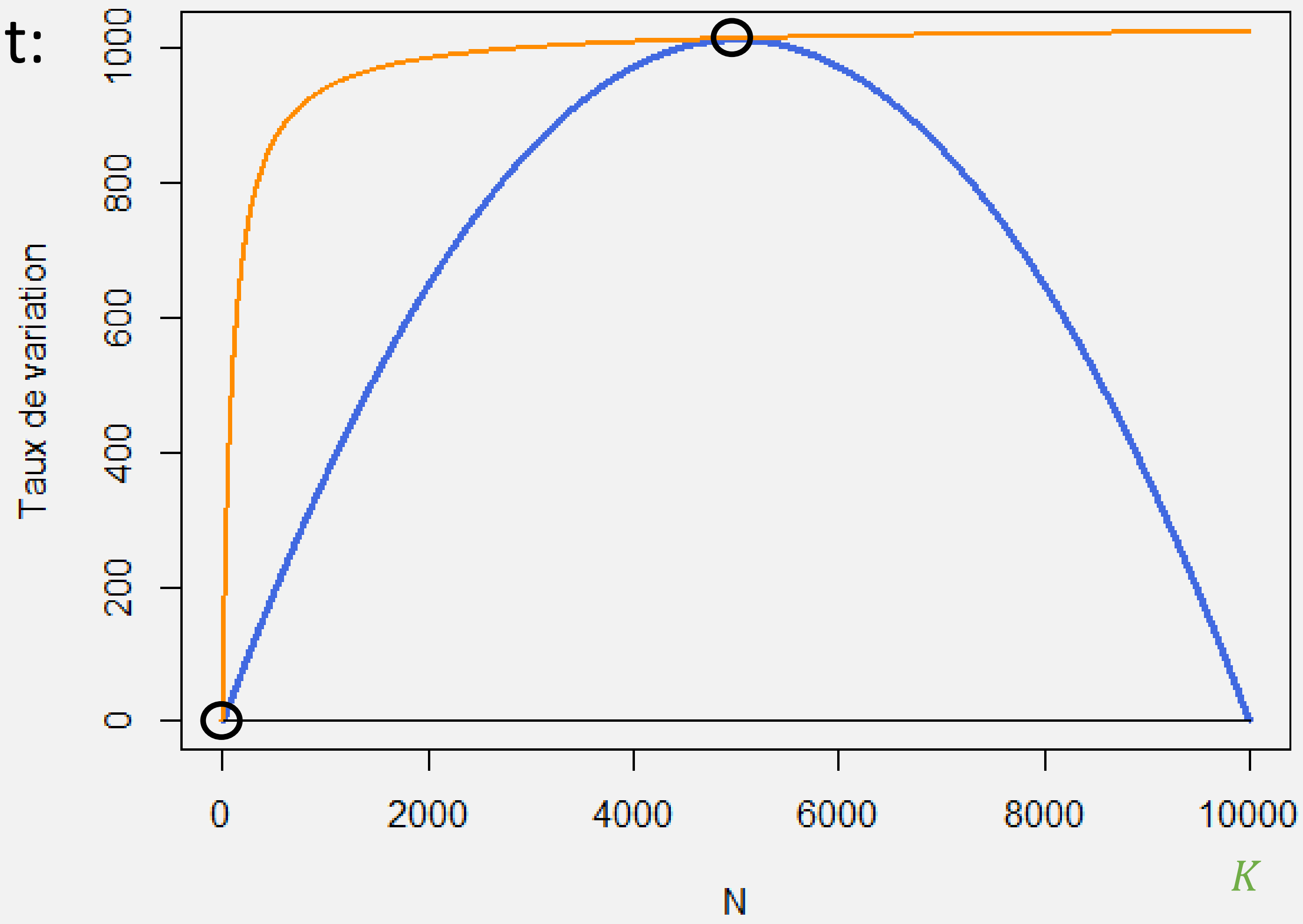
$$\underbrace{r\bar{N}\left(1-\frac{\bar{N}}{K}\right)}_{\text{logistic growth}} = \frac{cB\bar{N}}{\underbrace{a+\bar{N}}_{\text{grazing}}}$$

$B = 20.7$

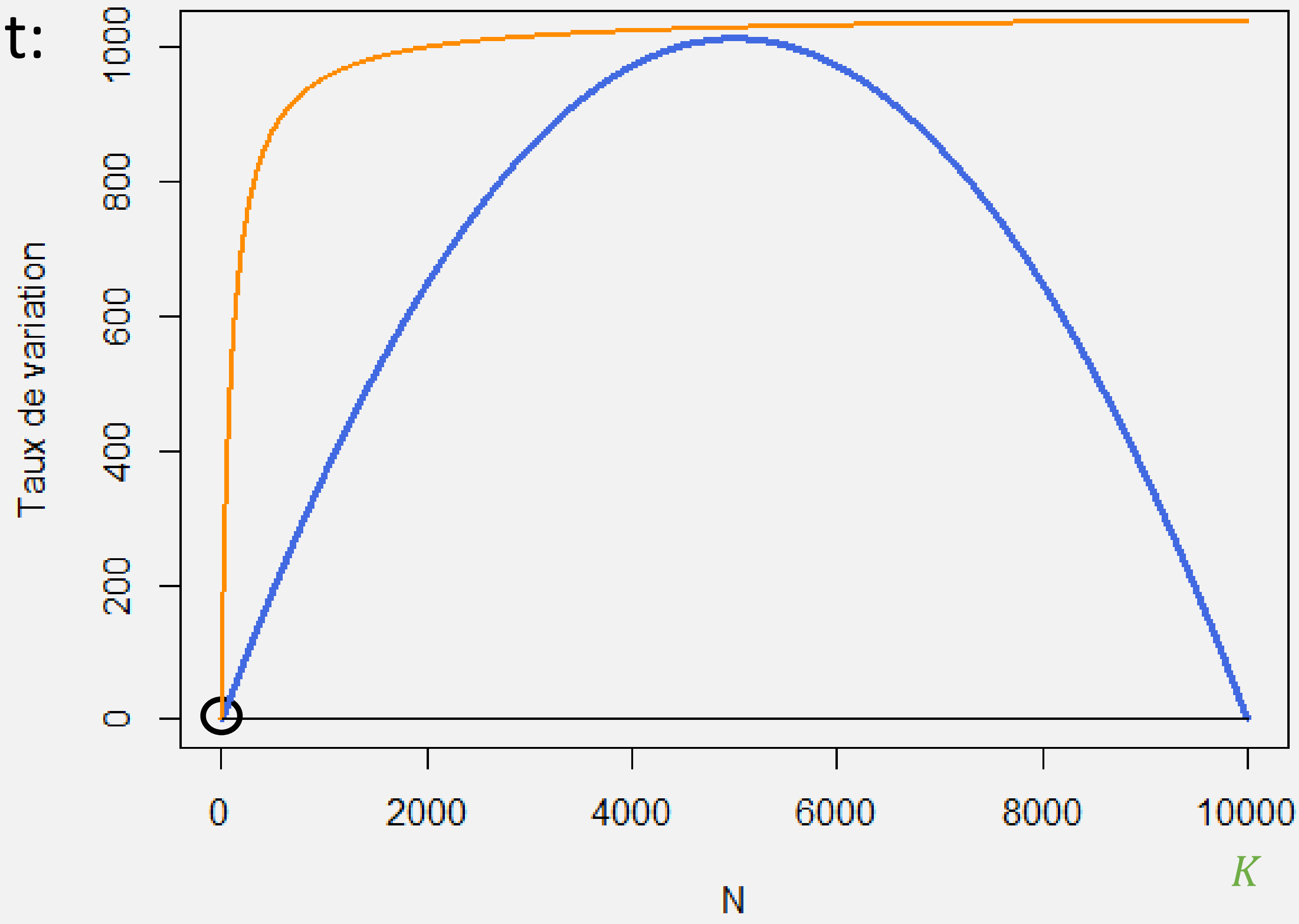


Equilibria

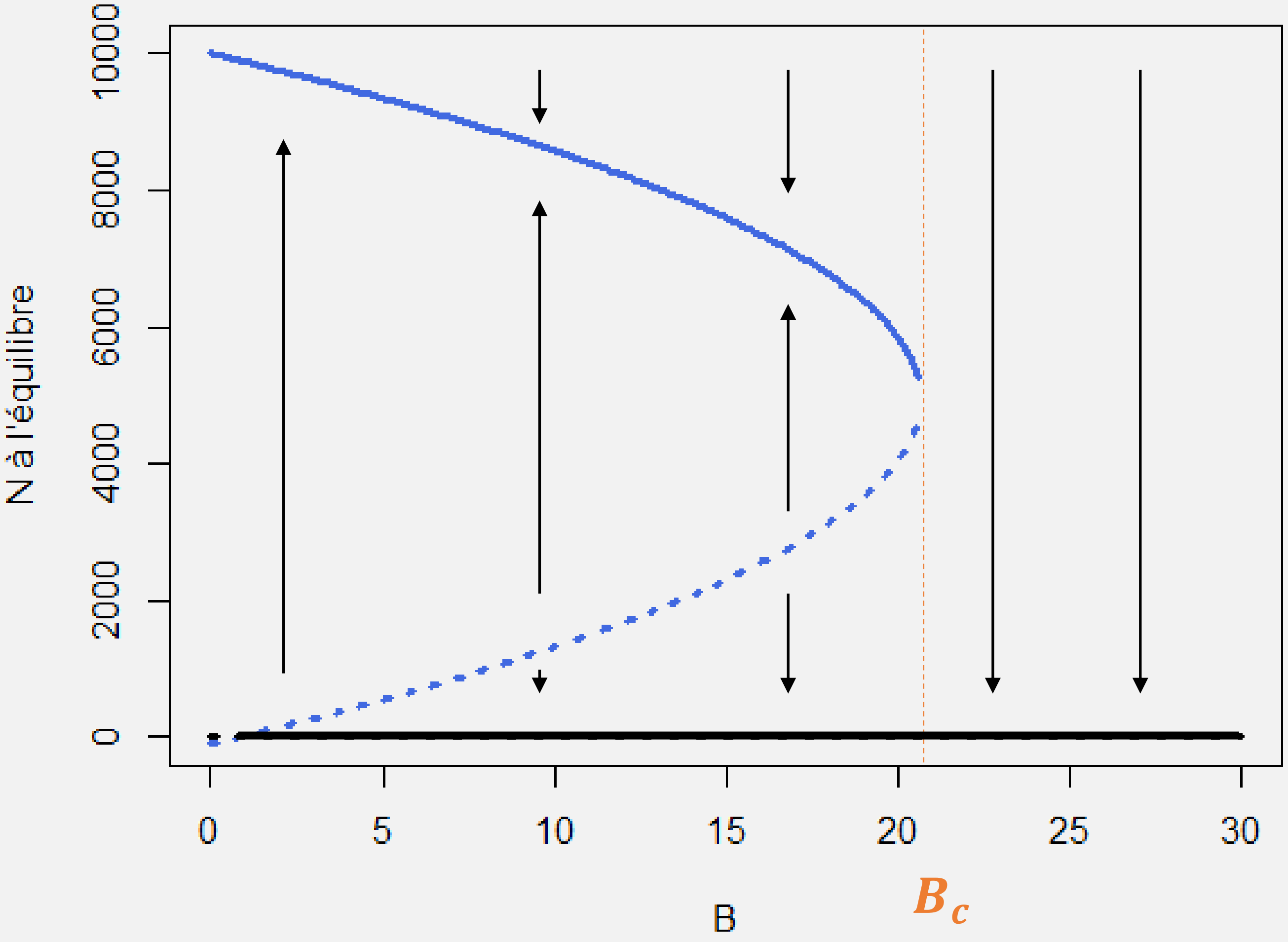
- Equilibium: any $\bar{N}$ such that:

$$\underbrace{r\bar{N}\left(1-\frac{\bar{N}}{K}\right)}_{\text{logistic growth}} = \frac{cB\bar{N}}{\underbrace{a+\bar{N}}_{\text{grazing}}}$$

$B = 21$



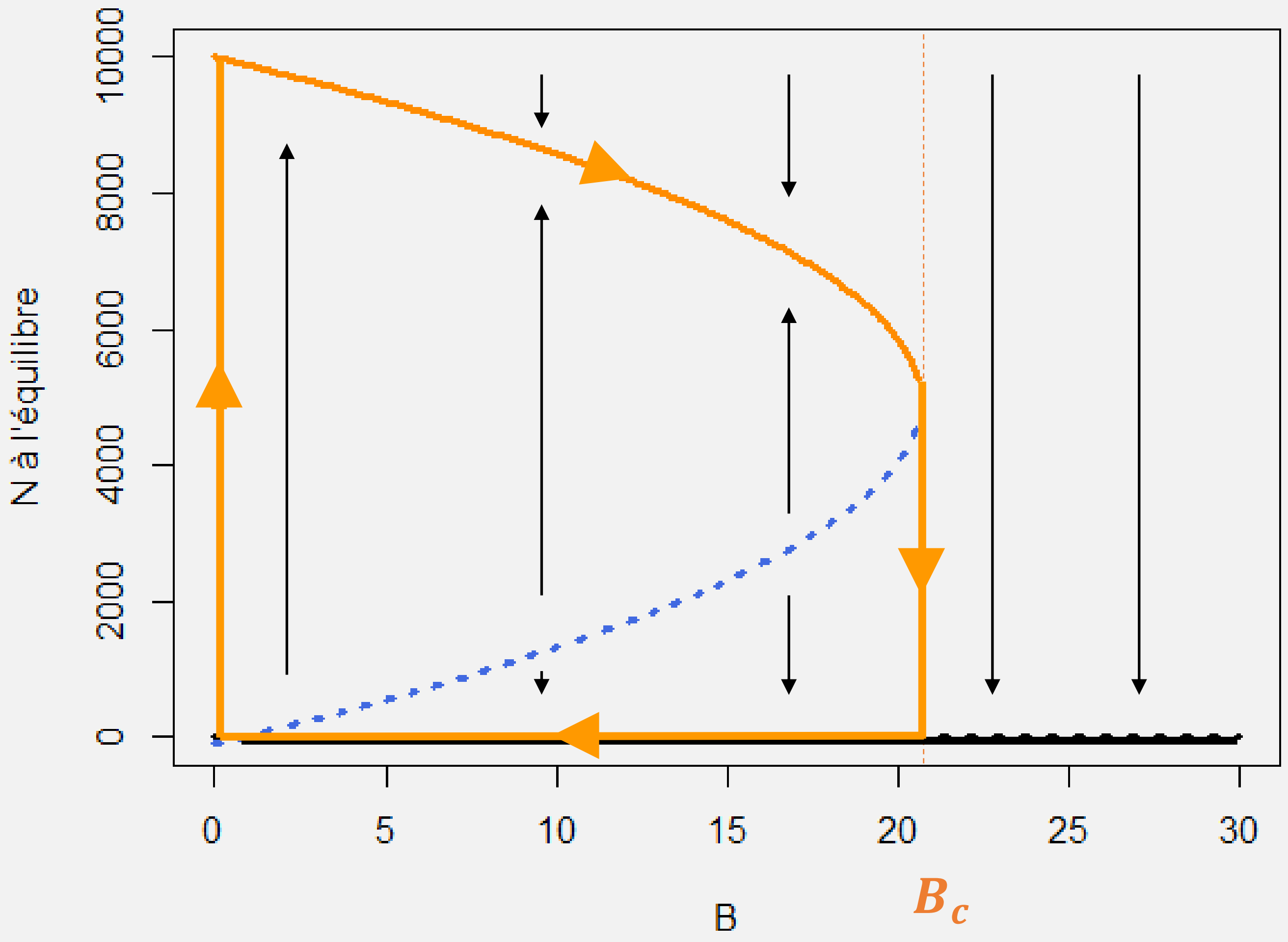
Catastrophic bifurcation



Density of grazers beyond which vegetation suddenly dies out (tipping point)

Discontinuous bifurcation (abrupt extinction that is difficult to reverse)

Hysteresys

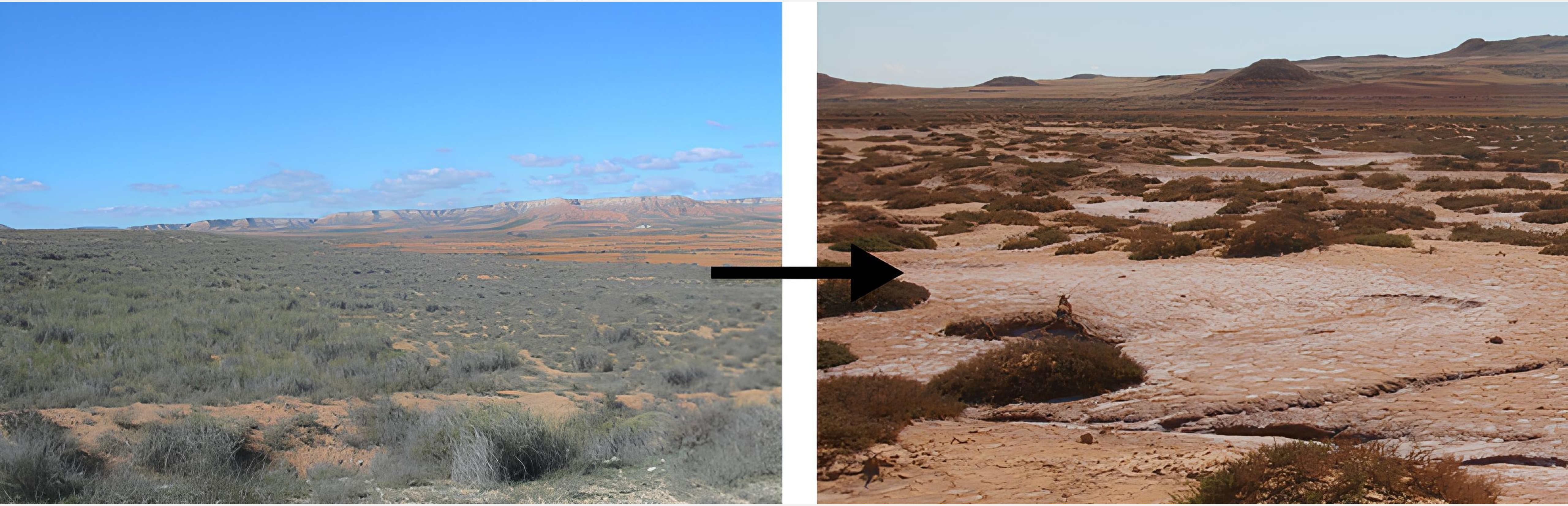


Density of grazers beyond which vegetation suddenly dies out (tipping point)

Discontinuous bifurcation (abrupt extinction that is difficult to reverse)

Overgrazing

Photos taken about 100 meters apart. The area on the right was overgrazed until the 1950s. Following its degradation, the area was abandoned. No regeneration of the ecosystem has been observed to date.



Semi-arid ecosystem: El Planerón Bird Sanctuary, Zaragoza, Spain

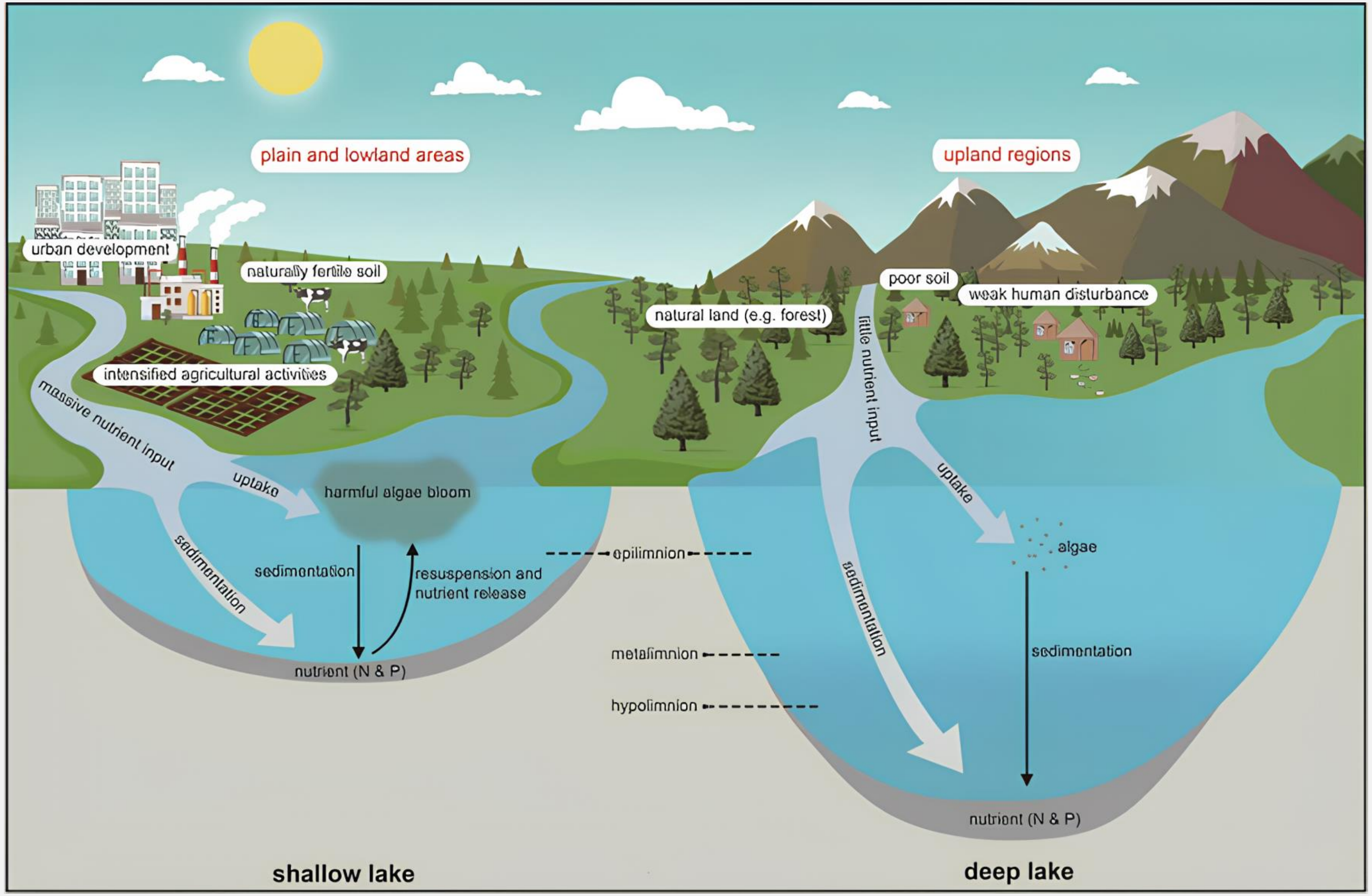
Ecosystèmes et transitions catastrophiques, Sonia Kéfi
https://sfecologie.org/regard/r37-hysteresis-sonia-kefi/

Shifts due to pollution or loss of biodiversity

Eutrophication of shallow lakes

Example of two lakes, one of which is clear and the other has become turbid

Why are shallow lakes prone to eutrophication?

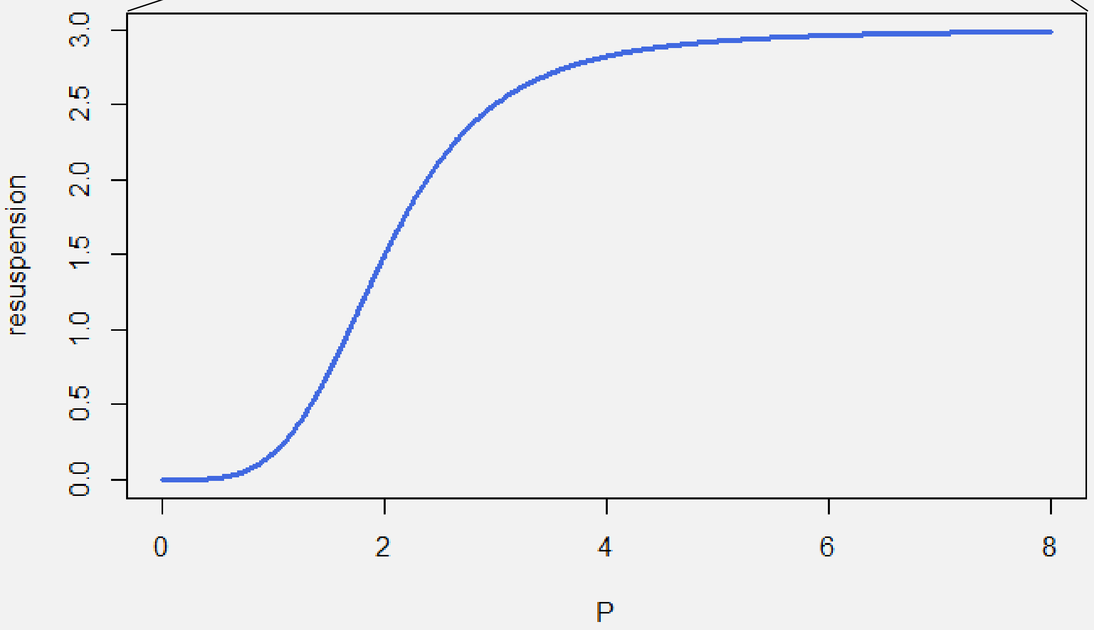


Lake eutrophication model

- Phosphorus concentration: P
- Contribution from the watershed (inflow): r
- Sedimentation rate: s
- Resuspension rate: r
- Model due to

Carpenter et al (1999) Management of eutrophication for lakes subject to potentially irreversible change. *Ecological applications*

$$\frac{dP}{dt} = A - sP + \underbrace{\frac{rP^q}{a^q + P^q}}_{\text{resuspension}}$$



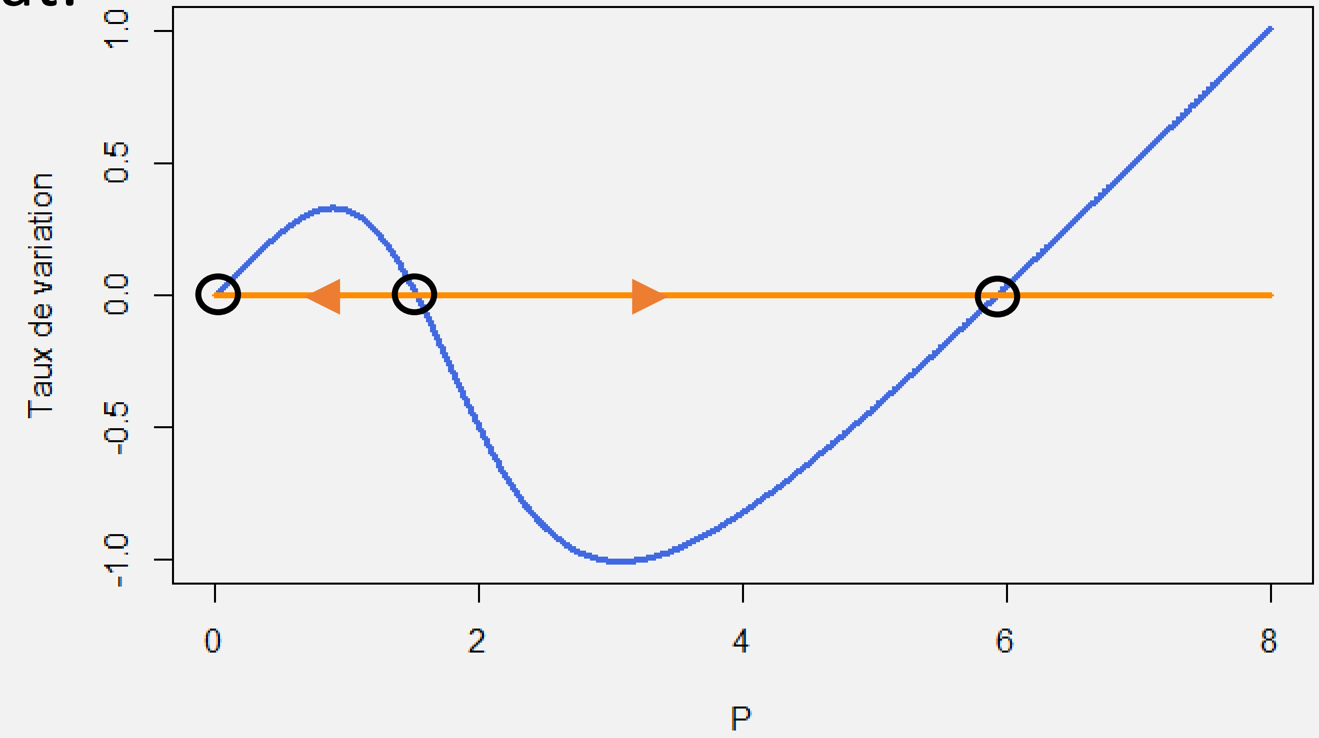
Equilibria

- Equilibrium: any $\bar{P}$ such that:

$$A = s\bar{P} - \underbrace{\frac{r\bar{P}^q}{a^q + \bar{P}^q}}_{\text{resuspension}}$$

$A = 0$

Bi-stability between clear and turbid



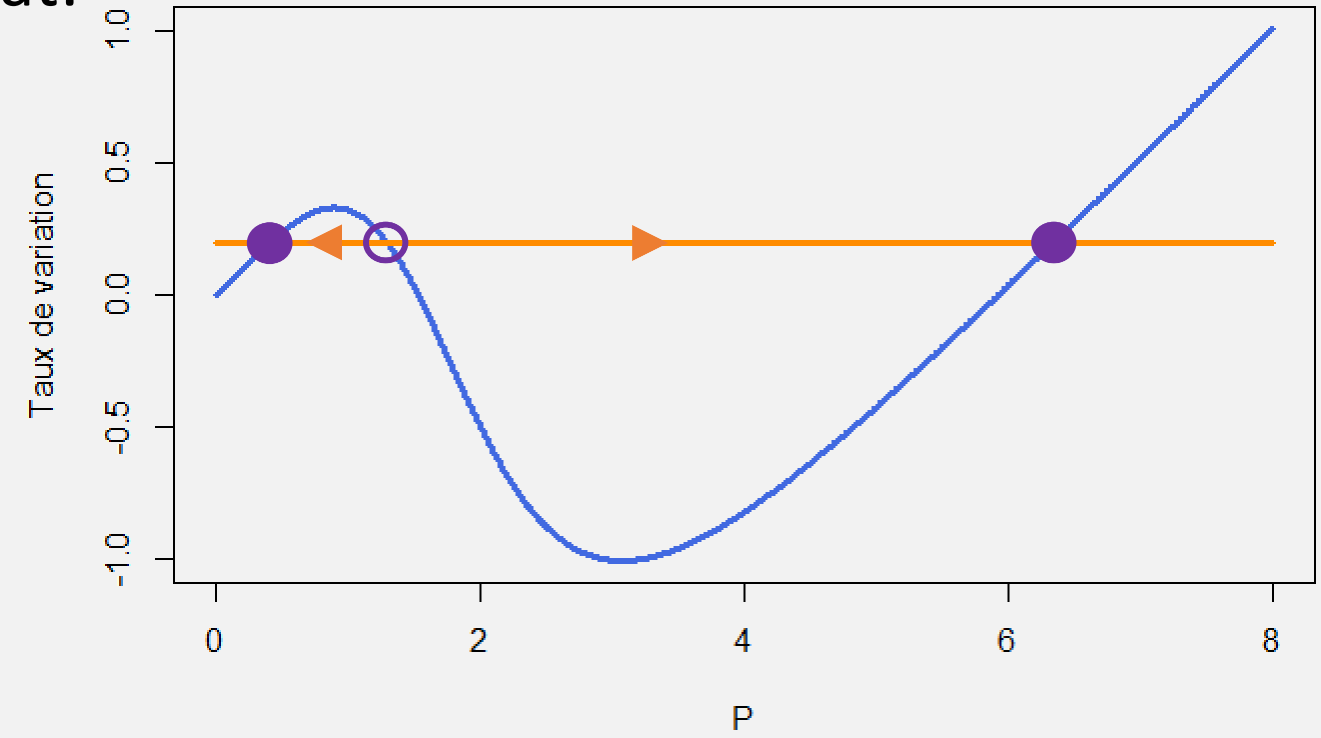
Equilibres

- Equilibrium: any $\bar{P}$ such that:

$$A = s\bar{P} - \underbrace{\frac{r\bar{P}^q}{a^q+\bar{P}^q}}_{\text{resuspension}}$$

A = 0,2

Bi-stability between clear and turbid



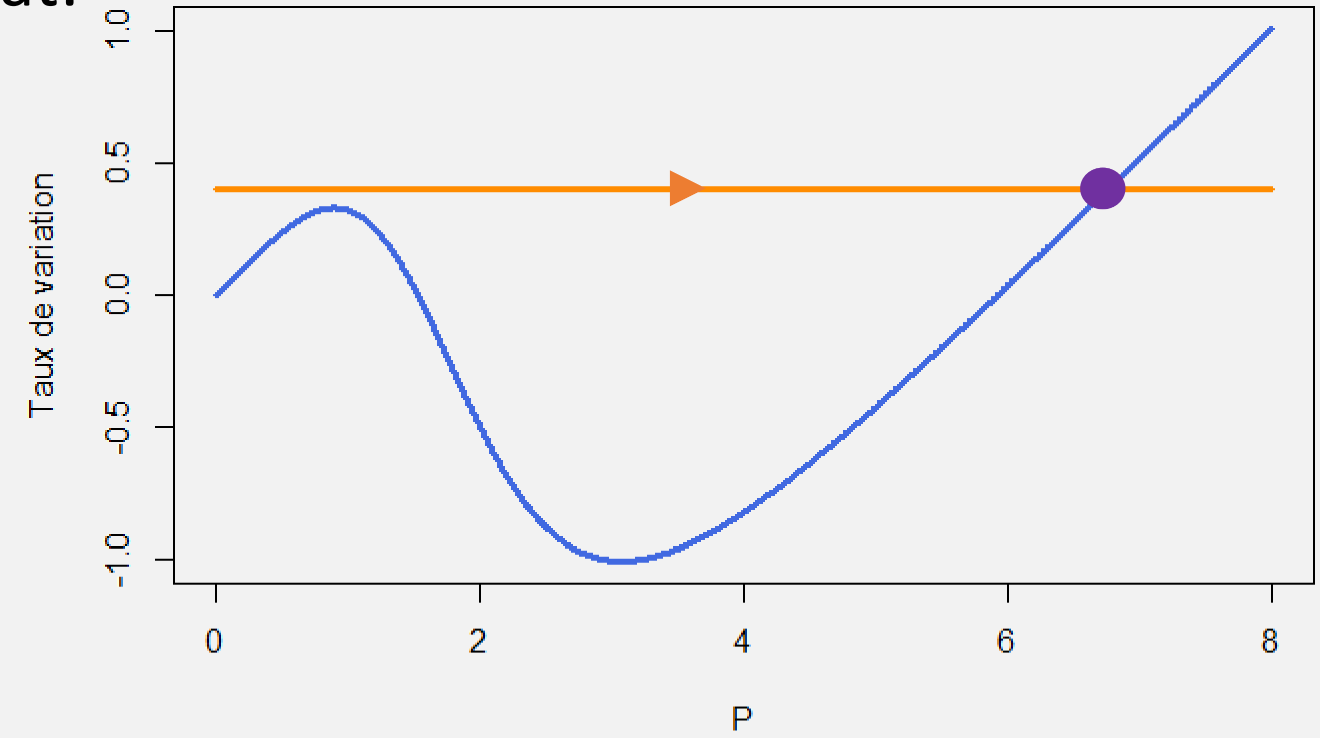
Equilibres

- Equilibrium: any $\bar{P}$ such that:

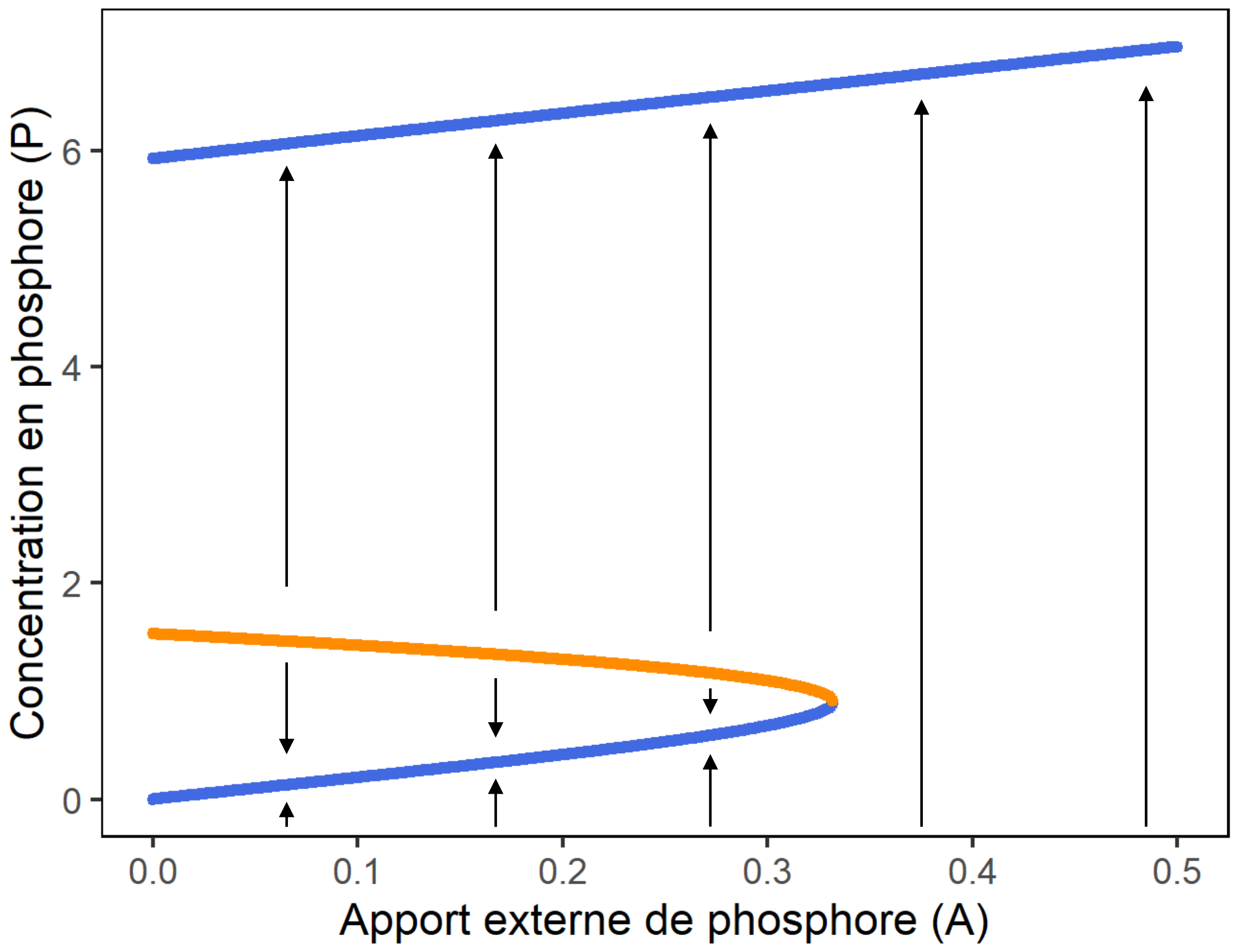
$$A = s\bar{P} - \underbrace{\frac{r\bar{P}^q}{a^q+\bar{P}^q}}_{\text{resuspension}}$$

$\mathbf{A = 0,4}$

Mono-stability of the turbid equilibrium



Catastrophic bifurcation



Critical inflow of phosphorus beyond which the state of the lake changes abruptly (tipping point)

Discontinuous bifurcation (abrupt and irreversible transition)

Corals, sea urchins, and parrotfish

Coral reefs

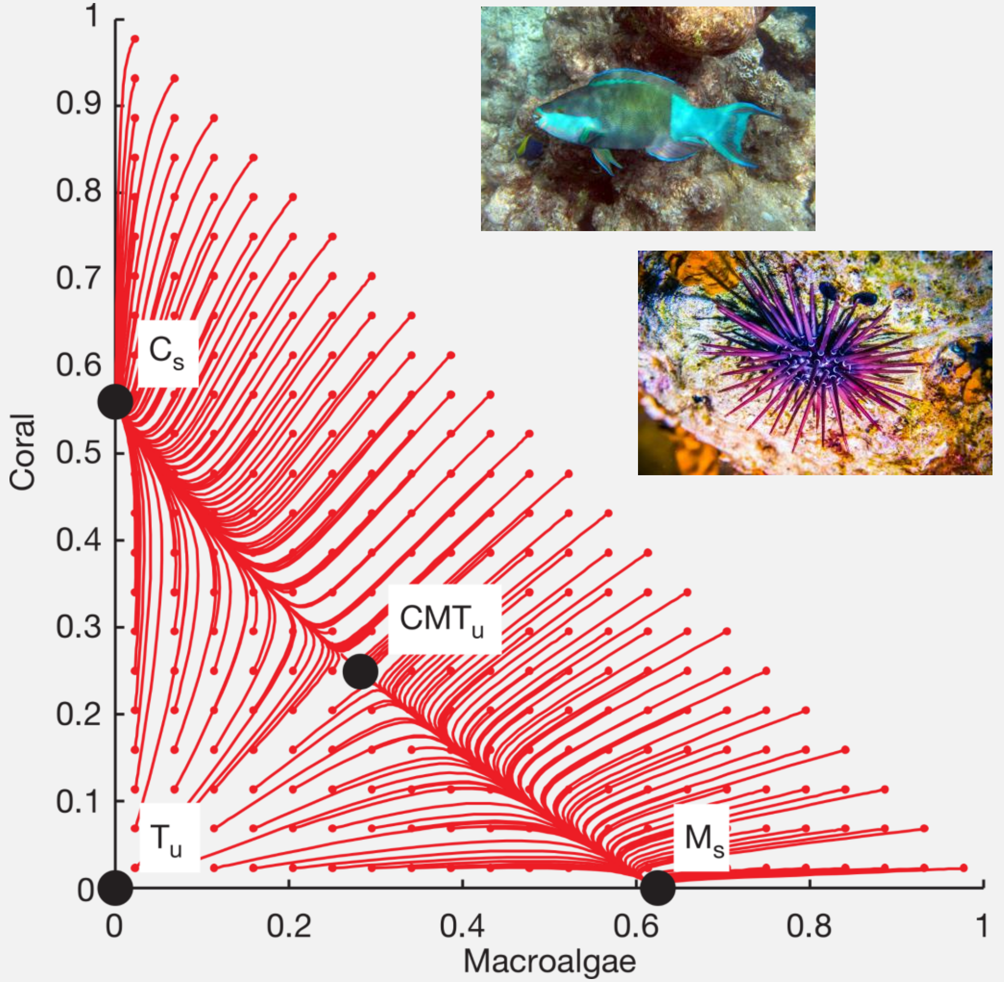
- Proportion of the seabed occupied by
  - Corals: C
  - Macro-algae: M
  - Algal turf: $G = 1 - M - C$
- Grazing intensity (by sea urchins and parrotfishes): b
- Model due to

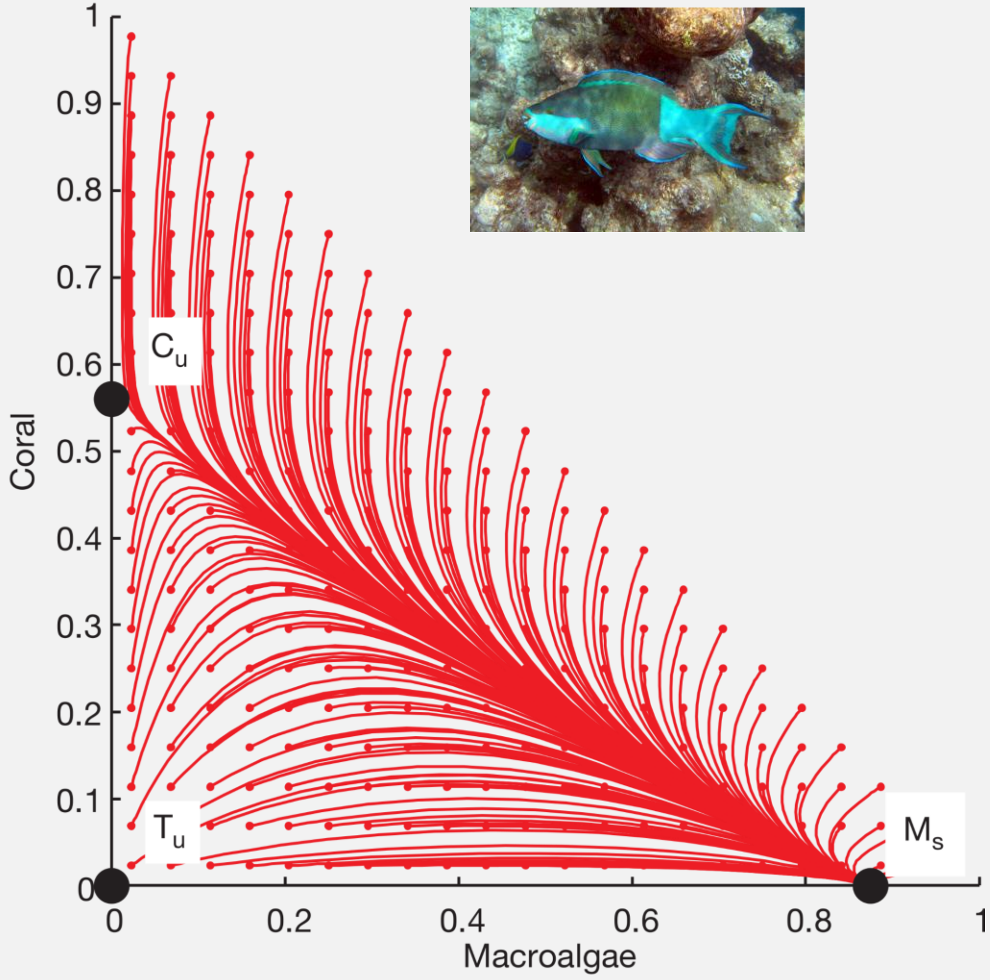
Mumby et al (2007) Thresholds and the resilience of Caribbean coral reefs. *Nature*

$$\begin{cases} \dfrac{dM}{dt} = \underbrace{aMC + cMG}_{\text{colonisations}} - \dfrac{bM}{\underbrace{G + M}_{\text{grazing}}} \\ \dfrac{dC}{dt} = \underbrace{kGC - aMC}_{\text{colonisations}} - \underbrace{dC}_{\text{mortality}} \end{cases}$$

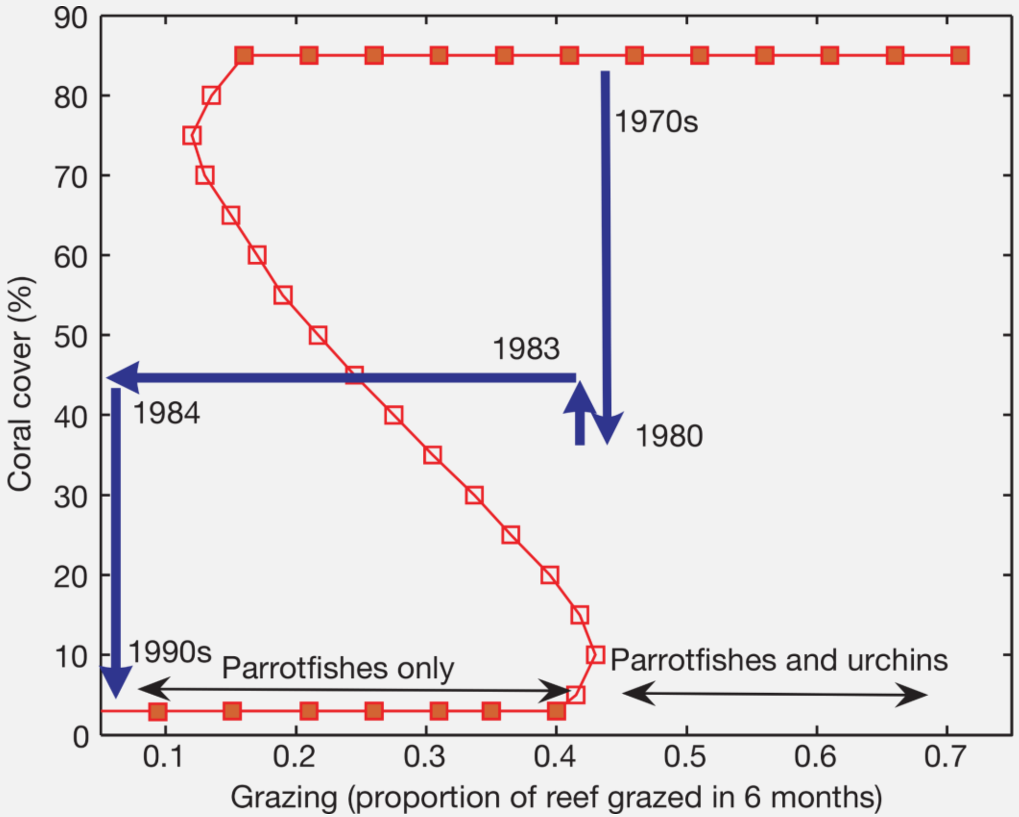
Equilibria, bi-stability and bifurcation

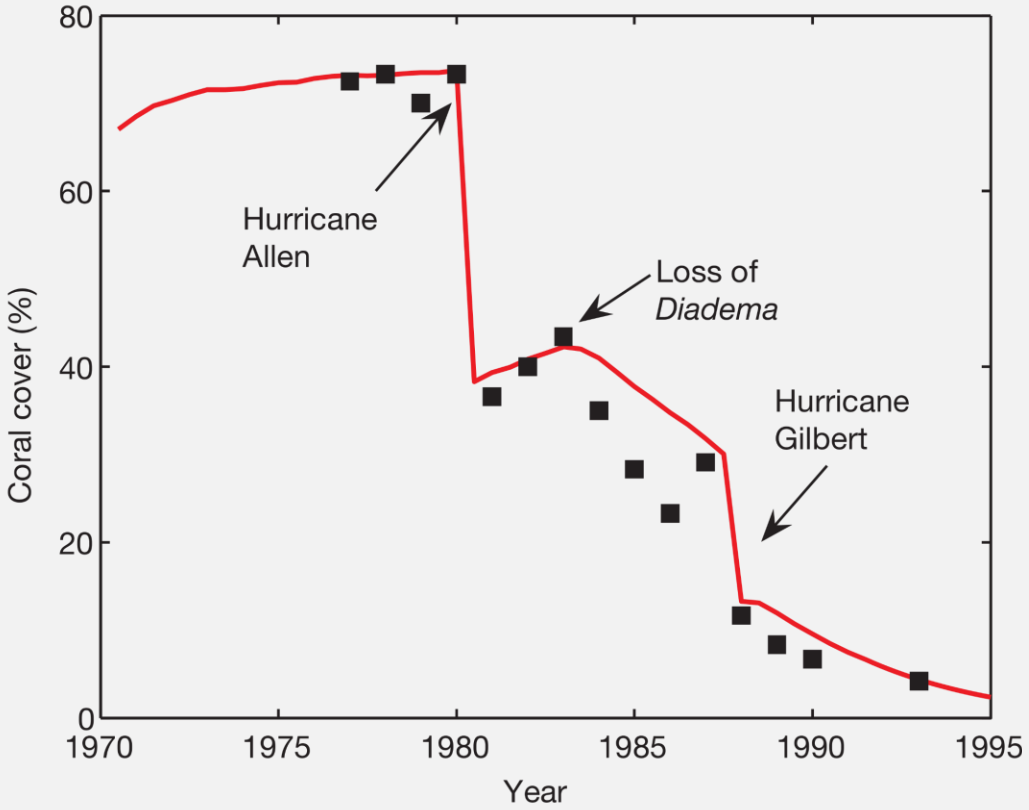
reduction in grazing intensity, *b* →





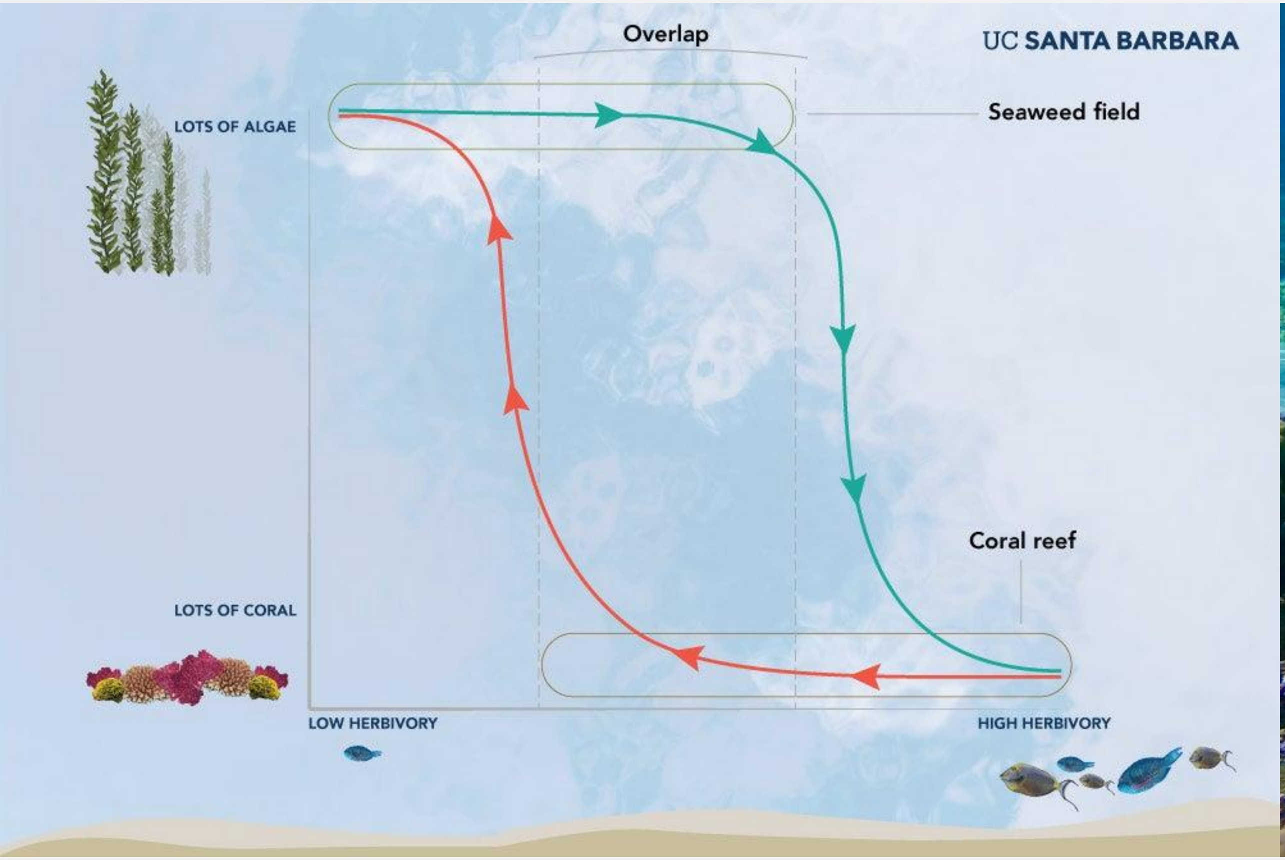
Coral hysteresis in the Caribbean





Mumby et al (2007) Thresholds and the resilience of Caribbean coral reefs. *Nature*

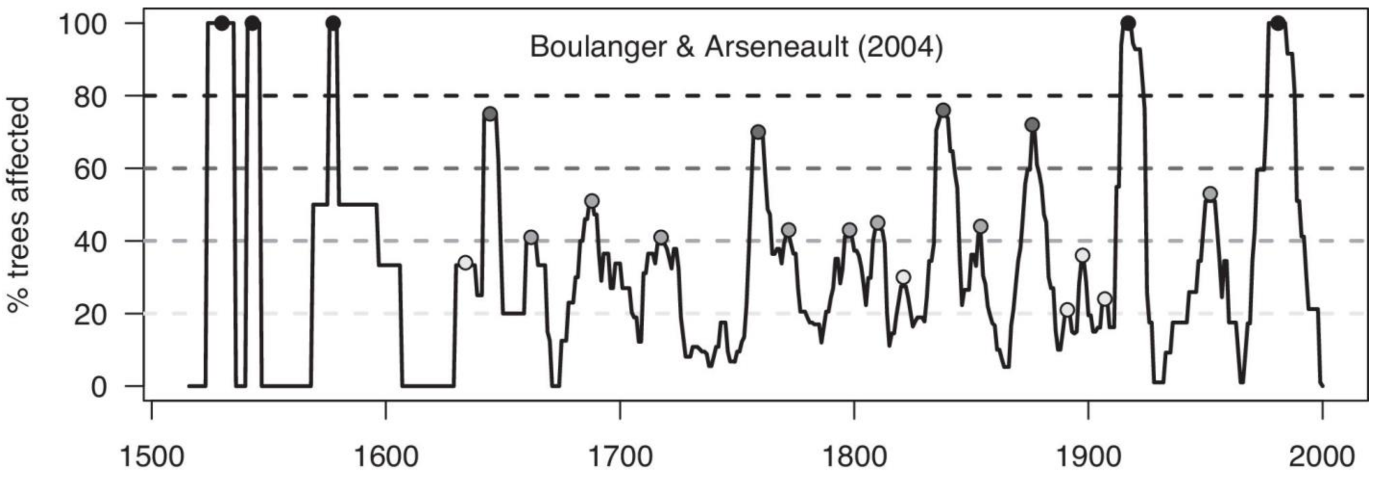
Coral hysteresis in Moorea



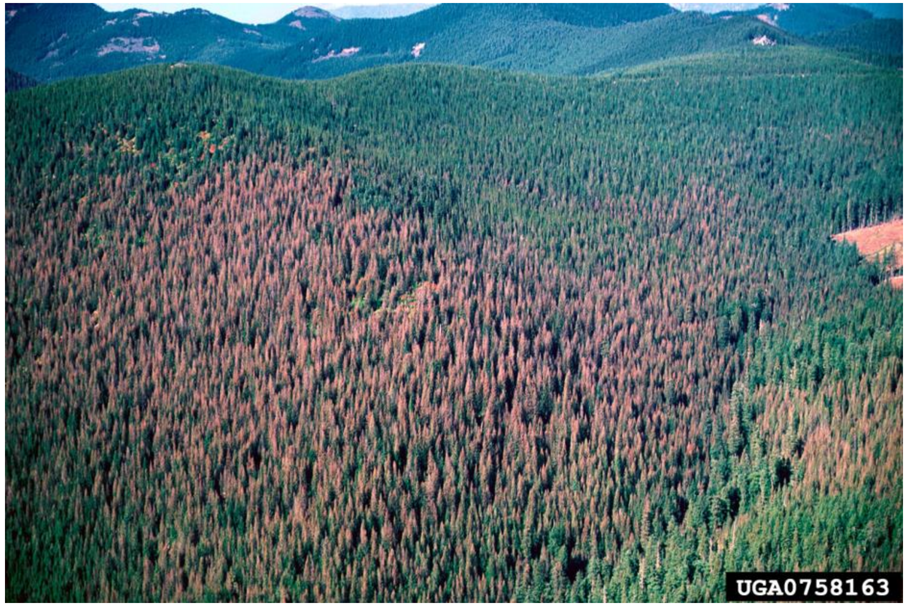
Schmitt et al (2019) Experimental support for alternative attractors on coral reefs. *Proceedings of the National Academy of Sciences*

Spruce budworm

- *Choristoneura fumiferana:* moth native to North America
- Recurring infestations every 30 years



Boulanger & Arseneault (2004) Spruce budworm outbreaks in eastern Québec over the last 450 years. Can. J. For. Res



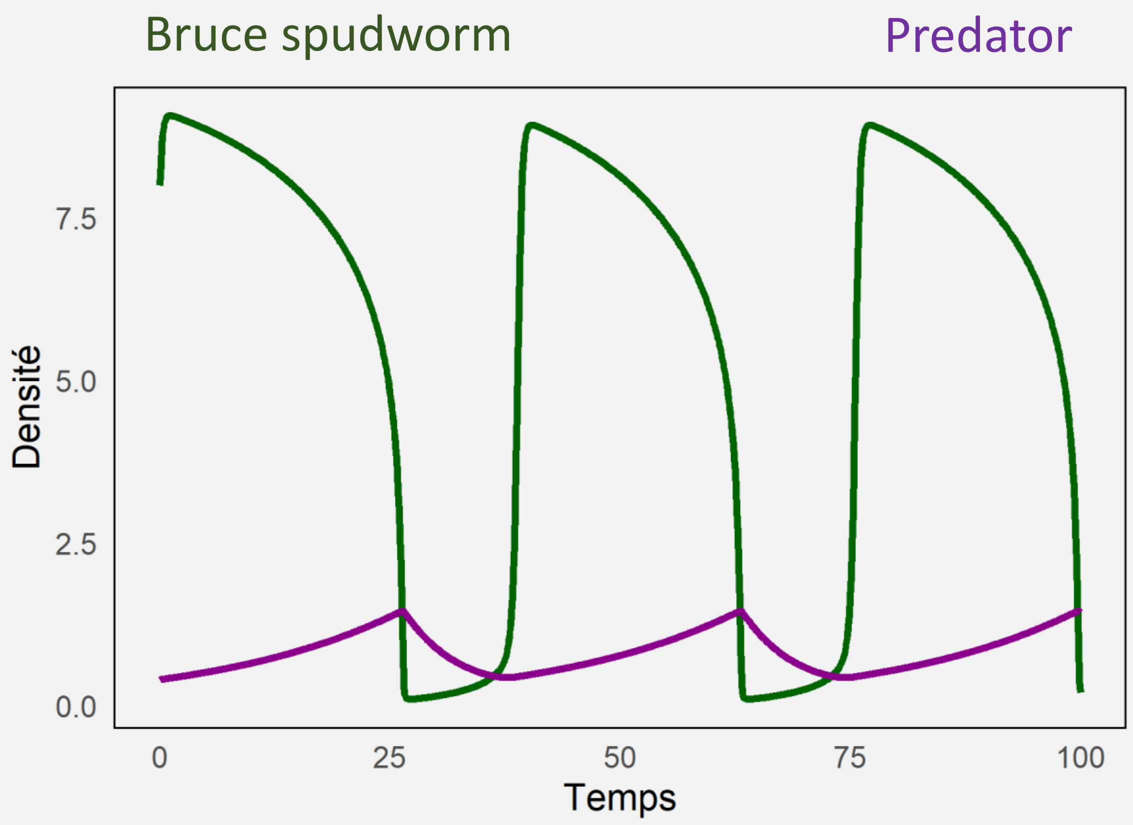
Spruce budworm

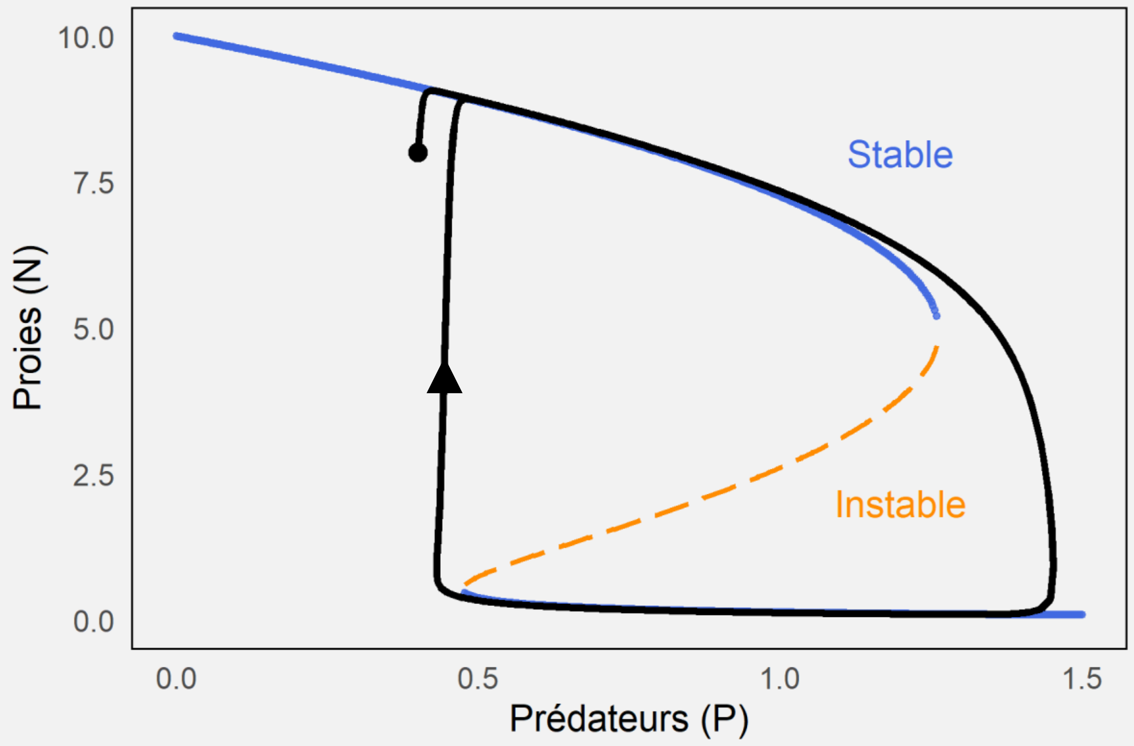
- Budworm density: N
- Predator density: P
- « Numerical response »: n
- Predator mortality: m
- Model due to

Ludwig et al (1978) Qualitative analysis of insect outbreak systems: the spruce budworm and forest. *Journal of animal ecology*

$$\begin{cases} \dfrac{dN}{dt} = rN\left(1 - \dfrac{N}{K}\right) - \underbrace{\dfrac{bPN^2}{a^2 + N^2}}_{\text{predation}} \\ \dfrac{dP}{dt} = n\dfrac{PN^2}{a^2 + N^2} - mP \end{cases}$$

Bruce spudworm dynamical hysteresys



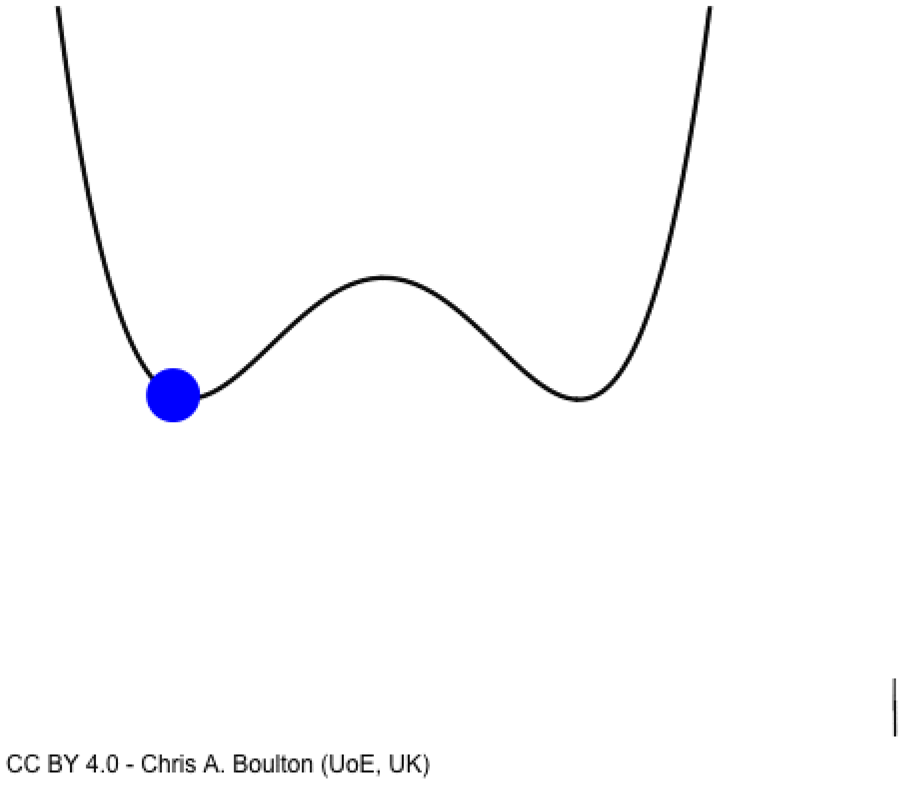


Tipping points and early warning signals

Tipping point: bi-stability -> mono-stability

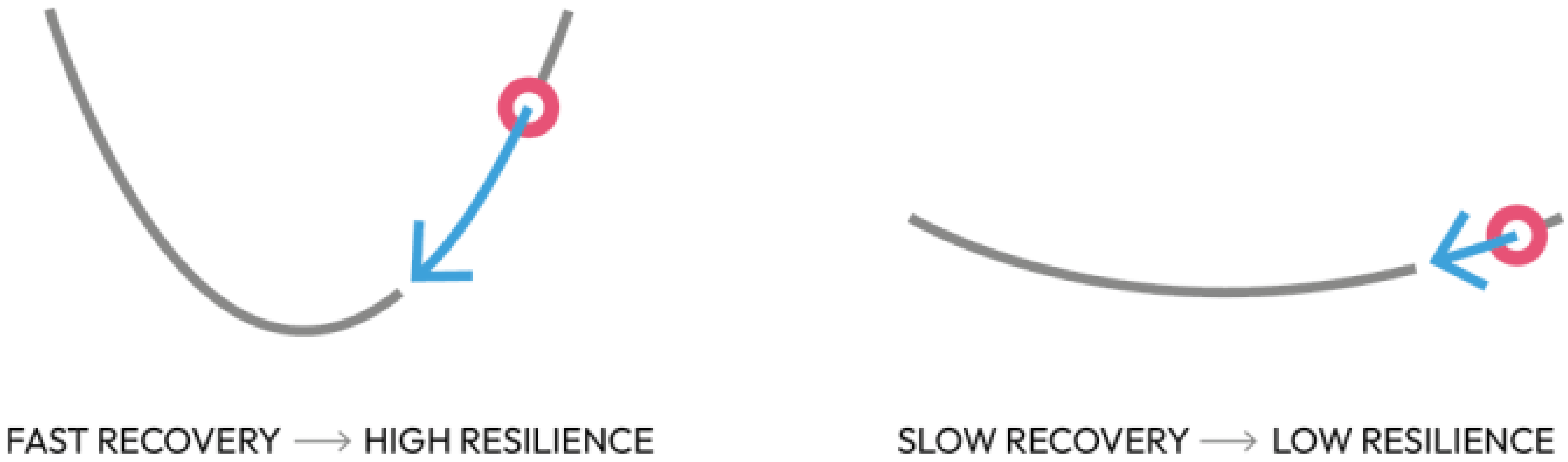
Lenton et al (2023) The Global Tipping Points Report 2023. University of Exeter, UK
https://report-2023.global-tipping-points.org/about/

Tipping point: movie



Boulton, Chris (2022). Tipping Point Animation. figshare. Figure. https://doi.org/10.6084/m9.figshare.21206987.v1

Speed of return to equilibrium



Dakos et al (2024). Tipping point detection and early warnings in climate, ecological, and human systems. *Earth System Dynamics*

Resilience metrics

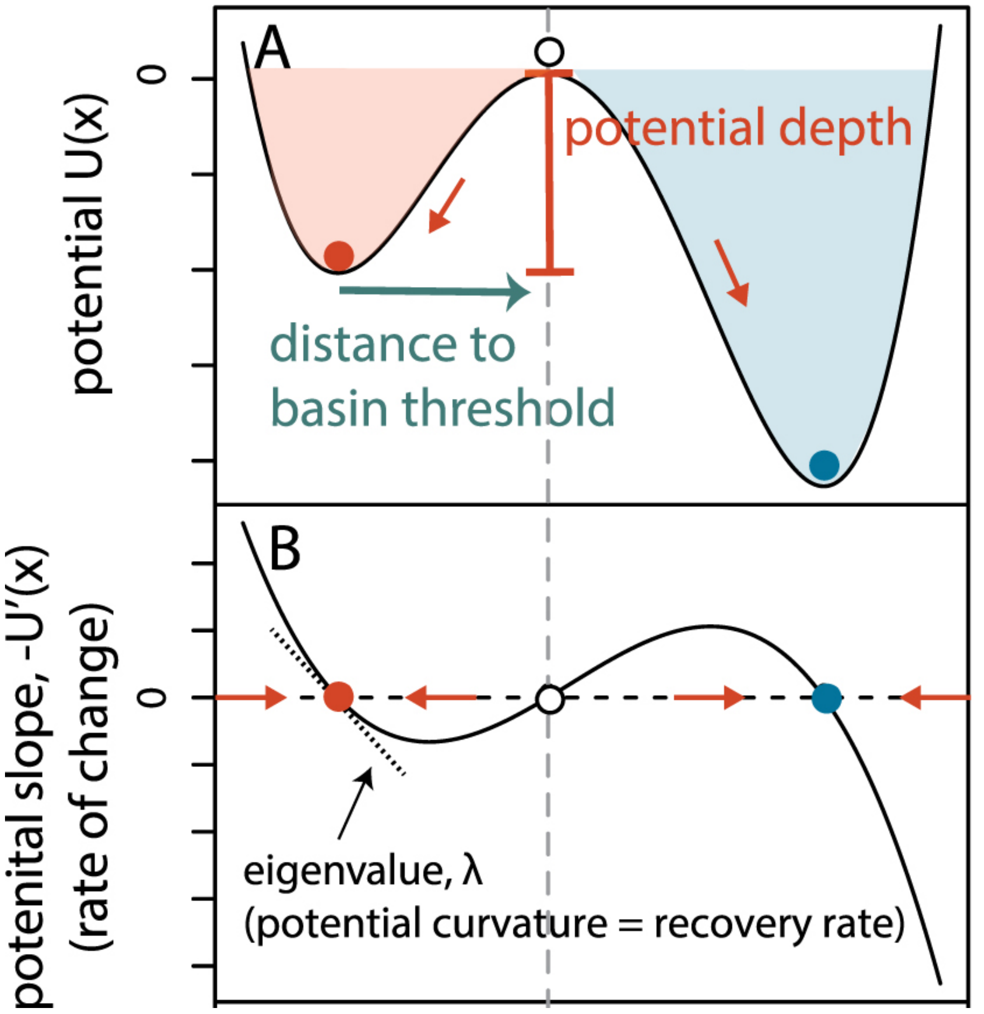
- Dynamical system:

$$\frac{dN}{dt} = f(N), \text{ with } \bar{N} \text{ an equilibrium s.t. } f(\bar{N}) = 0$$

- Potential function:

$$U(N) = -\int_{N_0}^{N} f(n)dn$$

- **Engineering** resilience:
  - Potential curvature: $\lambda = -f'(\bar{N})$
  - **Time to return to equilibrium**: $\tau_r = \frac{1}{\lambda}\ln\left(\frac{\bar{N}}{N}\right)$
  - **Variance**: $\mathrm{Var}(N(t)) = -\frac{\sigma}{2\lambda}$
  - **Autocorrelation** : $\mathrm{Corr}(N(t), N(t+1)) = e^{\lambda}$
- These three quantities are highly correlated



Dakos & Kéfi (2022) Ecological resilience: what to measure and how. *Environmental Research Letters*

Resilience metrics (bis)

- Dynamical system:

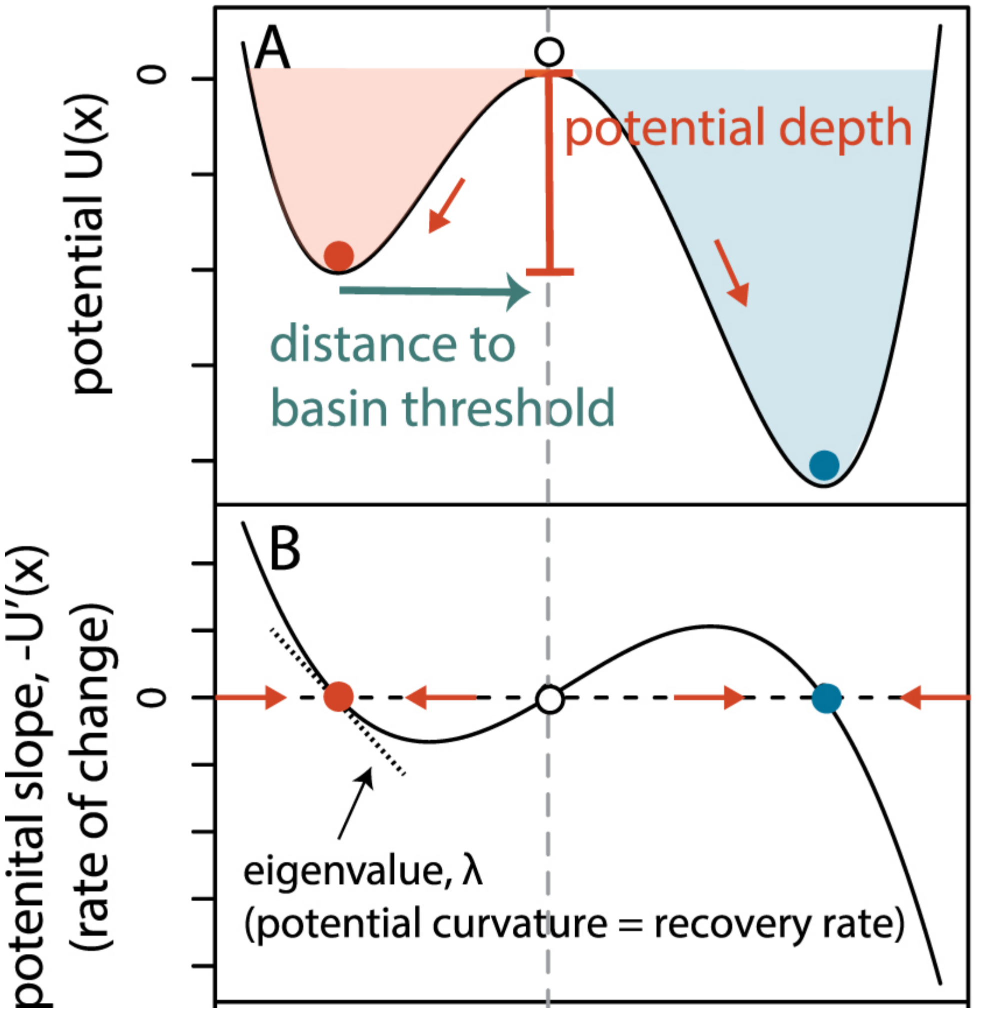
$$\frac{dN}{dt} = f(N), \text{ with } \bar{N} \text{ an equilibrium s.t. } f(\bar{N}) = 0$$

- Potential function:

$$U(N) = -\int_{N_0}^{N} f(n)dn$$

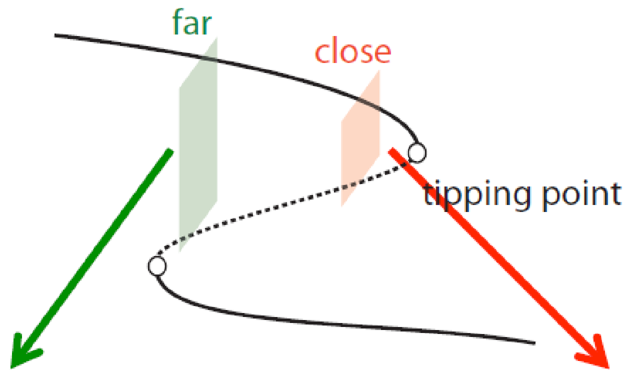
- Ecological resilience:
  - **Potential depth**: $|U(\bar{N}_o) - U(\bar{N})|$
  - **Distance to tipping point**: $|\bar{N}_o - \bar{N}|$
  - **Mean exit time**:

$$\tau_s = \frac{2\pi}{\sqrt{|\lambda|\lambda_o}} e^{\frac{2}{\sigma^2}|U(\bar{N}_o) - U(\bar{N})|}$$



Dakos & Kéfi (2022) Ecological resilience: what to measure and how. *Environmental Research Letters*

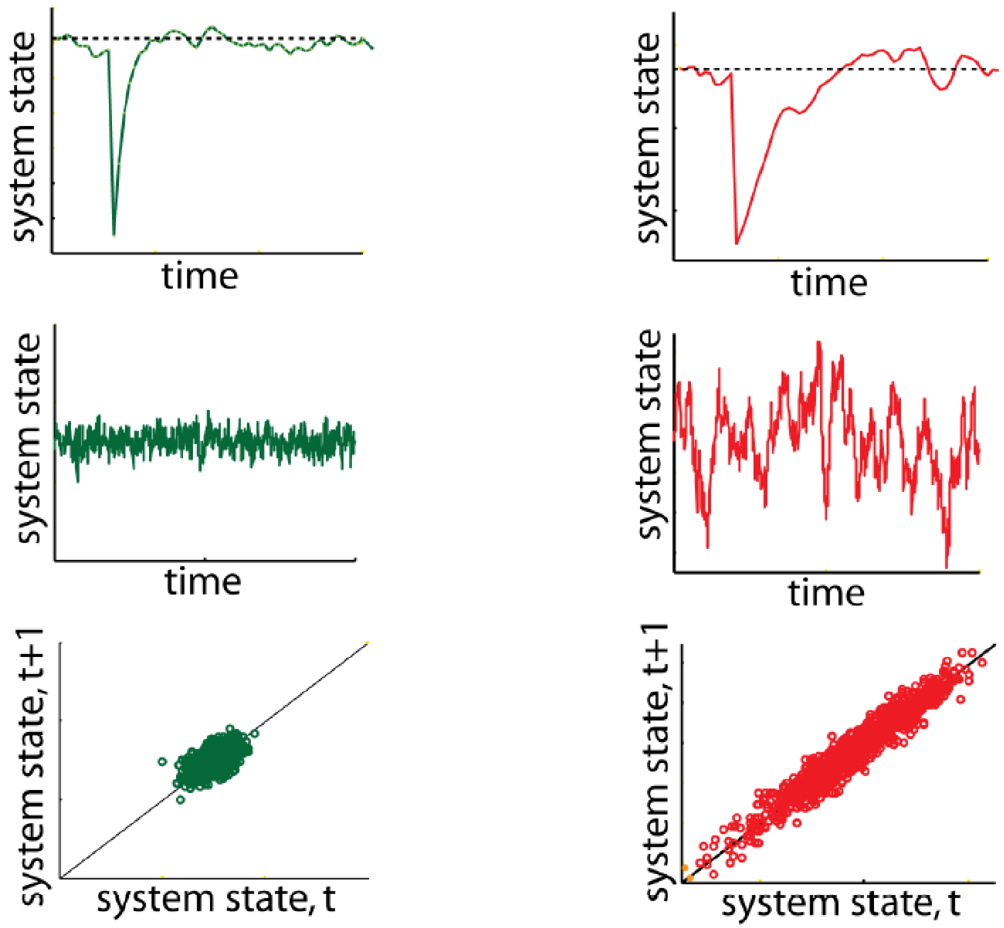
tipping point indicators



far from tipping

close to tipping

leading indicators (Early Warnings)

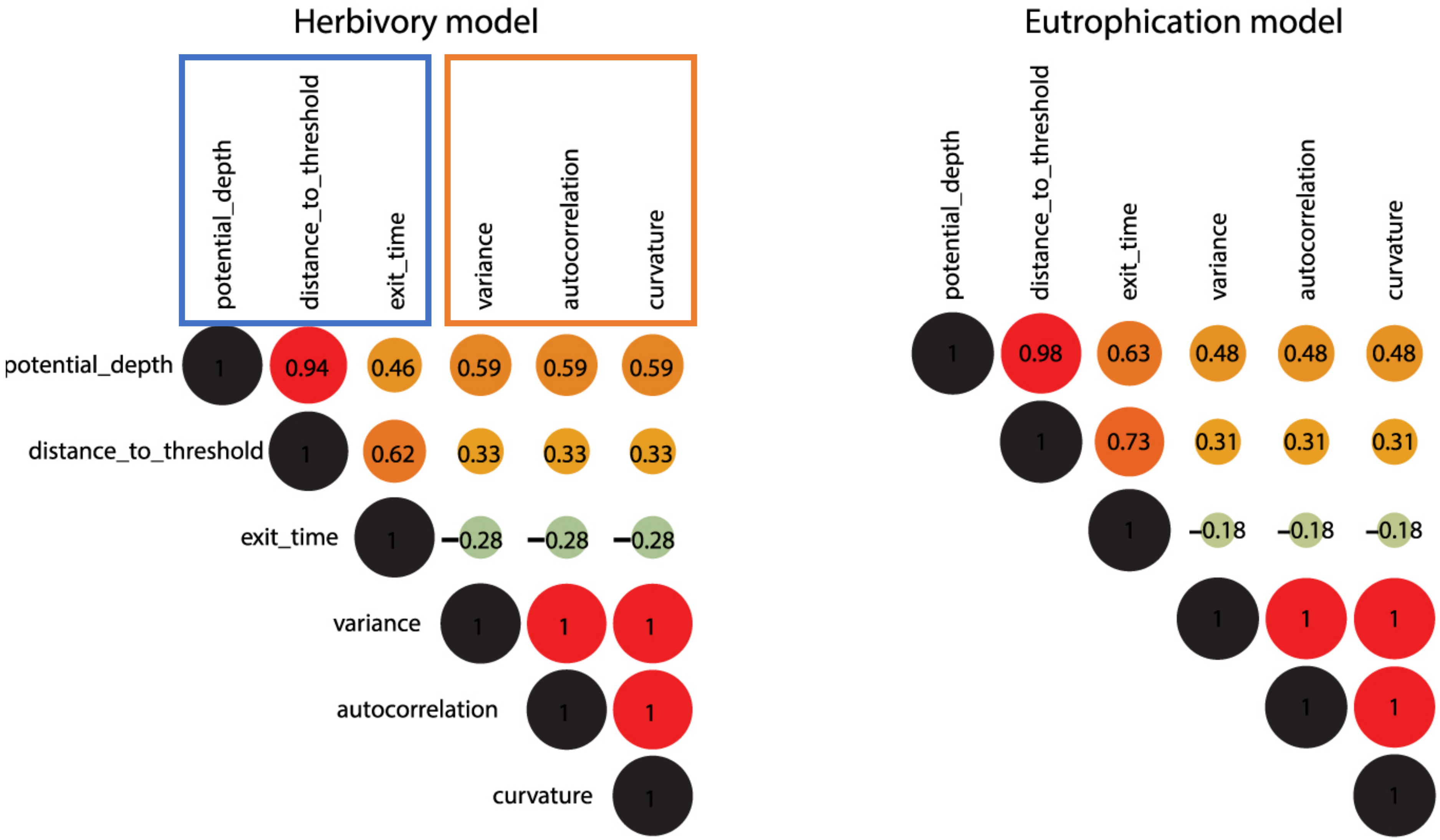


recovery time increases

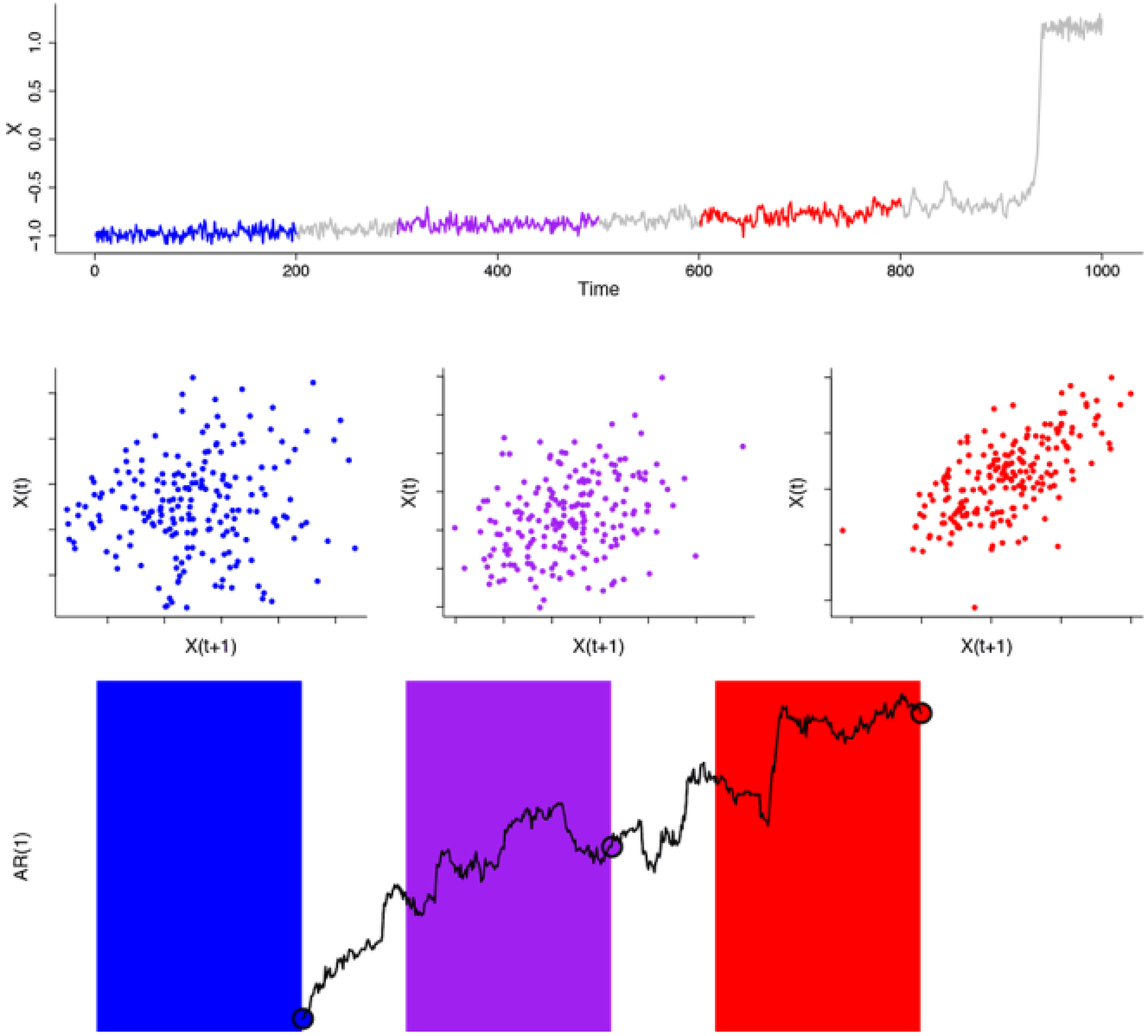
variance increases

autocorrelation rises

Engineering metrics are correlated to ecological metrics (réconciliation)

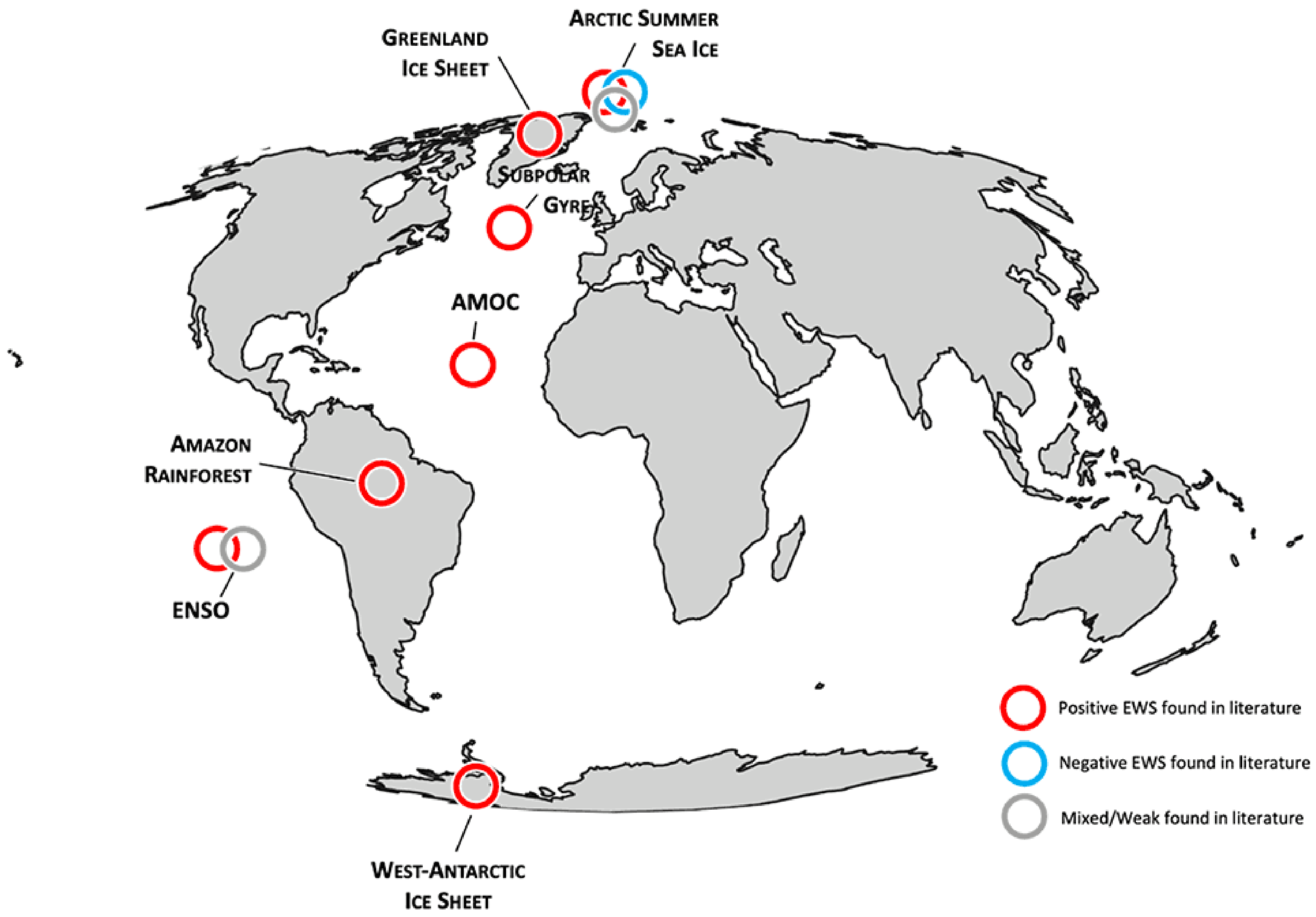


Early-warning signals



Near the tipping point, the **time to return to equilibrium** is longer (critical slowdown), which results in an increase in the **autocorrelation** of the signal.

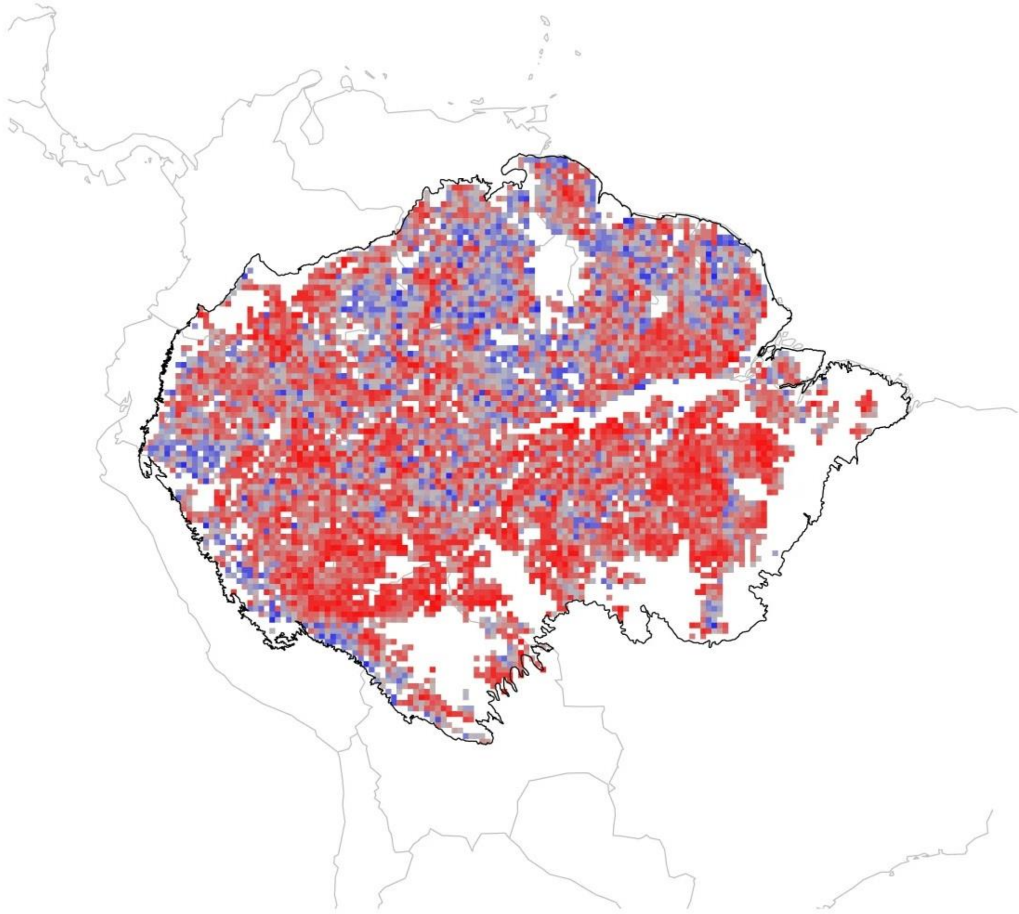
Empirical evidence of Early Warning Signals

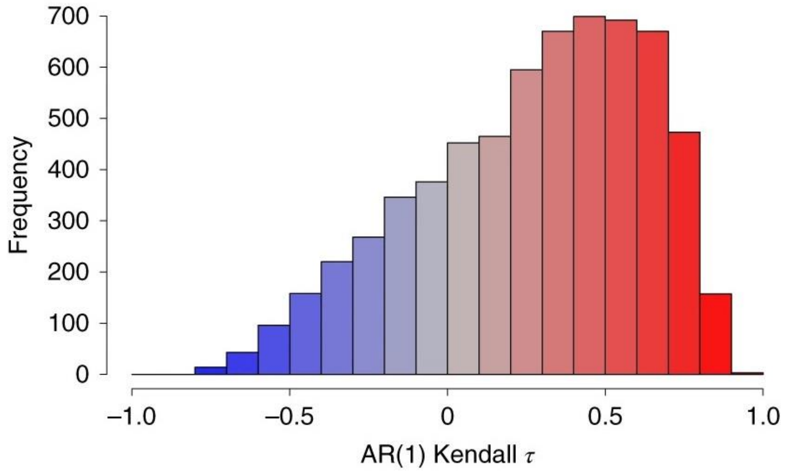


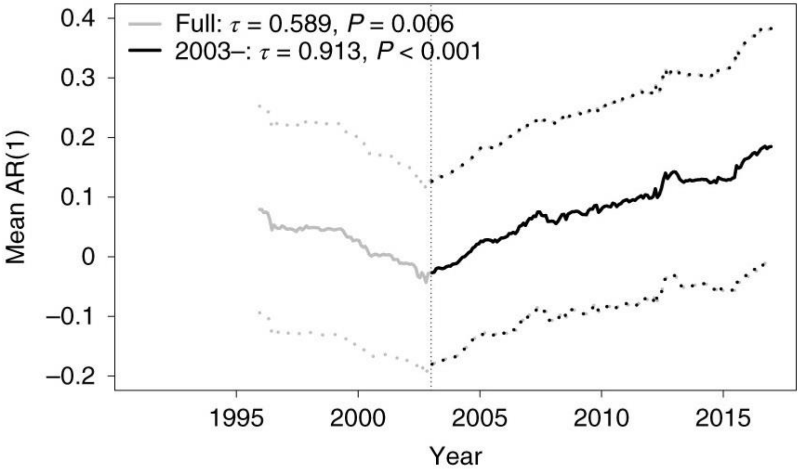
Dakos et al (2024). Tipping point detection and early warnings in climate, ecological, and human systems. *Earth System Dynamics*

Loss of resilience in the Amazon rainforest

optical depth of vegetation







Boulton et al (2022) Pronounced loss of Amazon rainforest resilience since the early 2000s. *Nature Climate Change*