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 dynamical systems in ecology

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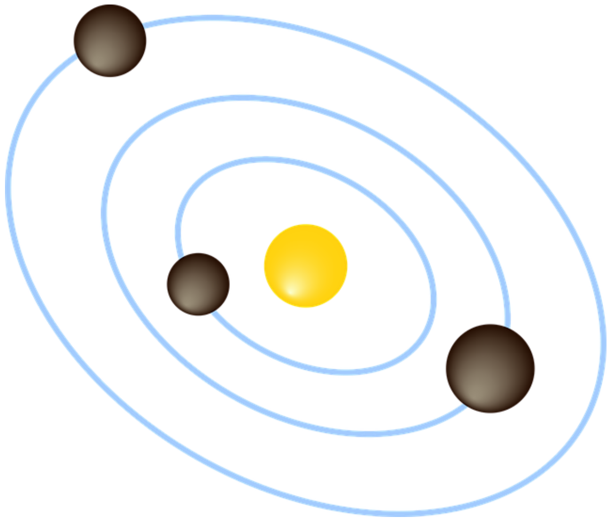
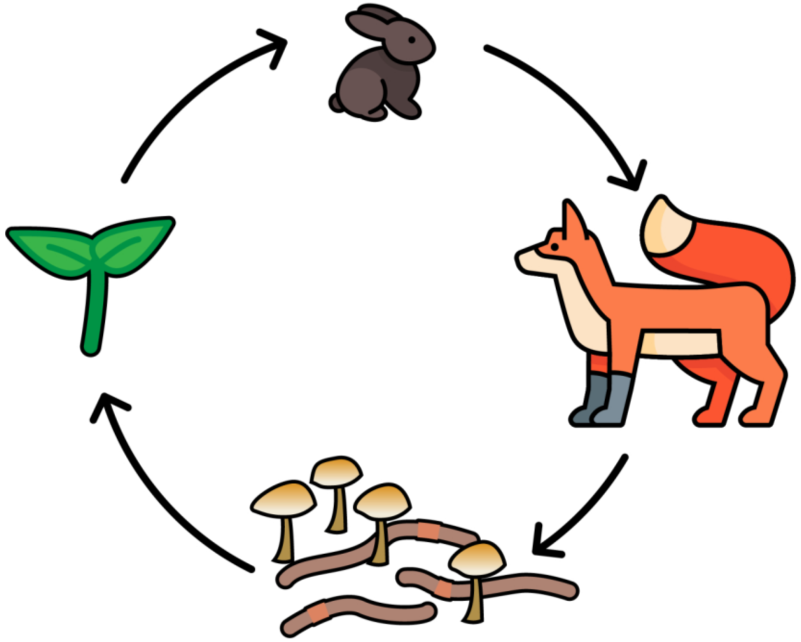
System?

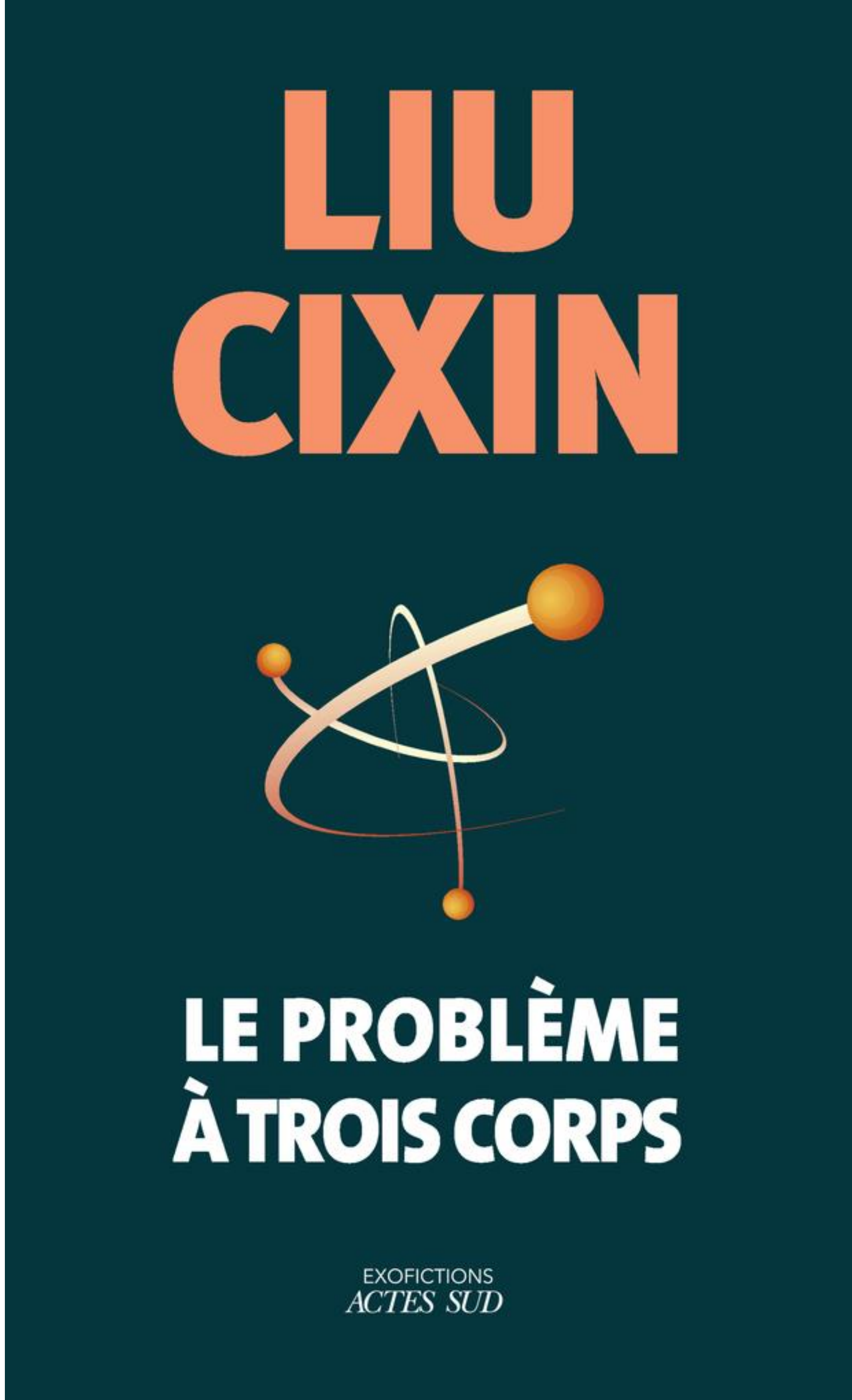
- A set of interconnected elements interacting together

solar system



ecosystem





Outline

- Can the dynamics of a system be predicted?
  1. One-body problem (one species)
  2. Two-body problem (two species)
  3. Three-body problem (three species)
- Notions of equilibrium and stability
  1. Dimension 1
  2. Dimension 2
- Notion of bistability
- Notion of transient dynamics

Can the dynamics of a system be predicted?

1. One-body problem (one species)

Non-overlapping genererations - discrete time

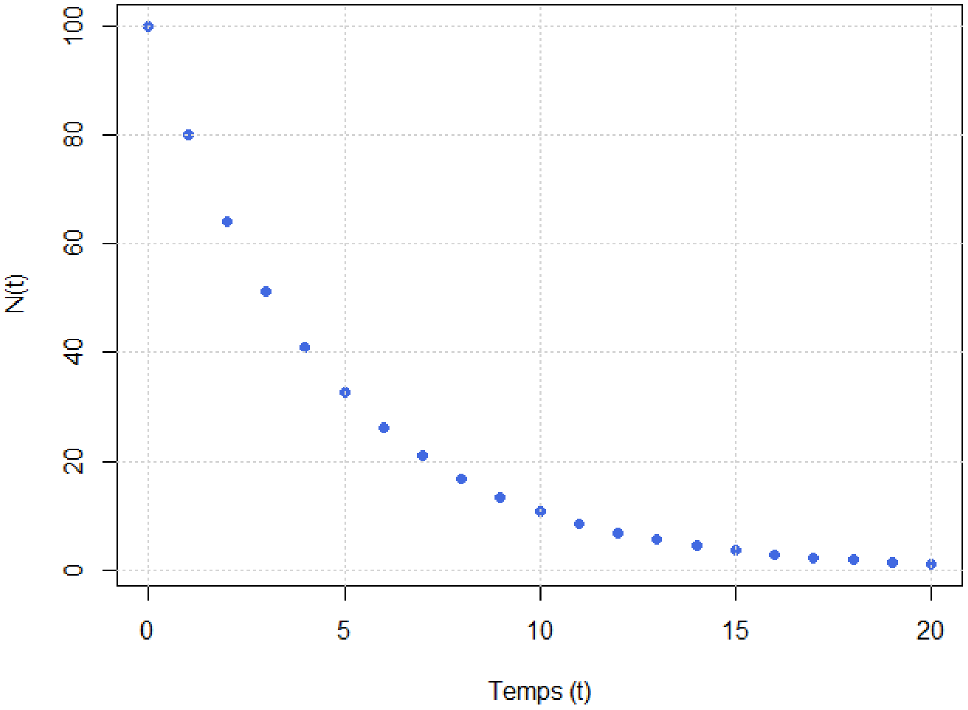
- Time: t [indep. variable]
- Population density: $N(t)$ [state variable]

  [number of individuals *per unit area*]
- Initial density: $N(0) = N_0$ [initial condition]
- Progeny number per individual: R [parameter]
- Population dynamics:

  $N(t+1) = R \times N(t)$ [recurrence eq.]
- Solution: $N(t) = R^t \times N_0$ [geom. growth]

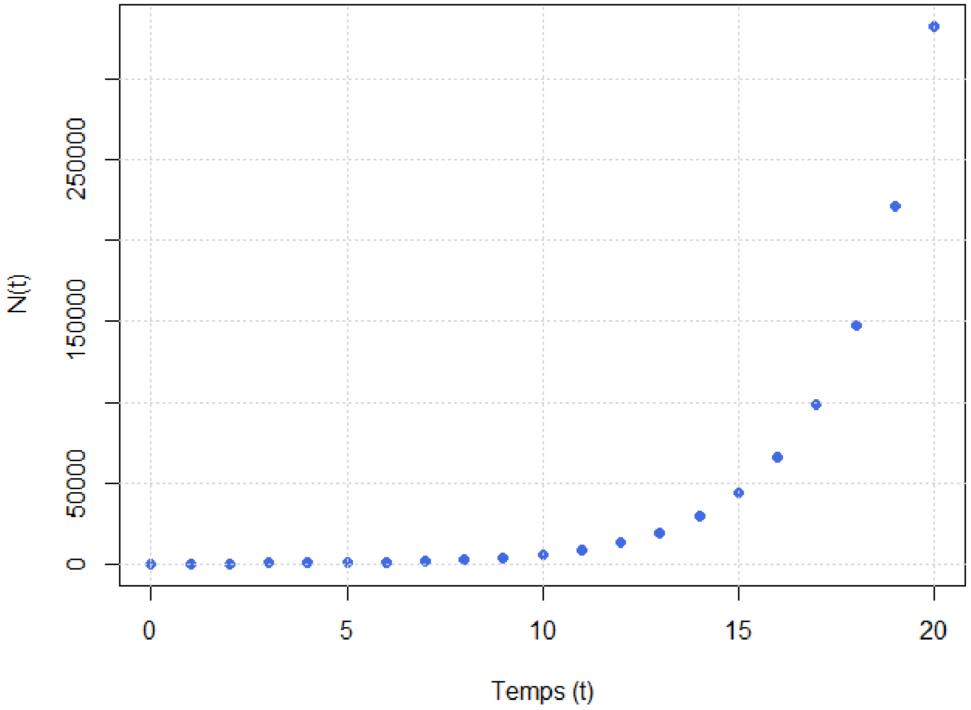
Geometric growth: $N(t) = R^t \times N_0$

If $R < 1$, pop. decreases down to extinction



$R = 0{,}8$

If $R > 1$, pop. increases limitless



$R = 1{,}5$

Overlapping generations - continuous time

- Time: t [indep. variable]
- Population density: $N(t)$ [state variable]

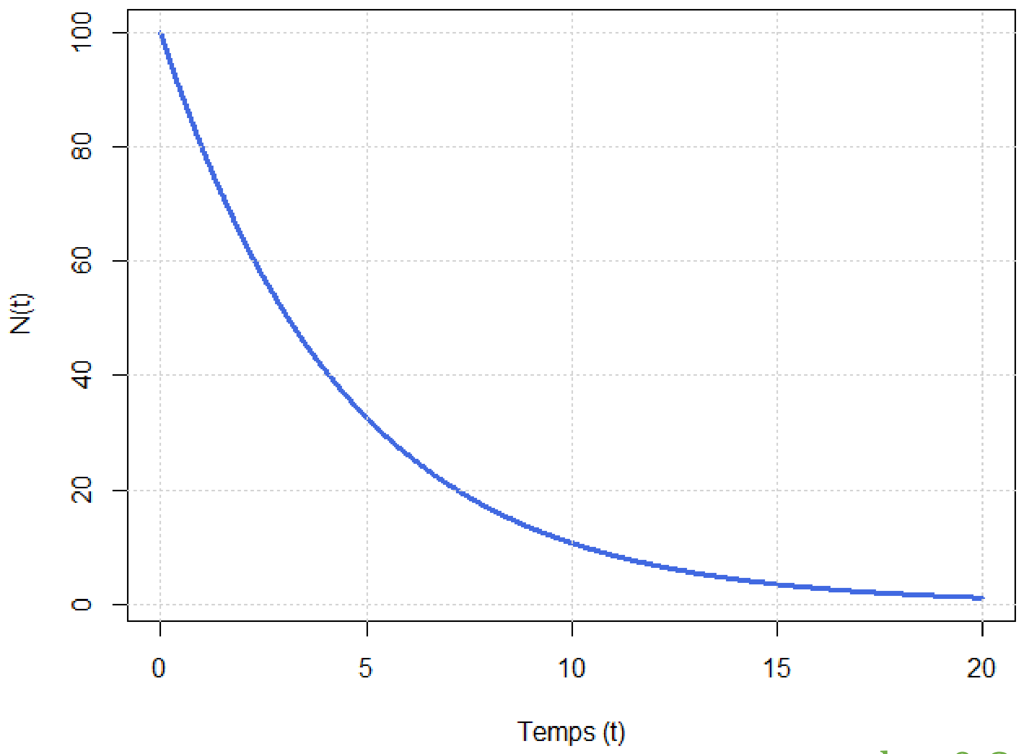
  [number of individual *per unit area*]
- Initial density: $N(0) = N_0$ [initial condition]
- Net reproduction per indiv. per unit time: r [parameter]
- Rate of change of pop. density per unit time:

$$\frac{dN}{dt}(t) = rN(t)$$ [differential eq.]

- Solution: $N(t) = e^{rt} \times N_0$ [exp. growth]

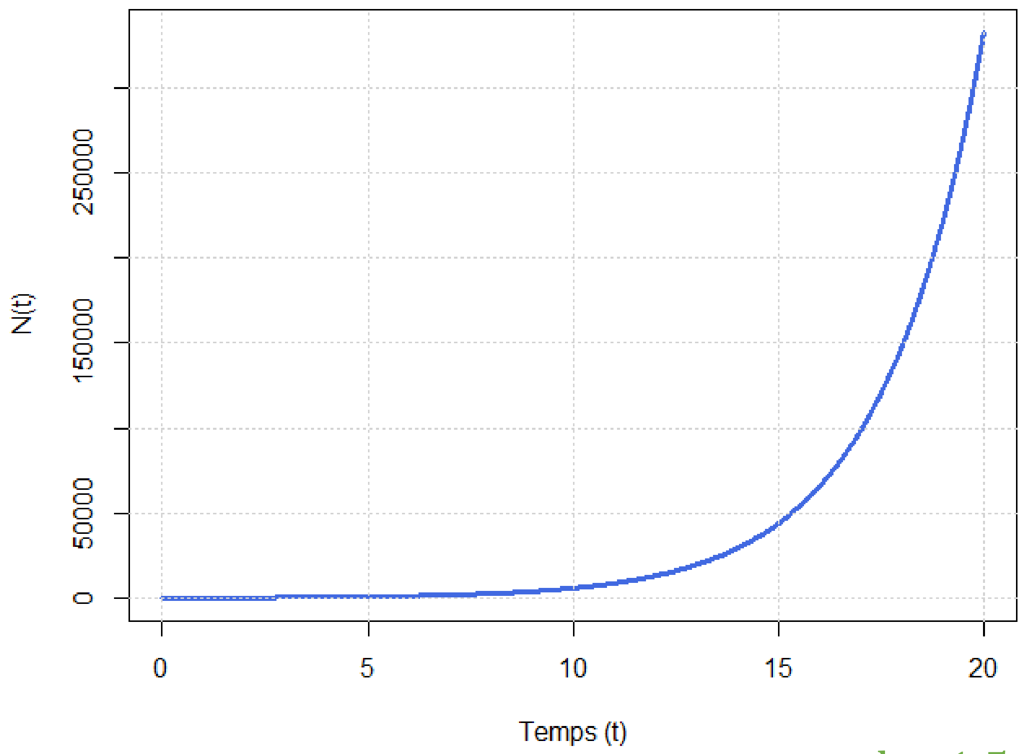
Exponential growth: $N(t) = e^{rt} \times N_0$

If $r < 0$, pop. Decreases exponentially



$r = \log 0{,}8$

If $r > 0$, pop. Increases exponentially



$r = \log 1{,}5$

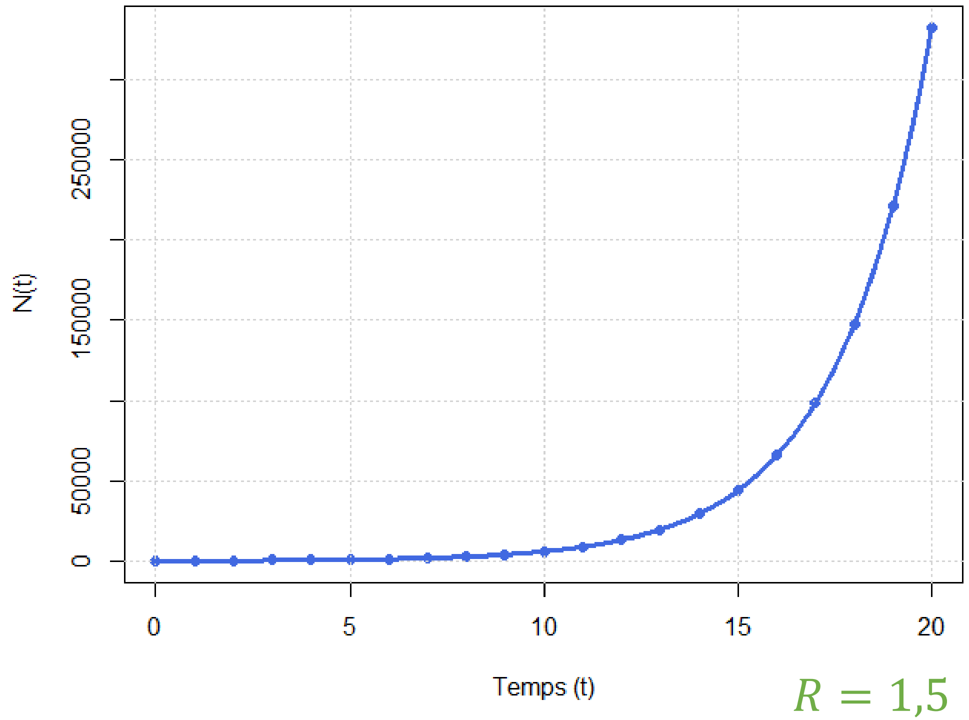
Geometric vs exponential growth

Geom. growth: $N(t) = R^t \times N_0$ [discrete time]

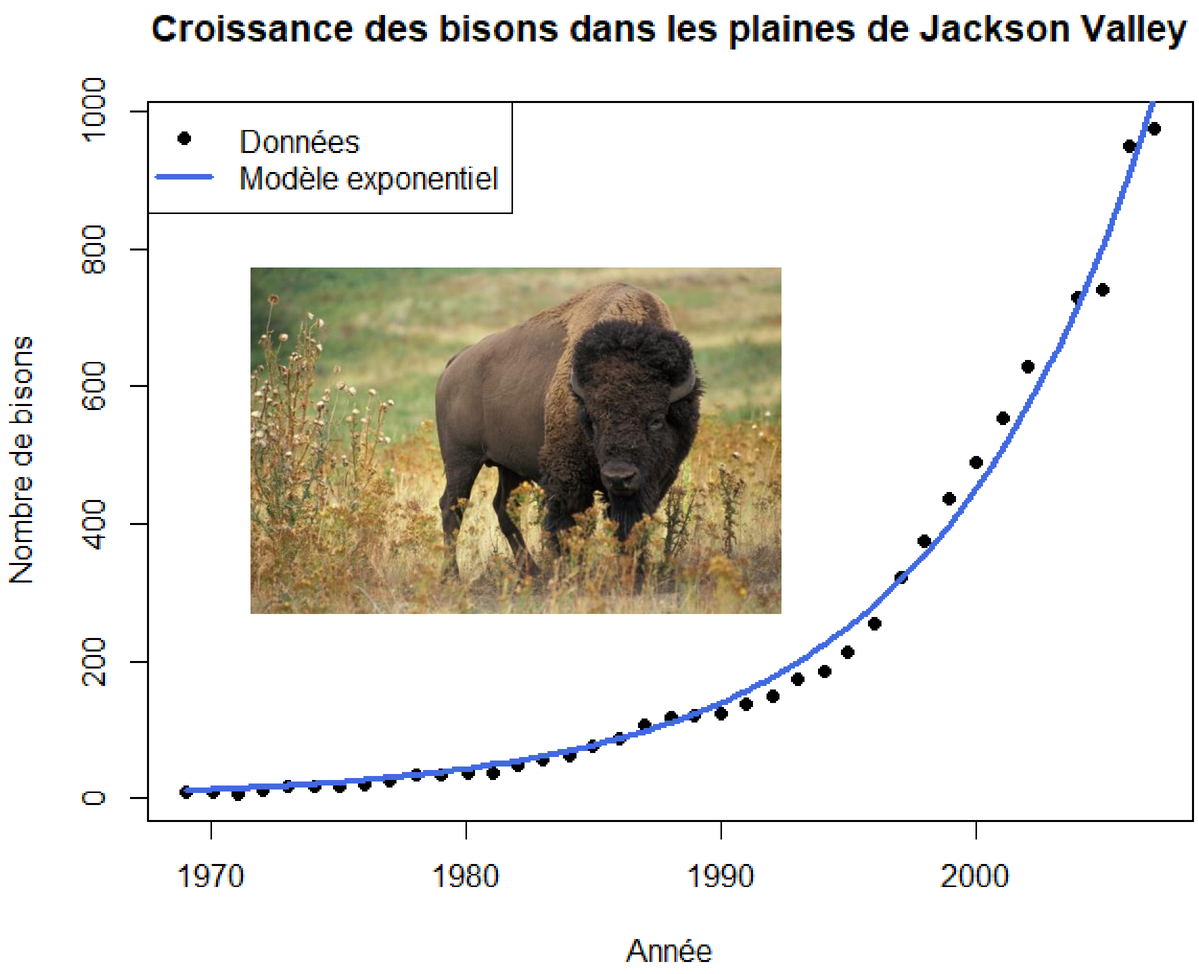
Exp. growth: $N(t) = e^{rt} \times N_0$ [continuous time]

Equivalence for: $R = e^r$

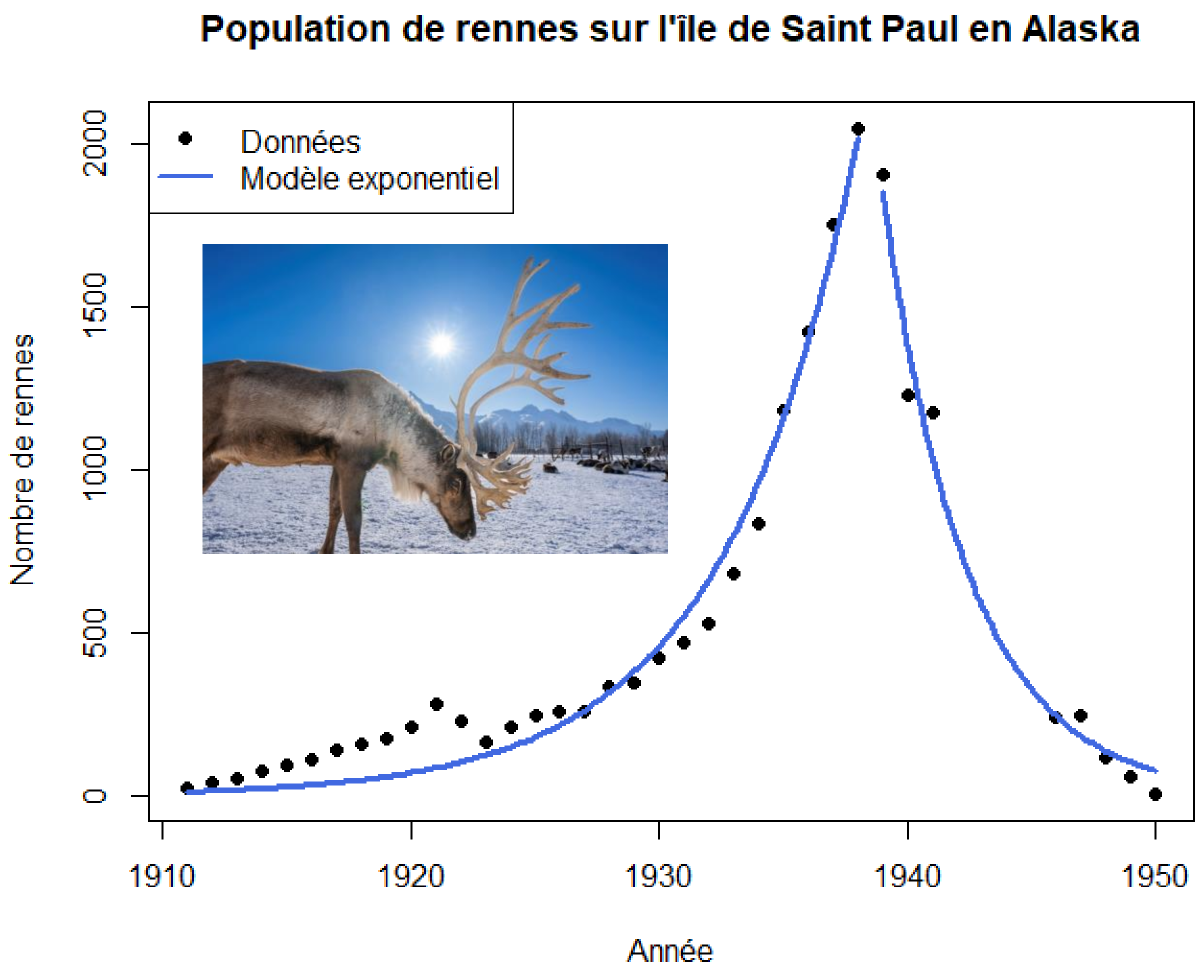
These are the same thing!



$R = 1{,}5$



Gates et al (2010) *American bison: status survey and conservation guidelines 2010*. IUCN.



Scheffer (1951) The rise and fall of a reindeer herd. *The Scientific Monthly*, *73*(6), 356-362.

Limits to growth

Logistic growth – continuous time

- Carrying capacity of the env.: K
- Differential eq.:

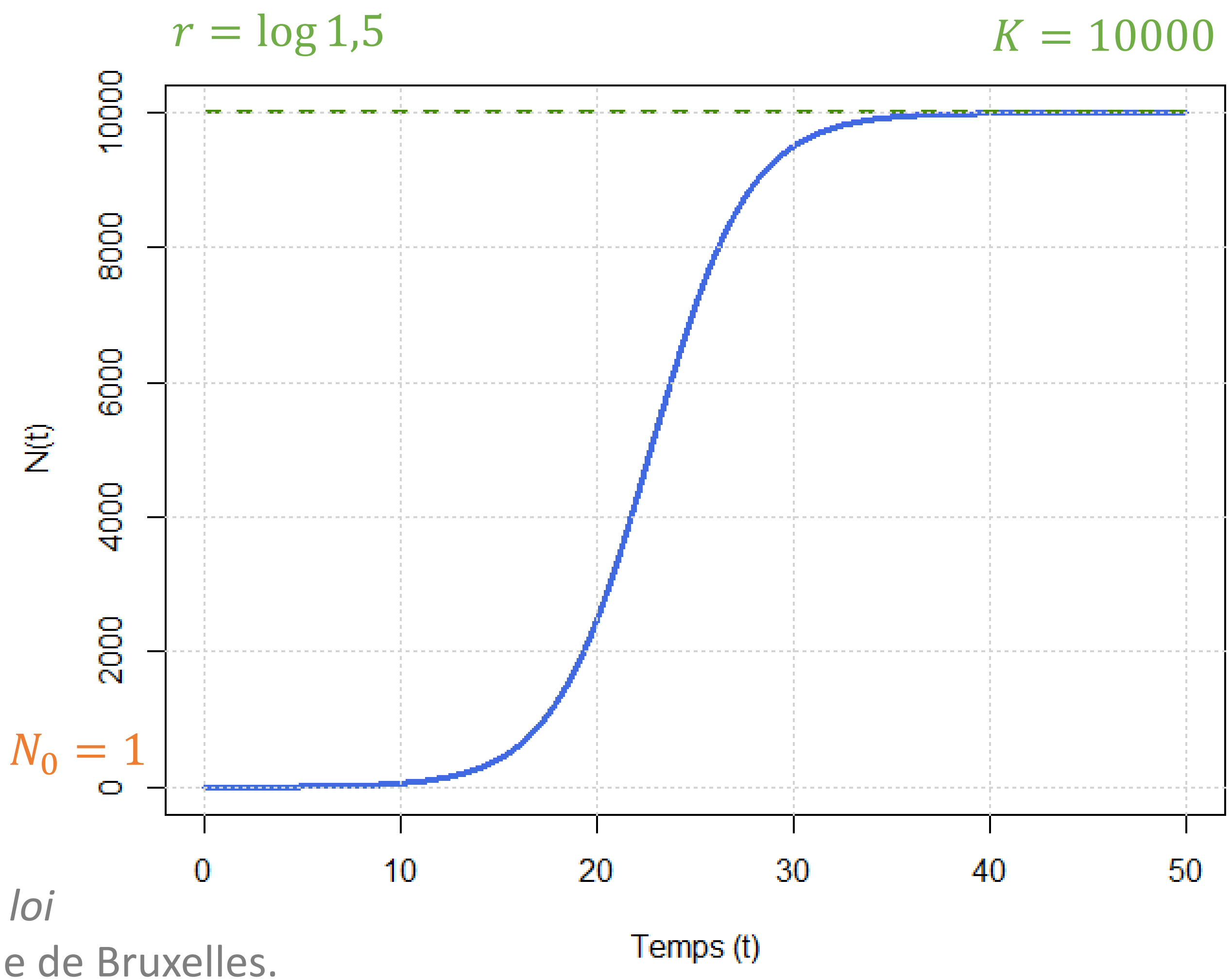
$$\frac{dN}{dt}(t) = rN(t)\left(1 - \frac{N(t)}{K}\right)$$

- Solution:

$$N(t) = \frac{K N_0}{N_0 + (K-1)e^{-rt}}$$

- Model due to

Verhulst (1844) *Recherches mathématiques sur la loi d'accroissement de la population*. Académie Royale de Bruxelles.



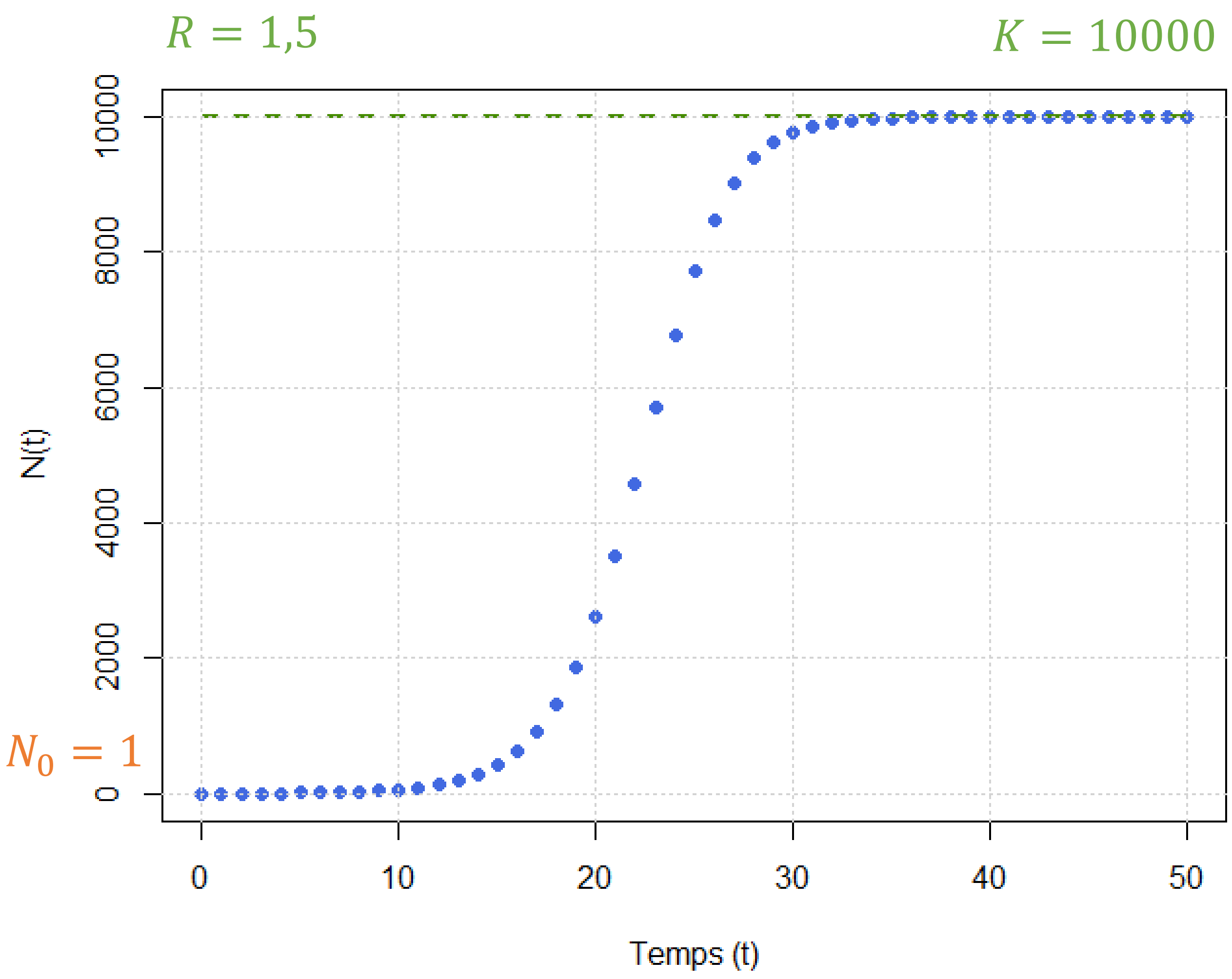
Logistic growth – discrete time

- Carrying capacity of the env.: K
- Recurrence eq.:

$$N(t+1) = R^{\left(1-\frac{N(t)}{K}\right)} N(t)$$

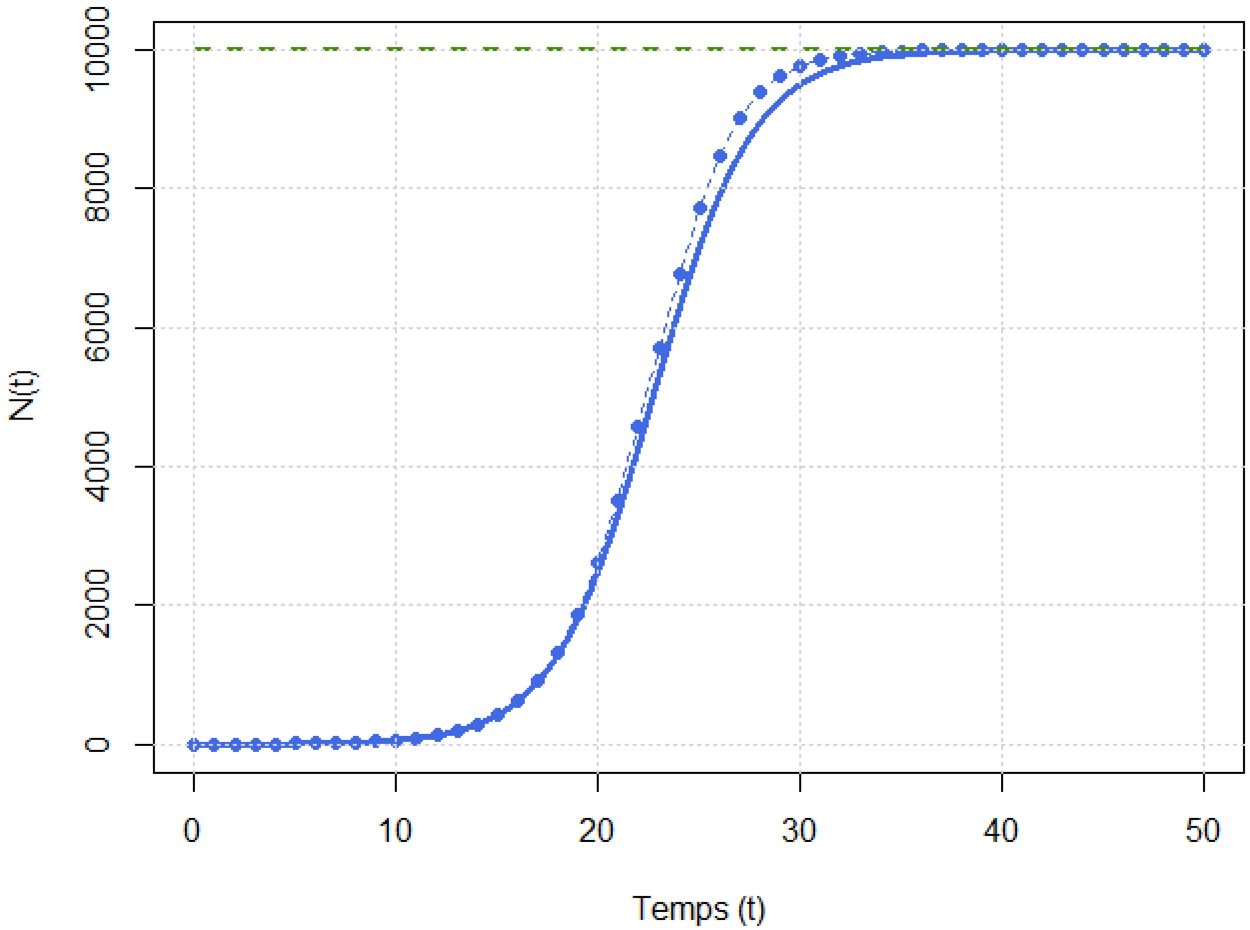
- No explicit solution
- Model due to

Ricker (1954), "Stock and recruitment", J. Fisheries Res. Board Can.



Ricker vs logistic - discrete vs continuous time

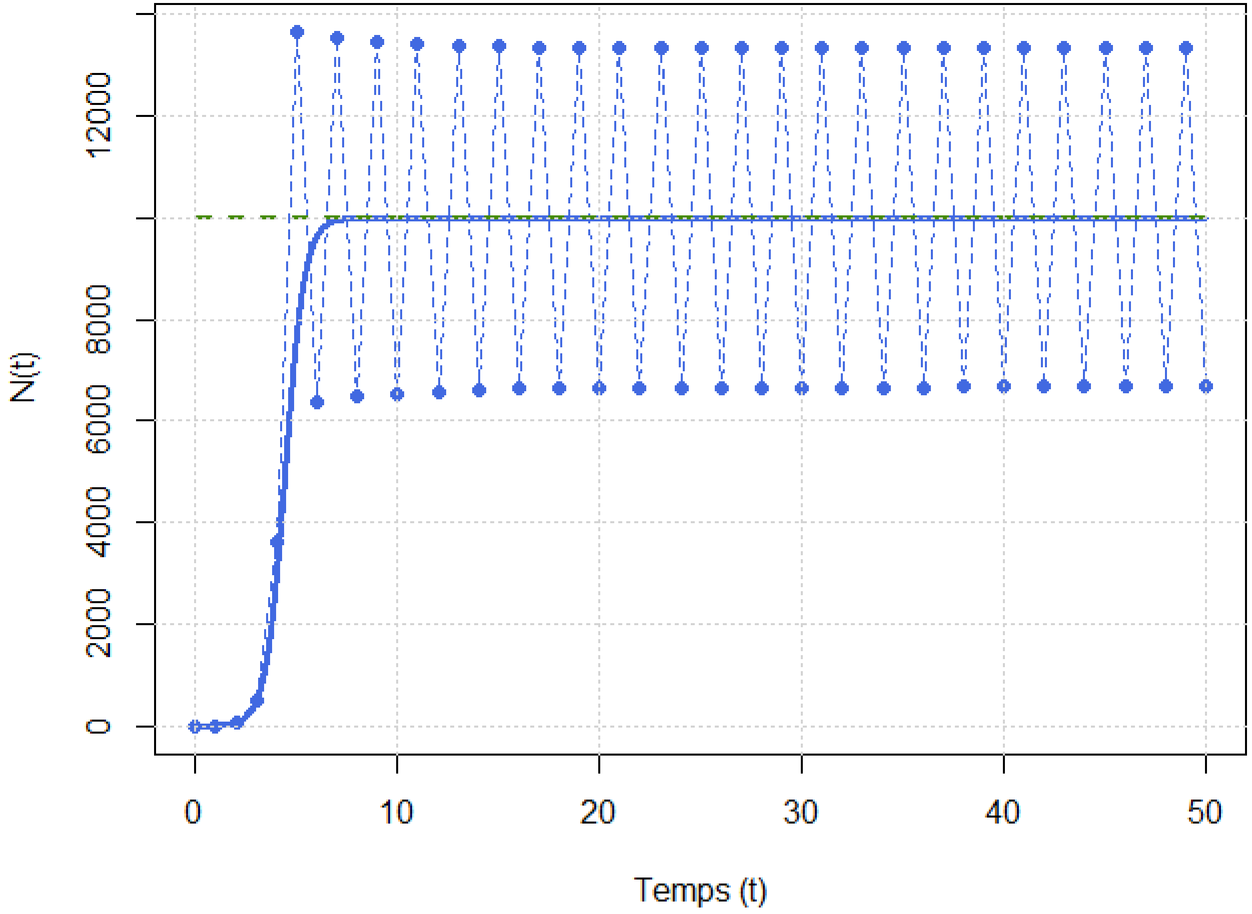
$R = 1,5$



Ricker's model is **not** an exact discrete-time analogue of continuous-time logistic growth

Ricker vs logistic - discrete vs continuous time

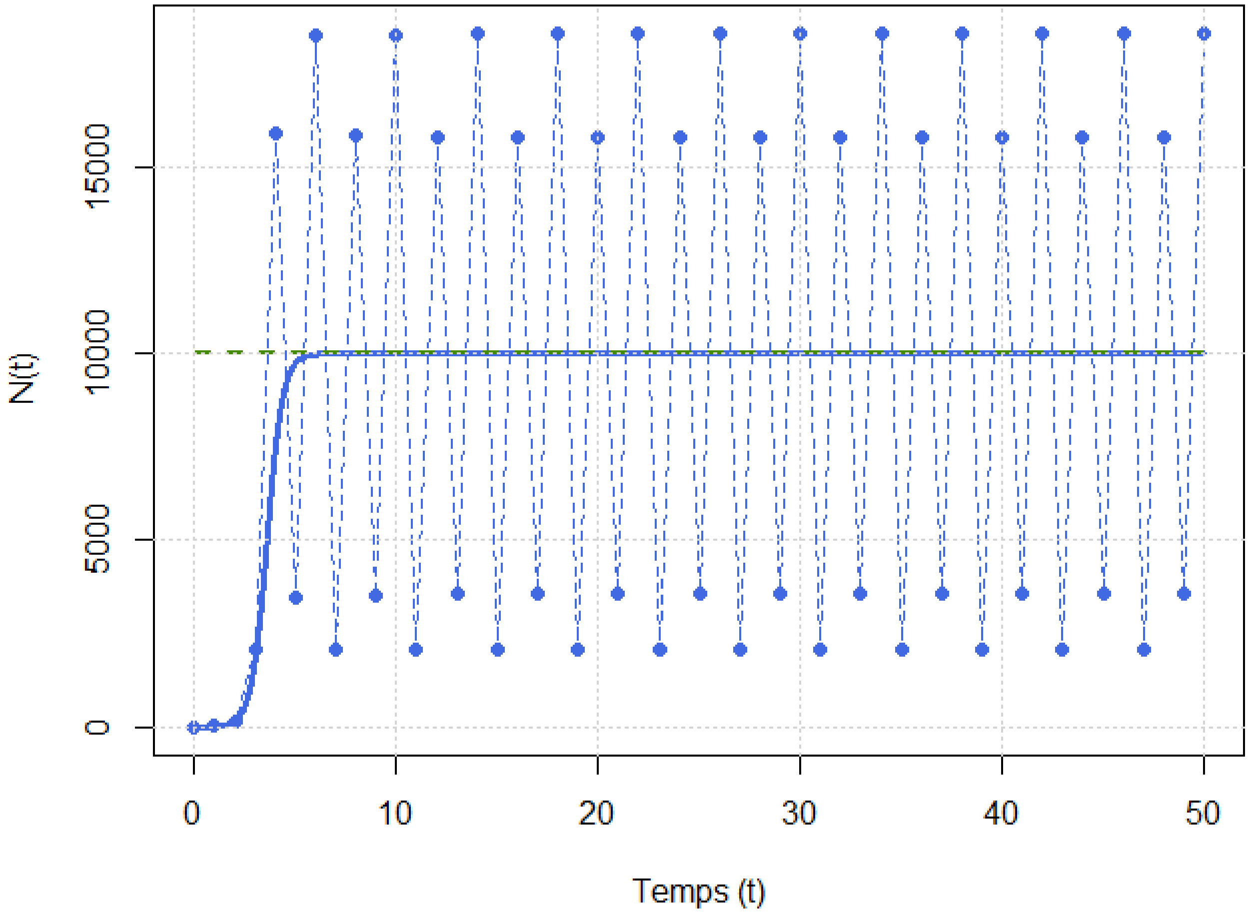
$R = 8$



Ricker's model can generate periodic oscillations of period 2

Ricker vs logistic - discrete vs continuous time

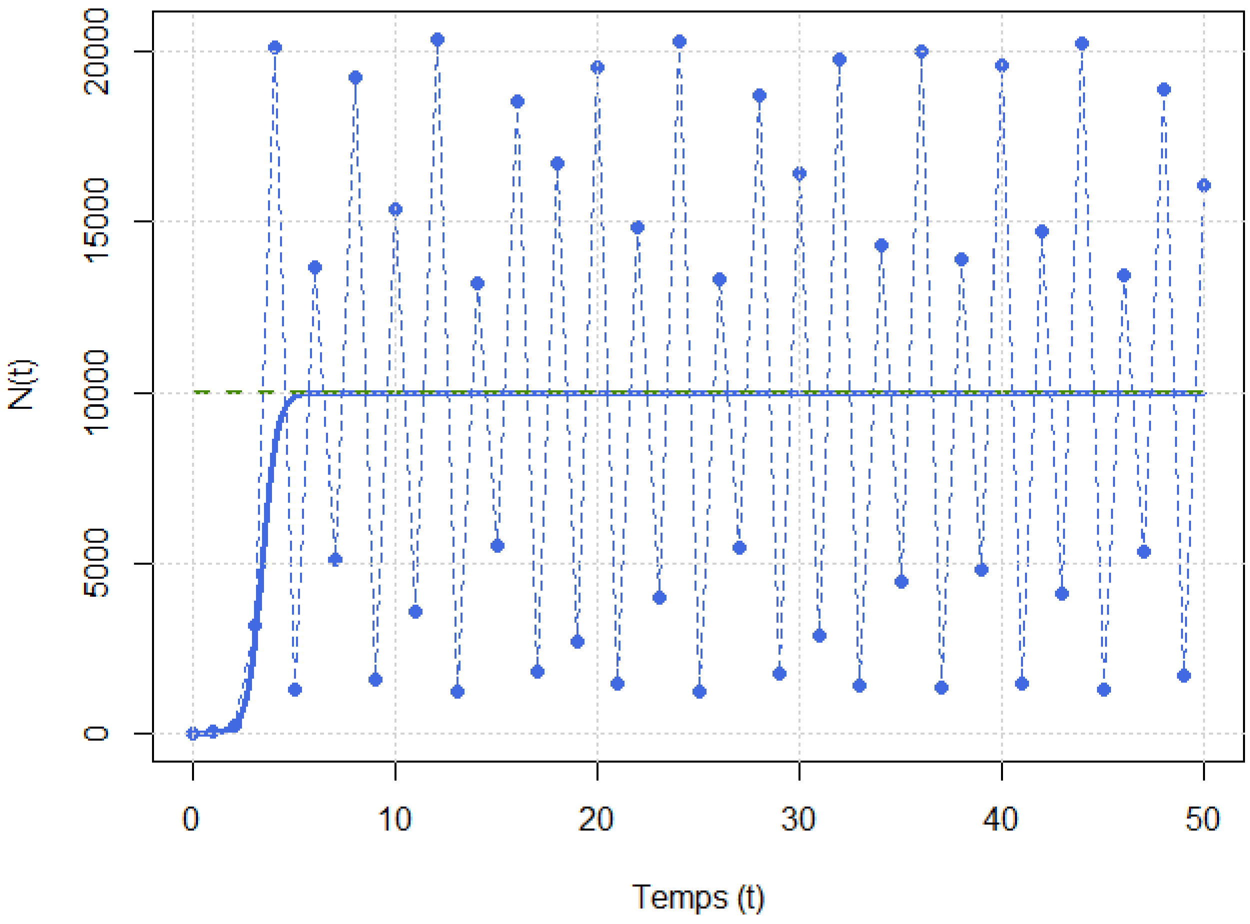
$R = 13$



Ricker's model can generate periodic oscillations of period 4 and more generally 2^n

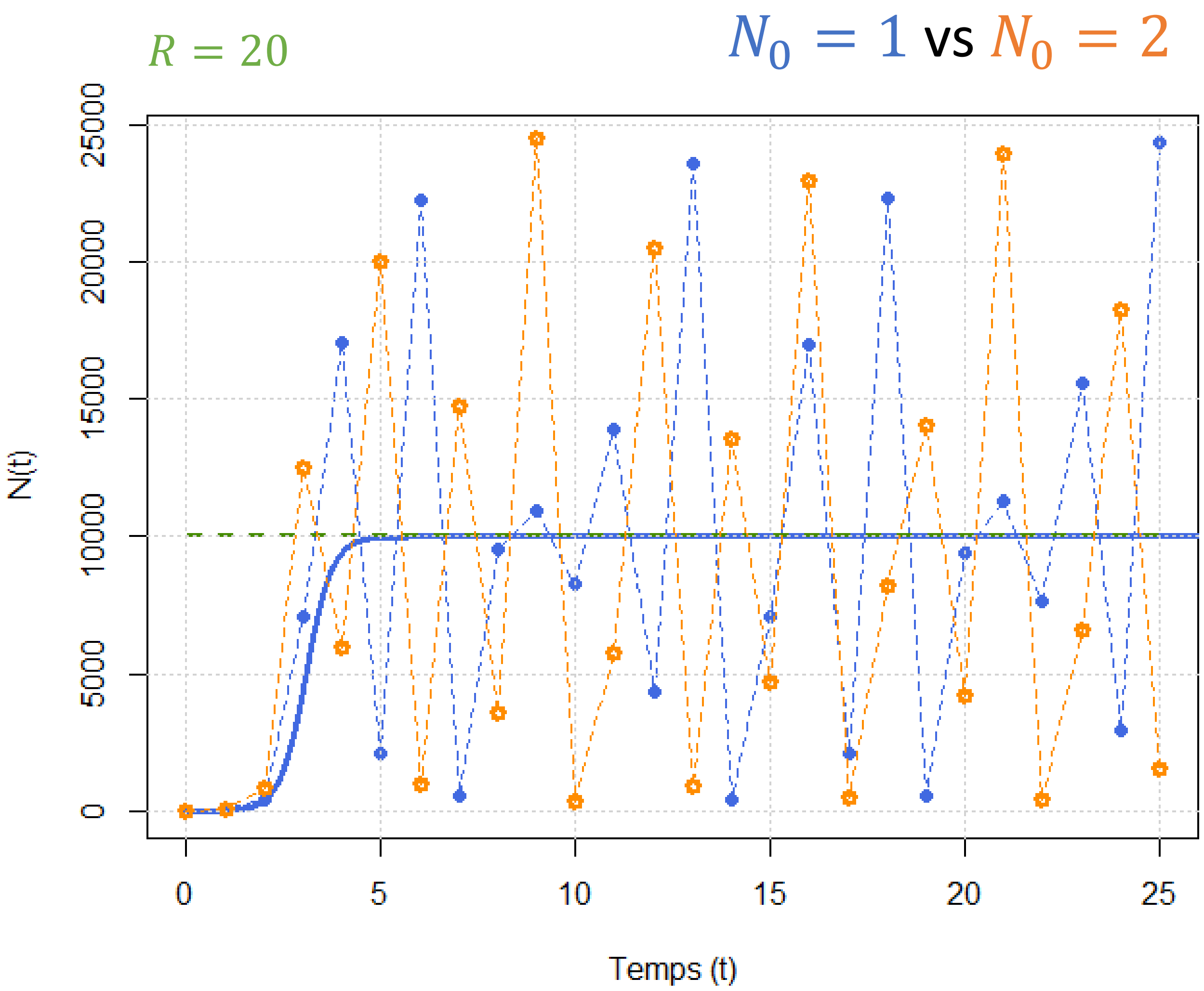
Ricker vs logistic - discrete vs continuous time

$R = 15$



Ricker's model can produce chaotic oscillations (loss of periodicity)

Deterministic chaos



A small difference in initial conditions generates large differences of trajectories

-> it is therefore impossible in this case to predict the dynamics of the system

May (1976). Simple mathematical models with very complicated dynamics. *Nature*.

Alternate logistic model – discrete time

- Carrying capacity of the env.: K
- Recurrence eq.:

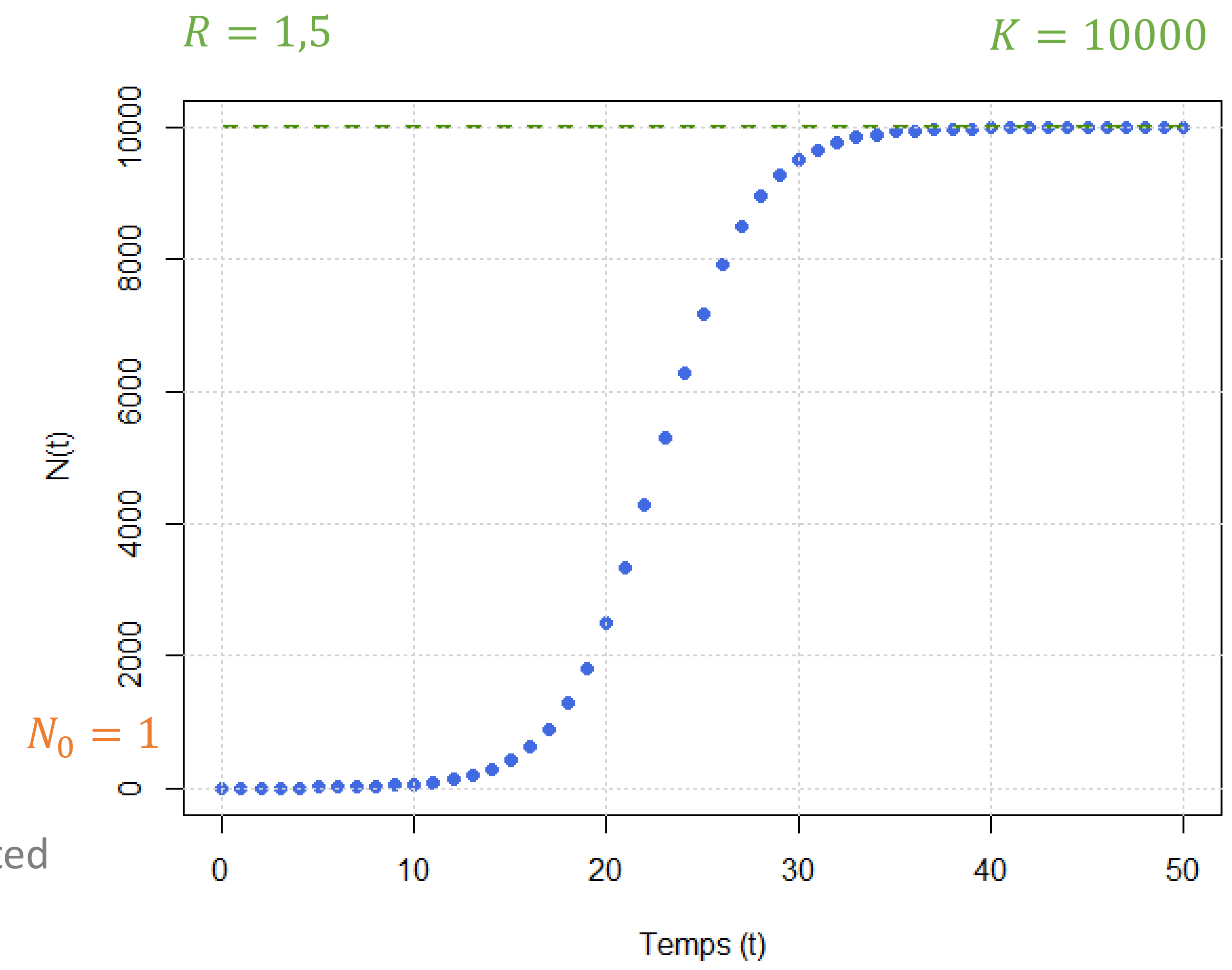
$$N(t+1) = \frac{RN(t)}{1 + \frac{N(t)}{K}(R-1)}$$

- Solution:

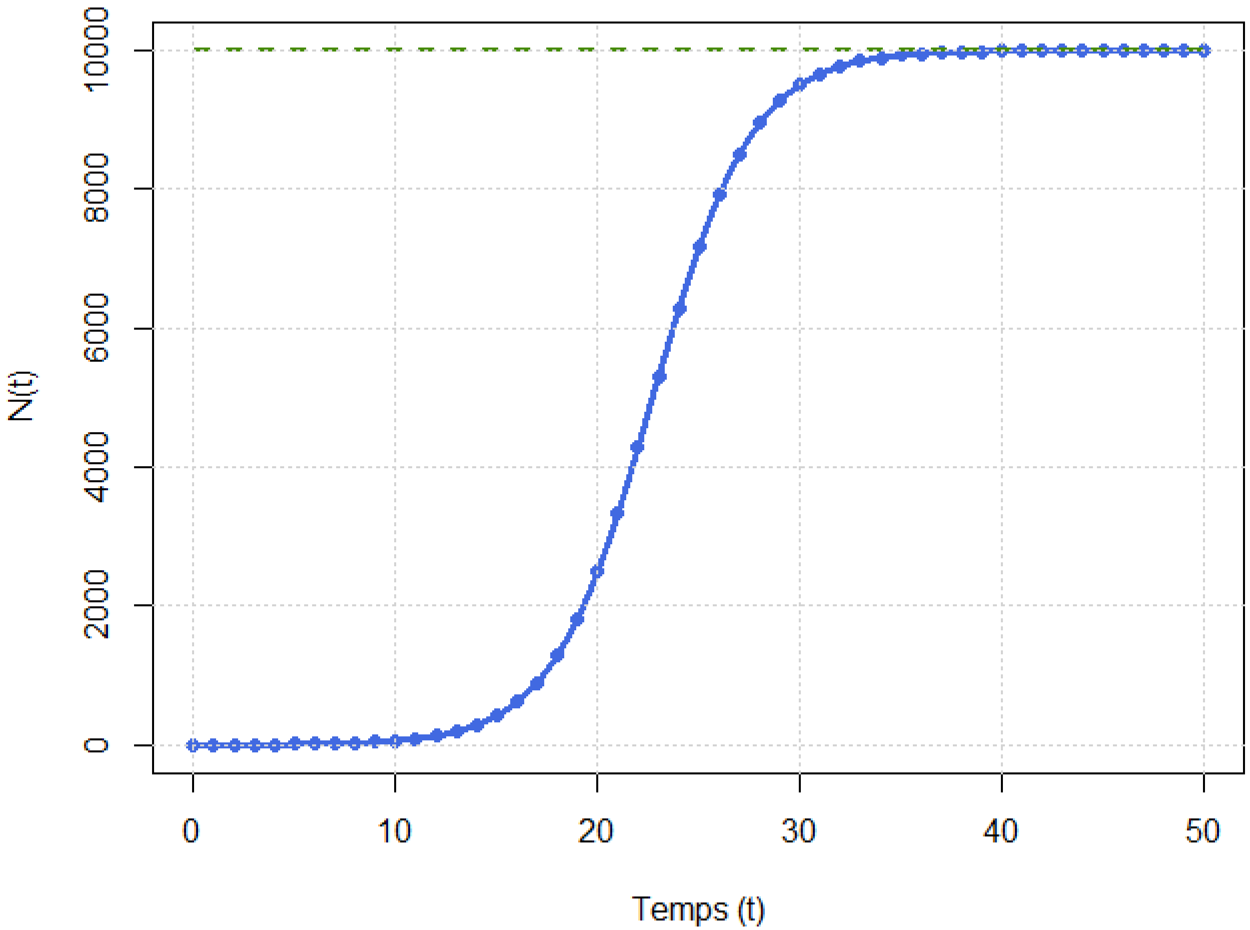
$$N(t) = \frac{KN_0}{N_0 + (K - N_0)R^{-t}}$$

- Model due to

Beverton & Holt (1957) On the Dynamics of Exploited Fish Populations, Fishery Investigations Series I



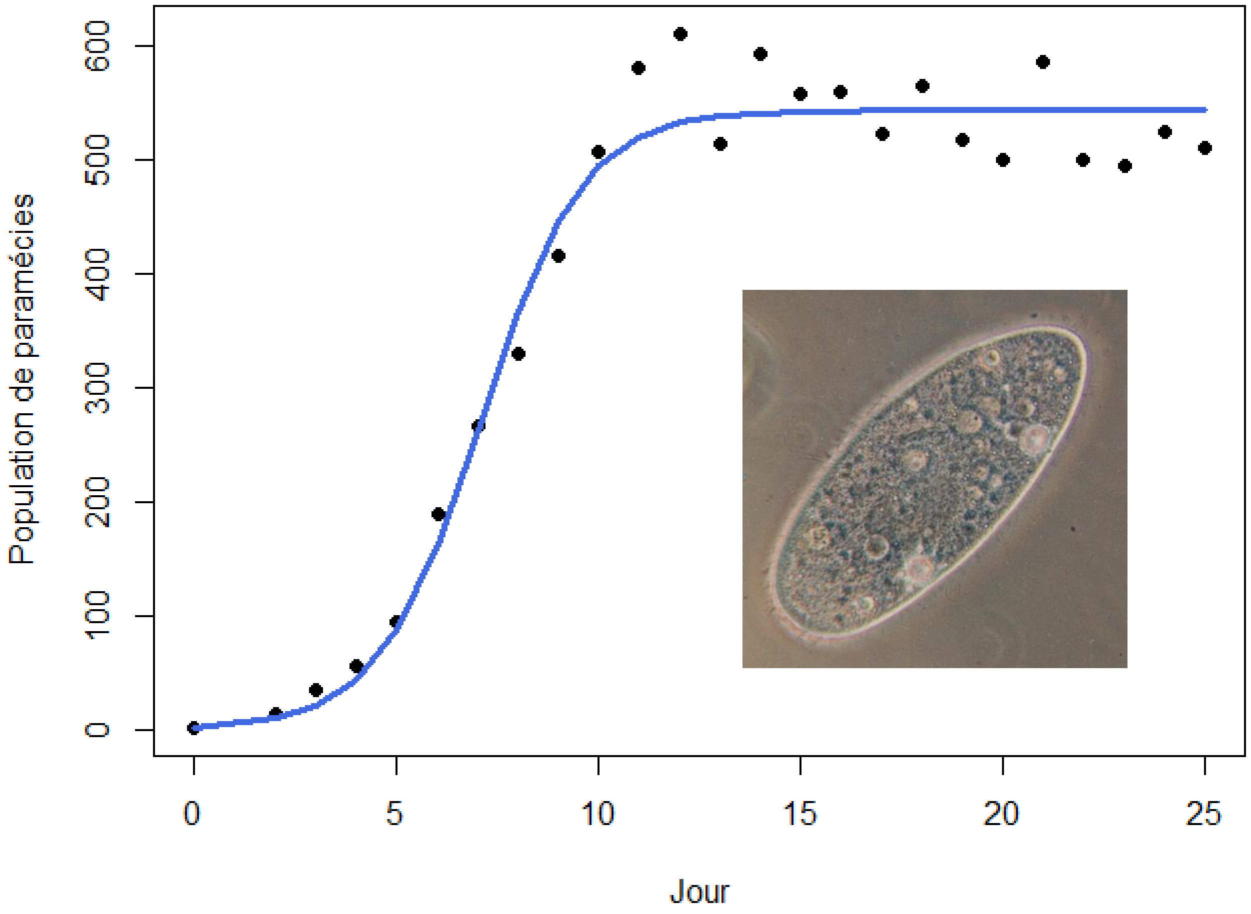
B-H vs logistic – discrete vs continuous time



Beverton-Holt's model is the exact discrete-time analogue of logistic growth in continuous time

-> No chaos!

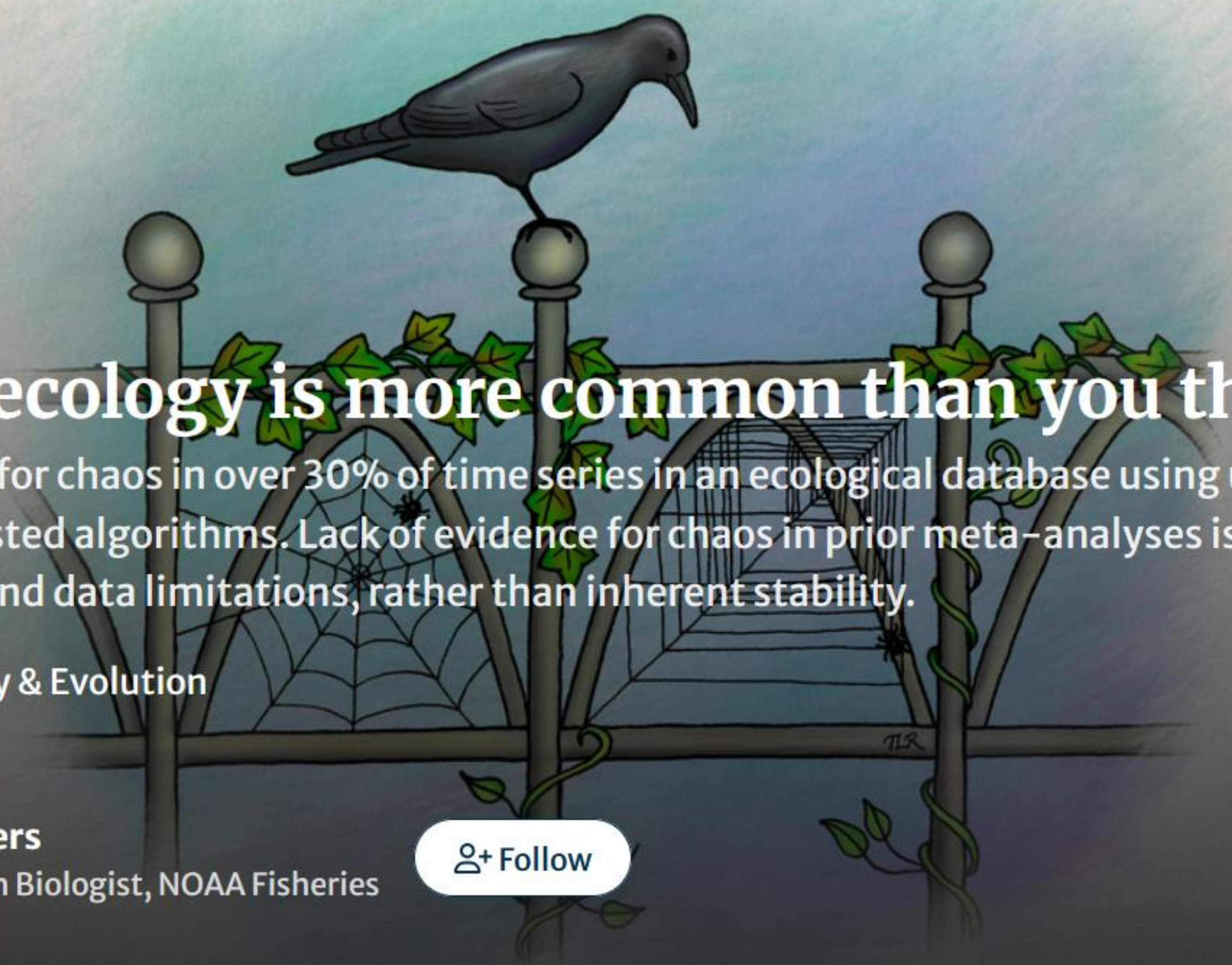
Logistic growth: paramecia as an example



Data from Gause (1934)'s famous experiments leading to the competitive exclusion principle in ecology

Gause (1934) Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science*

Is chaos possible in nature?



Behind the Paper

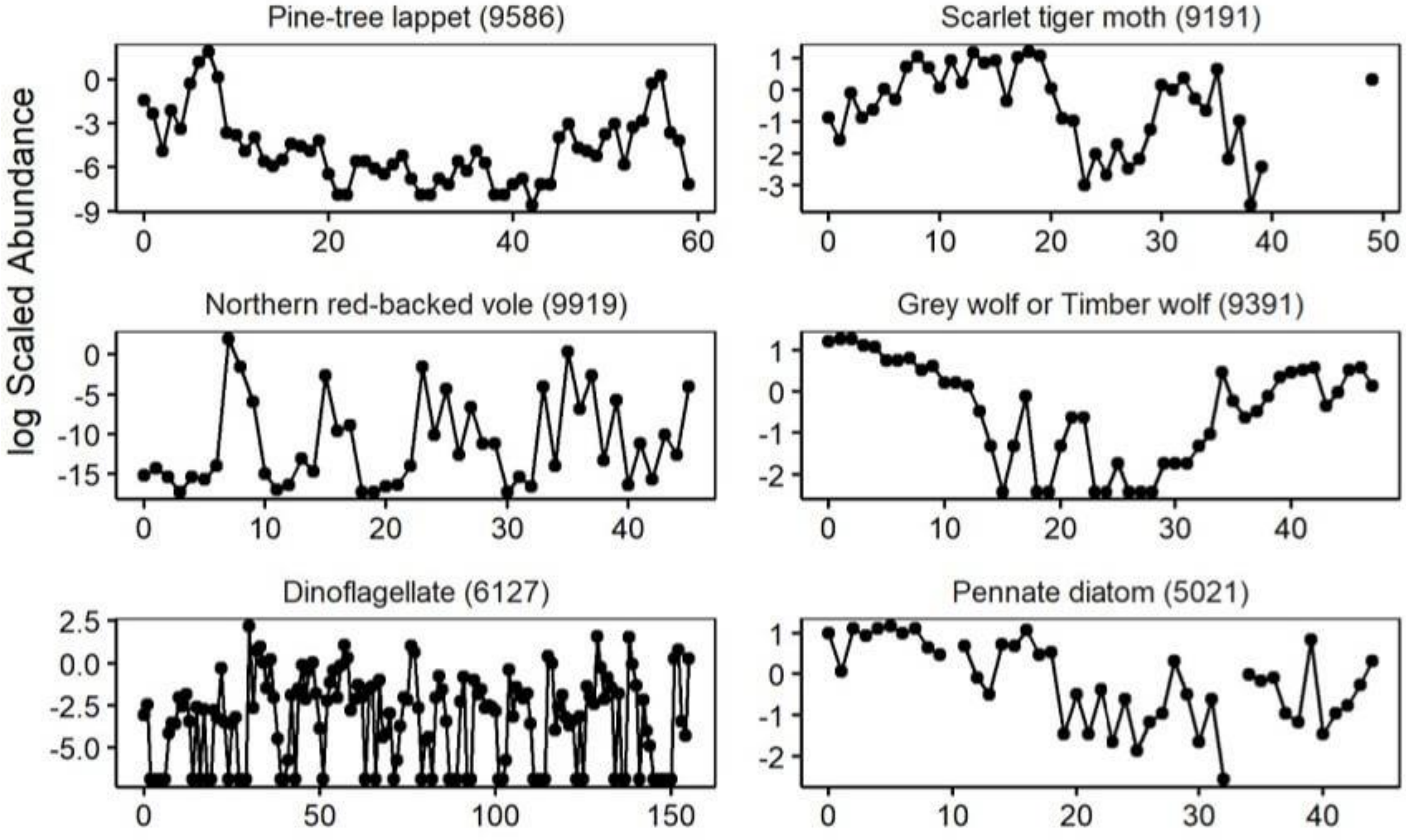
Chaos in ecology is more common than you think

We find evidence for chaos in over 30% of time series in an ecological database using updated, flexible, and rigorously tested algorithms. Lack of evidence for chaos in prior meta-analyses is likely the result of methodological and data limitations, rather than inherent stability.

Published in Ecology & Evolution
Jun 27, 2022

Tanya Rogers
Research Fish Biologist, NOAA Fisheries

Dynamics: chaotic non-chaotic



Rogers et al., Nature Ecol & Evol 2022

Summary of the 1-body problem (1 species)

Population dynamics of an « isolated » species can be described:

- In continuous-time, in which case it **will** converge to an equilibrium

  -> The dynamics of the system can be predicted

- In discrete-time, in which case it can
  - Converge to an equilibrium
  - Fluctuate periodically
  - Fluctuate chaotically

  -> The dynamics of the system can be unpredictable!

2. Two-body problem (two species)

Prey-predator model – continuous-time

- Prey density: $N(t)$
- Predator density: $P(t)$
- Prey reproductive rate: r
- Prey mortality rate due to predation: $aP(t)$
- Predator reproduction rate: $bN(t)$
- Predator mortality rate: m

- System of differential eq.:

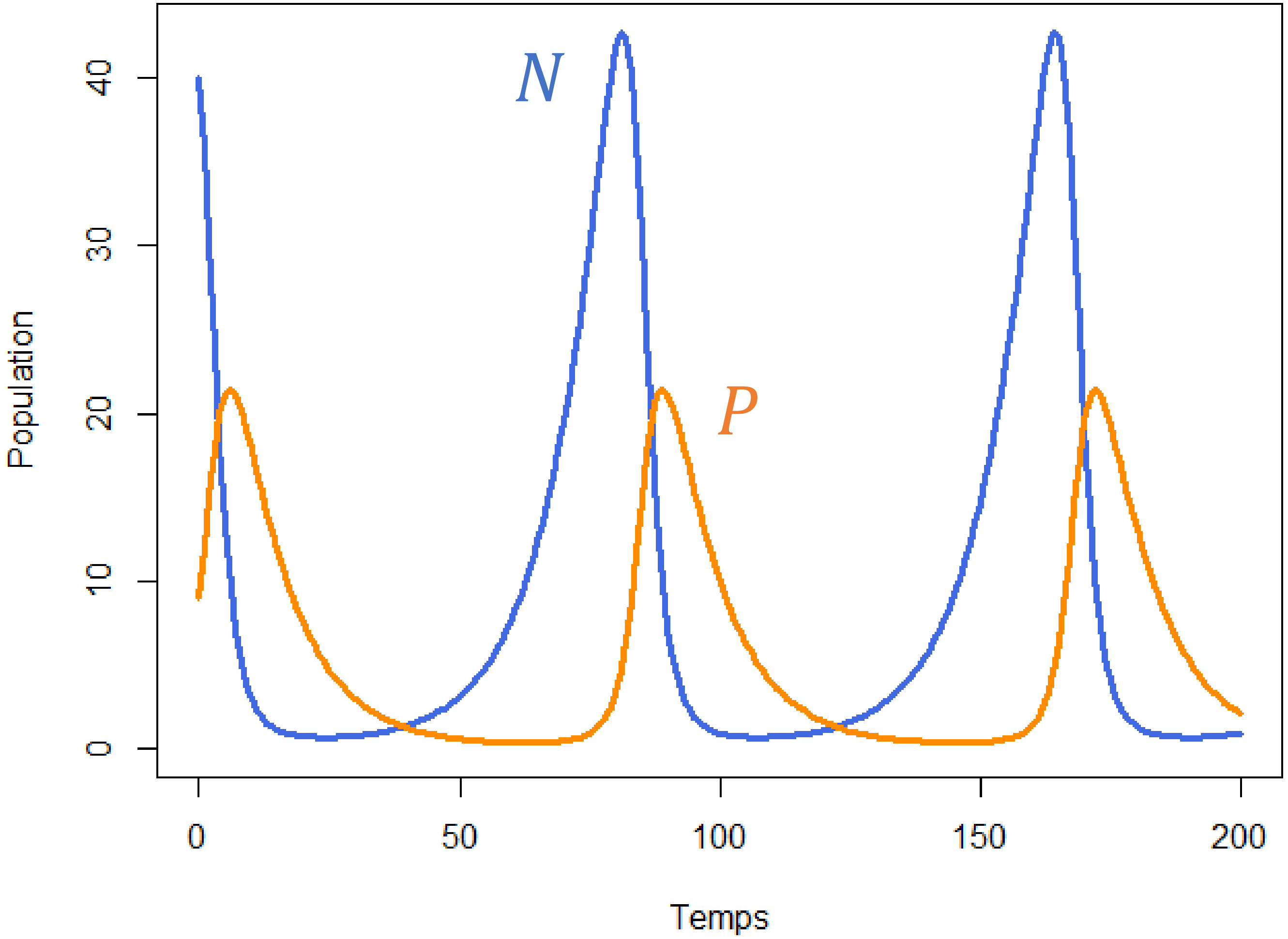
$$\begin{cases} \dfrac{dN}{dt}(t) = rN(t) - aP(t)N(t) \\ \dfrac{dP}{dt}(t) = bP(t)N(t) - mP(t) \end{cases}$$

- No explicit solution
- Model due to

Lotka (1925) Elements of Physical Biology.

Volterra (1926) Variazioni e fluttuazioni del numero d'individui in specie animali conviventi.

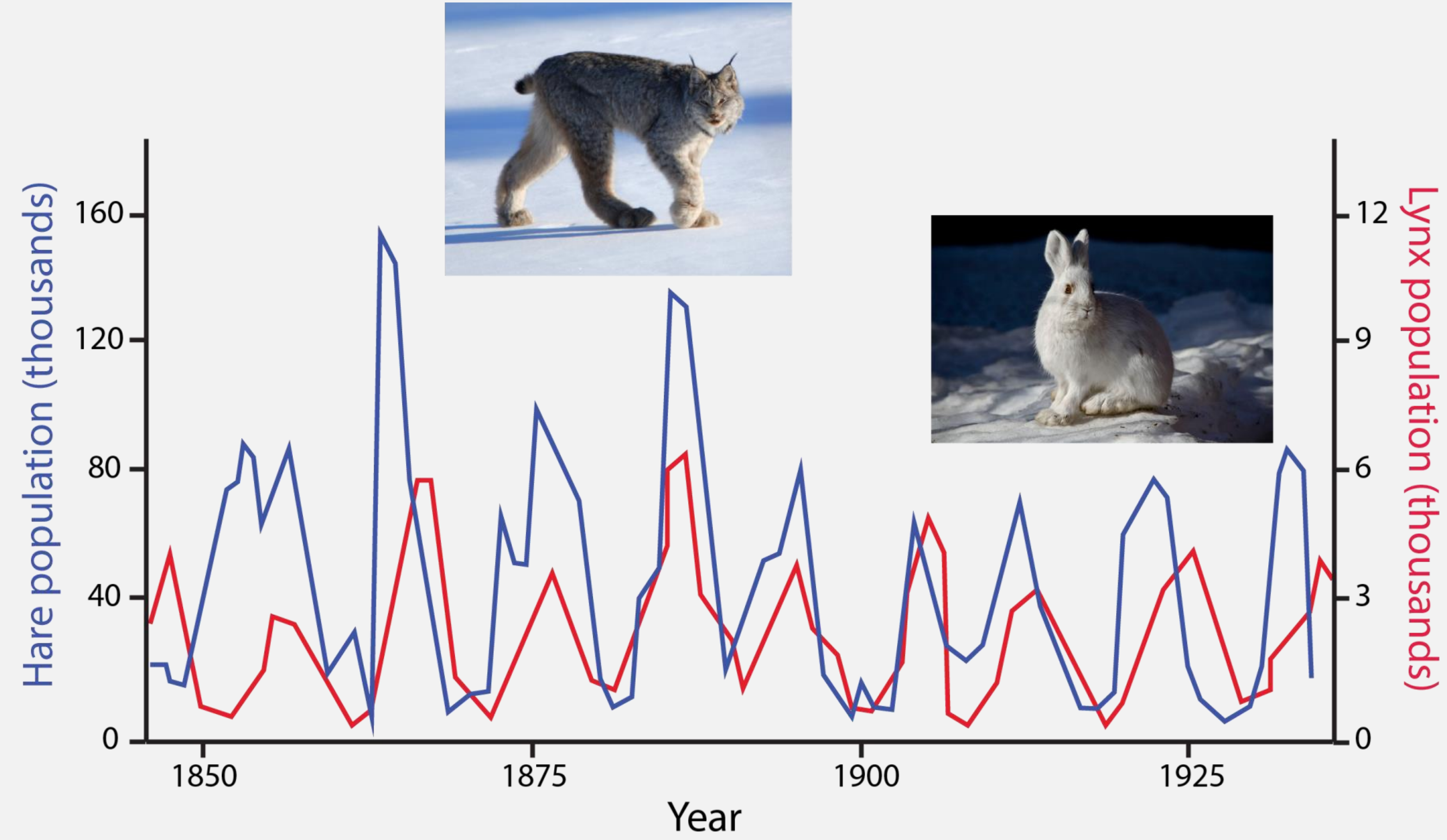
Prey-predator dynamics



Prey-predator interactions lead to periodic oscillations

The predator population regulates the prey pop., and conversely

Lynx and hare example in Canada



Host-parasitoid model – discrete-time

- Host density: $N(t)$
- Parasitoid density: $P(t)$
- Host reproductive number: R
- Host mortality due to parasitism: $aP(t)$
- Parasitoid number from infected host: b

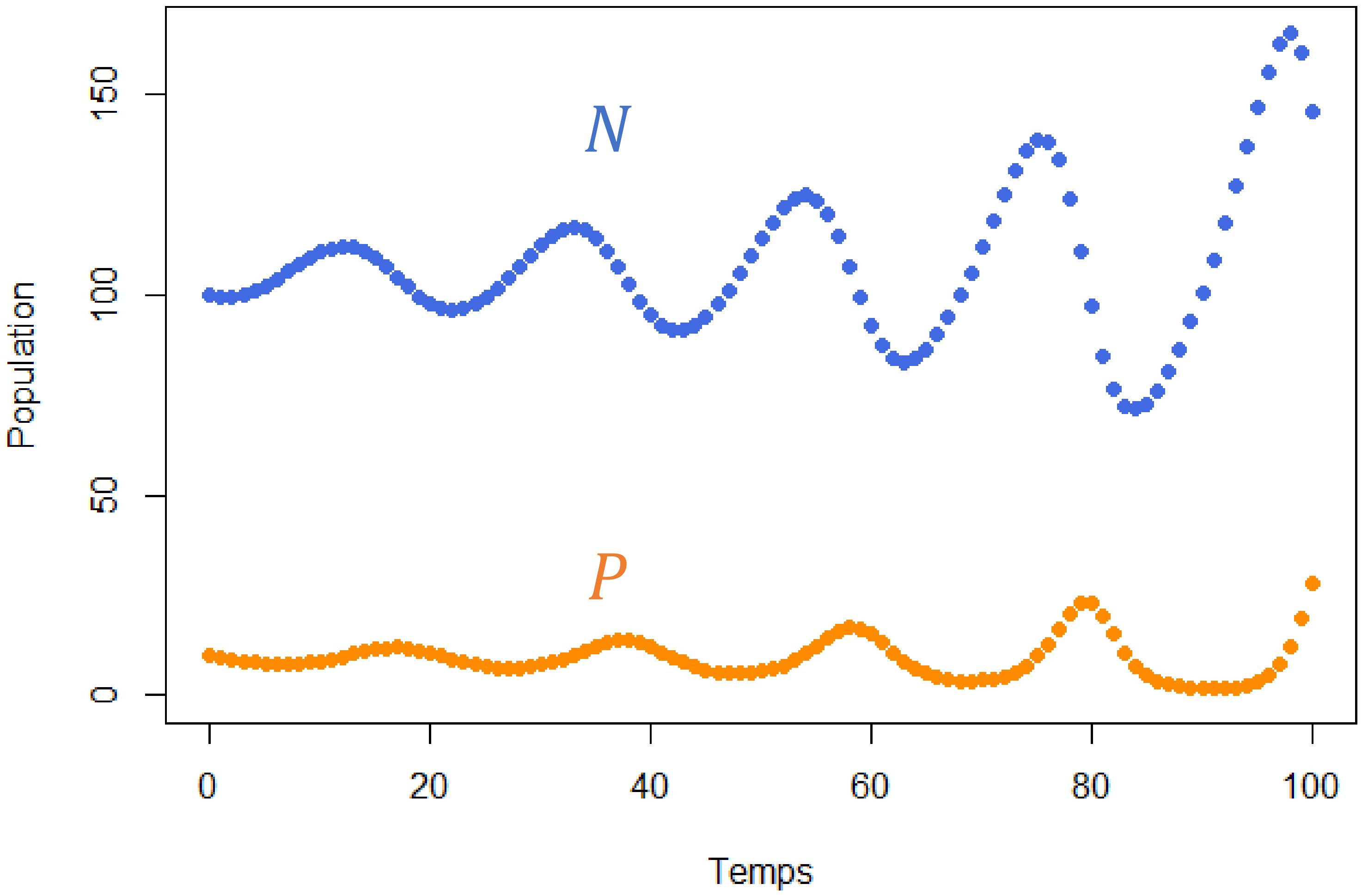
- Recurrence eq. system:

$$\begin{cases} N(t+1) = RN(t)e^{-aP(t)} \\ P(t+1) = bN(t)\left(1 - e^{-aP(t)}\right) \end{cases}$$

- No explicit solution
- Model due to

Nicholson & Bailey (1935) The Balance of Animal Populations. Part I. Proceedings of the Zoological Society of London

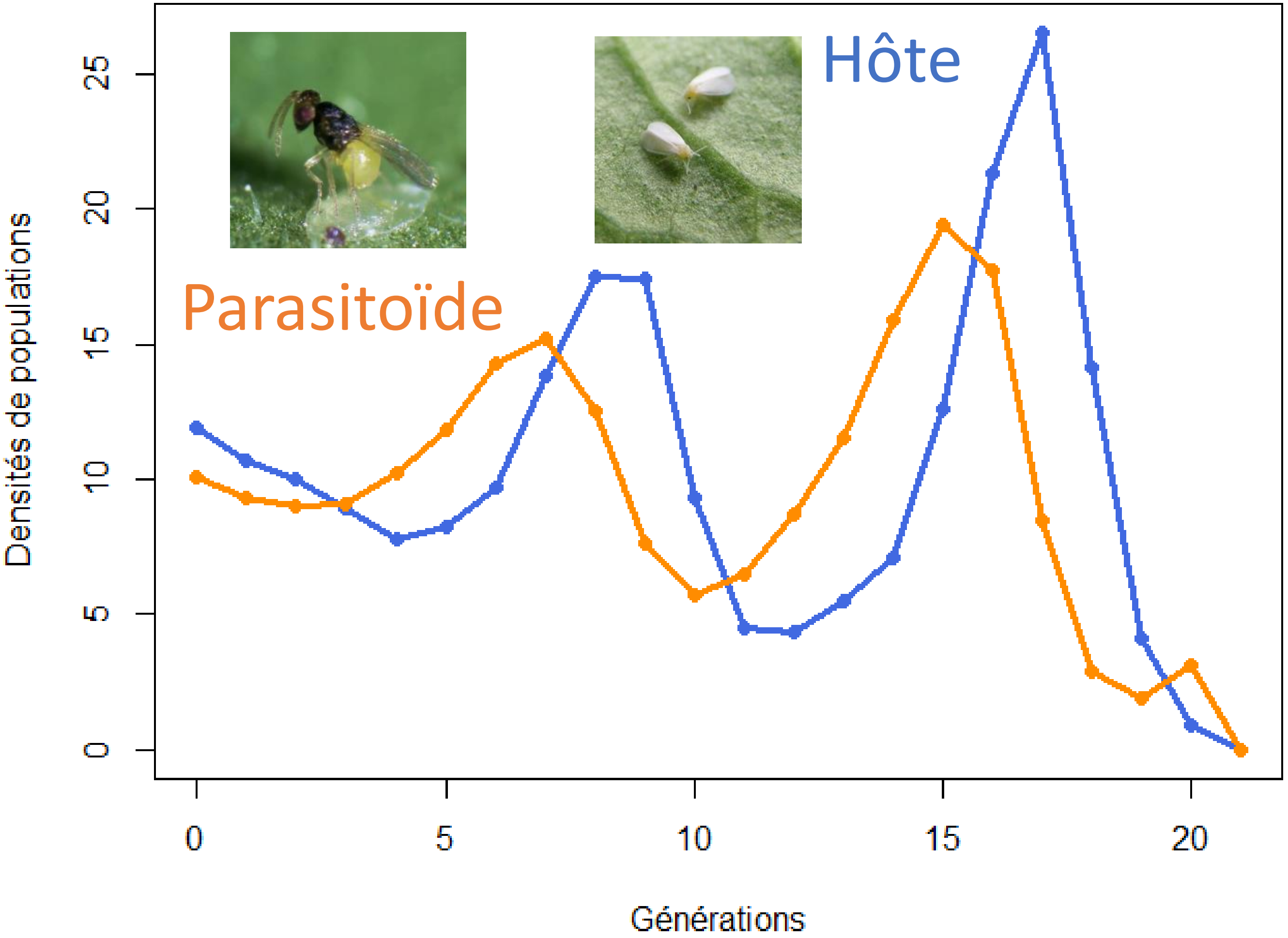
Host-parasitoid dynamics



Host-parasitoid interactions generate oscillations of ever-increasing magnitude

Nicholson-Bailey's model is not biologically well posed in the long run

Burnett (1958)'s experience

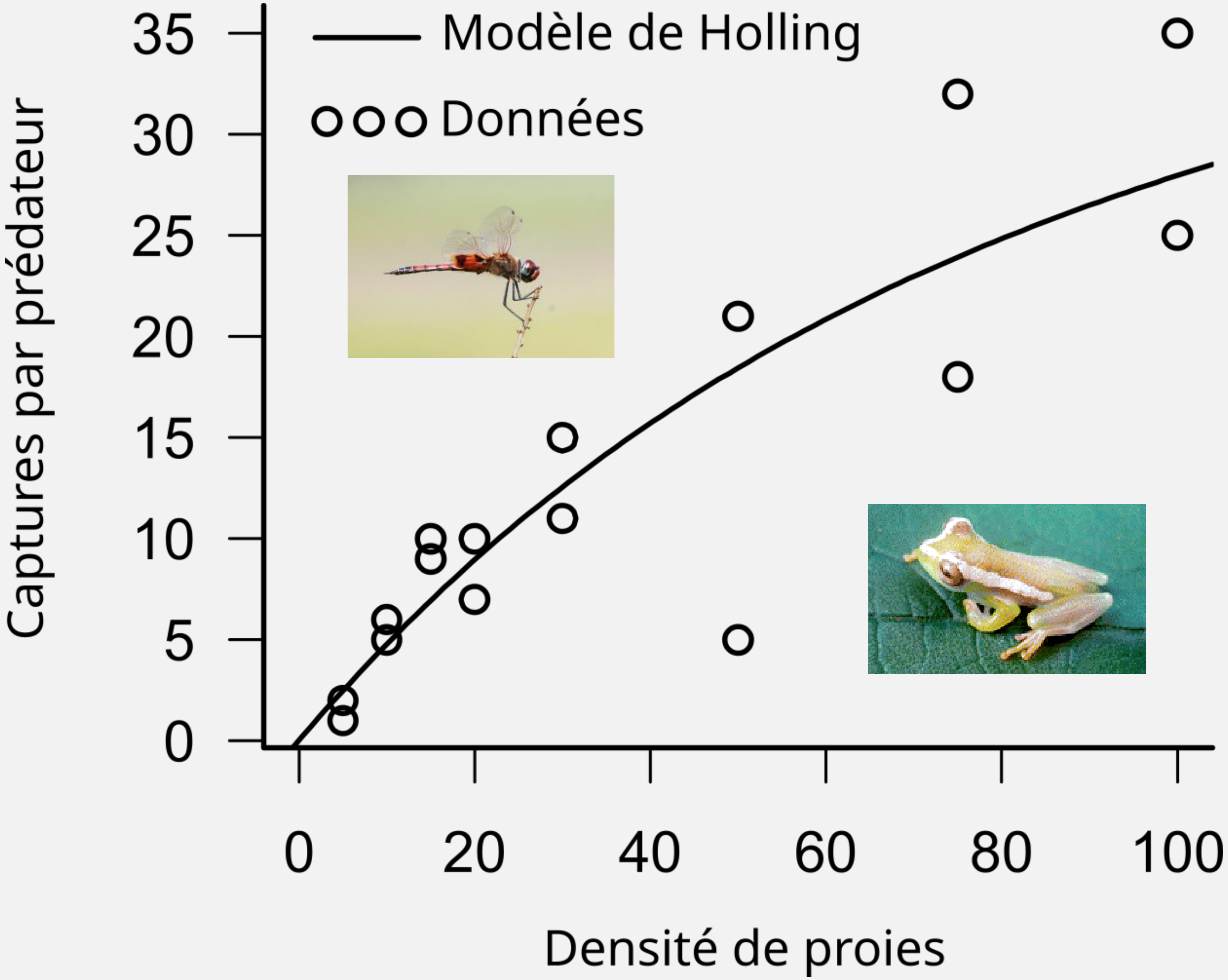


Experimental data with the whitefly *Trialeurodes vaporariorum* and its parasitoid *Encarsia formosa*.

The dynamics qualitatively correspond to those of the Nicholson-Bailey's model

Burnett, (1958) A model of host-parasite interaction. In Proceedings of the 10th International Congress of Entomology

Holling's functional response



The number of prey caught per predator tends to saturate with increasing prey density

Functional response:

$$f(N) = \frac{aN}{1 + ahN}$$

Holling (1965) The functional response of predators to prey density. Entomological Society of Canada

Bolker (2008) Ecological models and data in R

Prey-predator model – continuous-time (2)

- Logistic growth of the prey
- Predator « saturation » - prey number per predator per unit time:

$$f(N) = \frac{aN}{1+ahN}$$

- Predator attack rate: a
- Prey handling rate by predator: h
- Prey to predator conversion coefficient: e

- Differential eq. system:

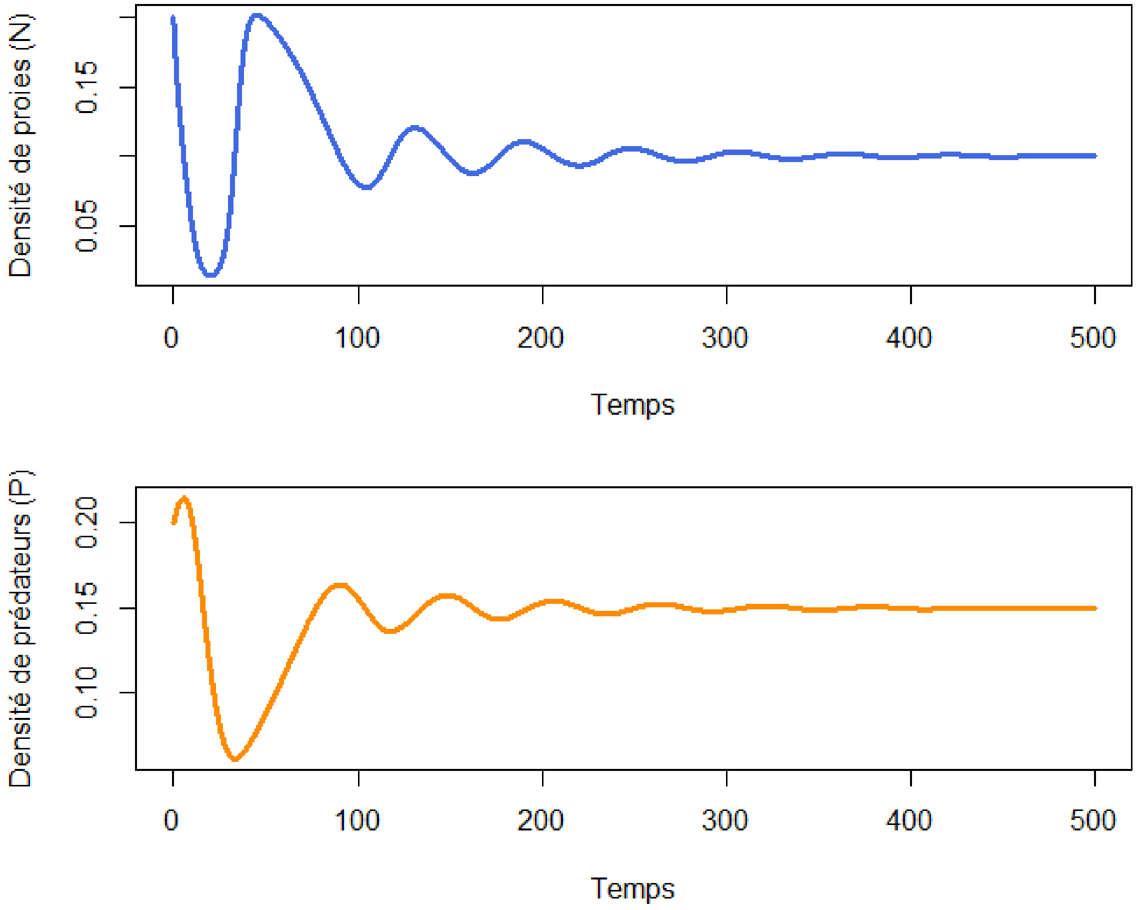
$$\begin{cases} \dfrac{dN}{dt} = rN\left(1 - \dfrac{N}{K}\right) - \dfrac{aPN}{1 + ahN} \\ \dfrac{dP}{dt} = e\,\dfrac{aPN}{1 + ahN} - mP \end{cases}$$

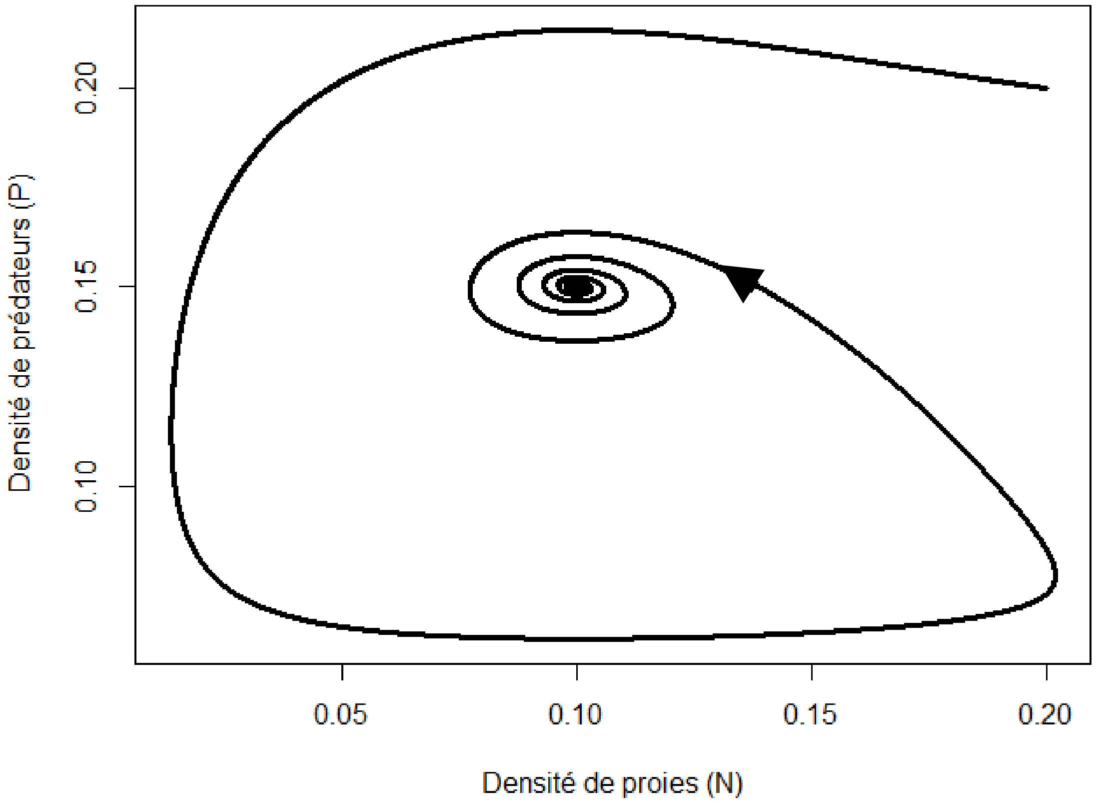
- No explicit solution
- Model due to

Rosenzweig & MacArthur (1963) Graphical representation and stability conditions of predator-prey interactions. The American Naturalist

Dumped oscillations – converging spiral

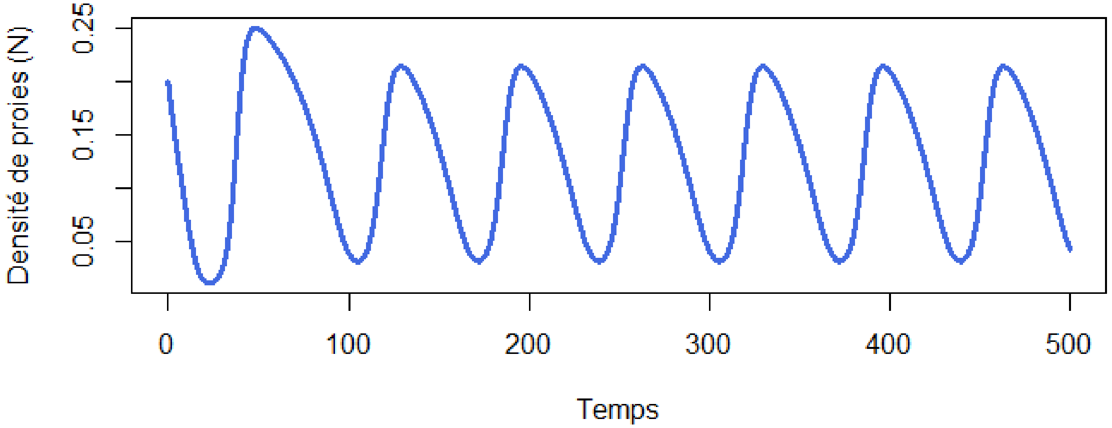
$r = 0.5, \boldsymbol{K = 0.25}, a = 5, h = 3, e = 0.5, m = 0{,}1$

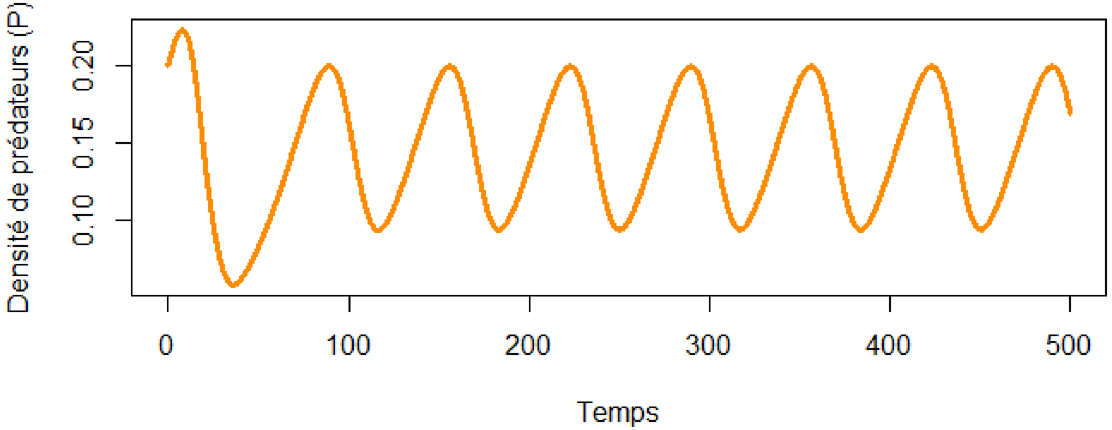


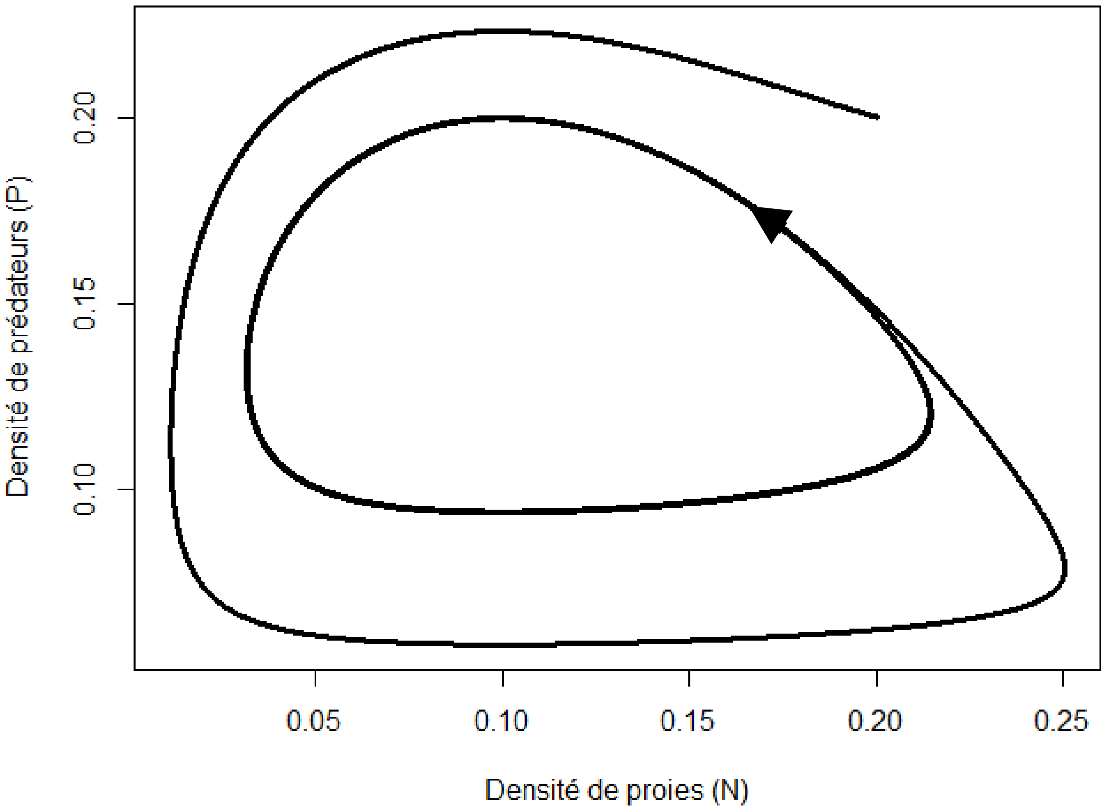


Sustained oscillations – limit cycle

$r = 0.5, \boldsymbol{K = 0.30}, a = 5, h = 3, e = 0.5, m = 0{,}1$







Host-parasitoid model – discrete time

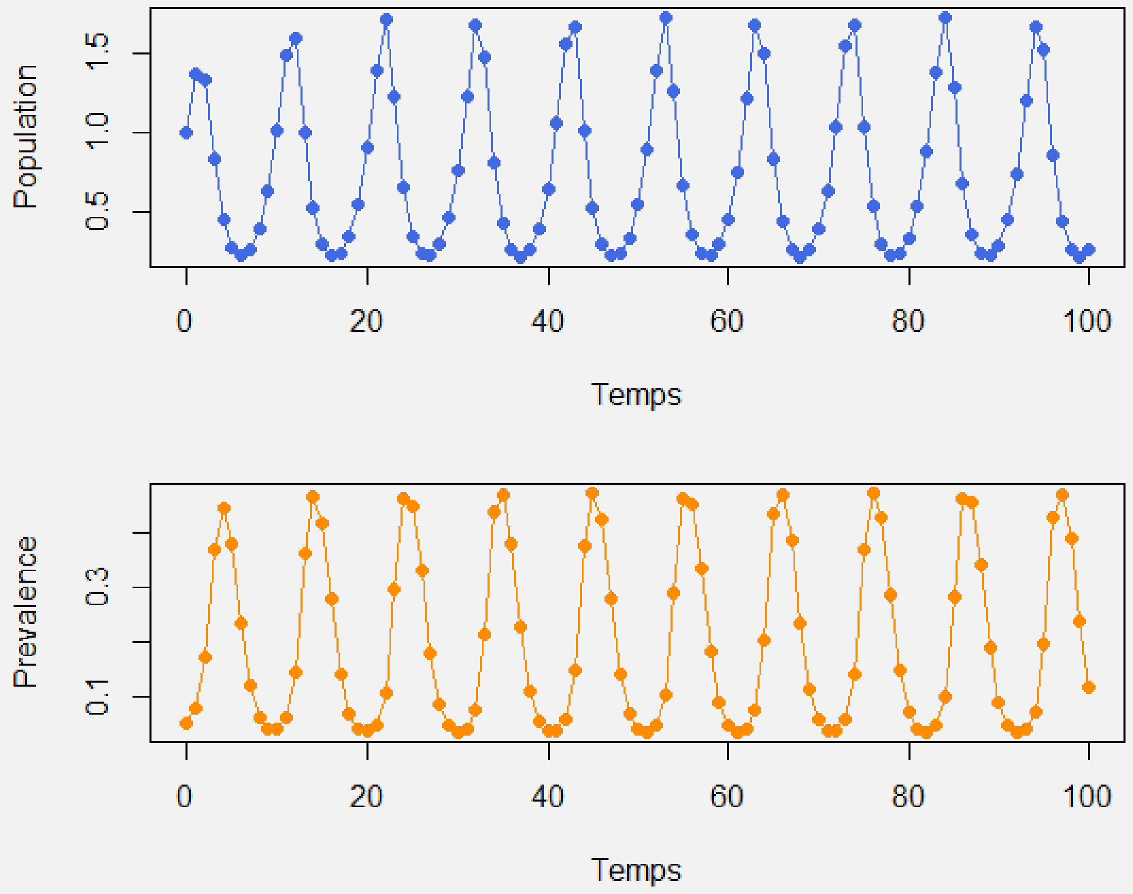
- Susceptible and infected host densities: $S(t)$ et $I(t)$
- Susceptible and infected host reproduction: b_S et b_I
- Force of infection: $aI(t)$
- Probability of parasite vertical transmission: p
- Recurrence eq. system:

$$\begin{cases} S(t+1) = b_S S(t) e^{-aI(t)} + (1-p) b_I \left(I(t) + S(t)\left(1 - e^{-aI(t)}\right)\right) \\ I(t+1) = p b_I \left(I(t) + S(t)\left(1 - e^{-aI(t)}\right)\right) \end{cases}$$

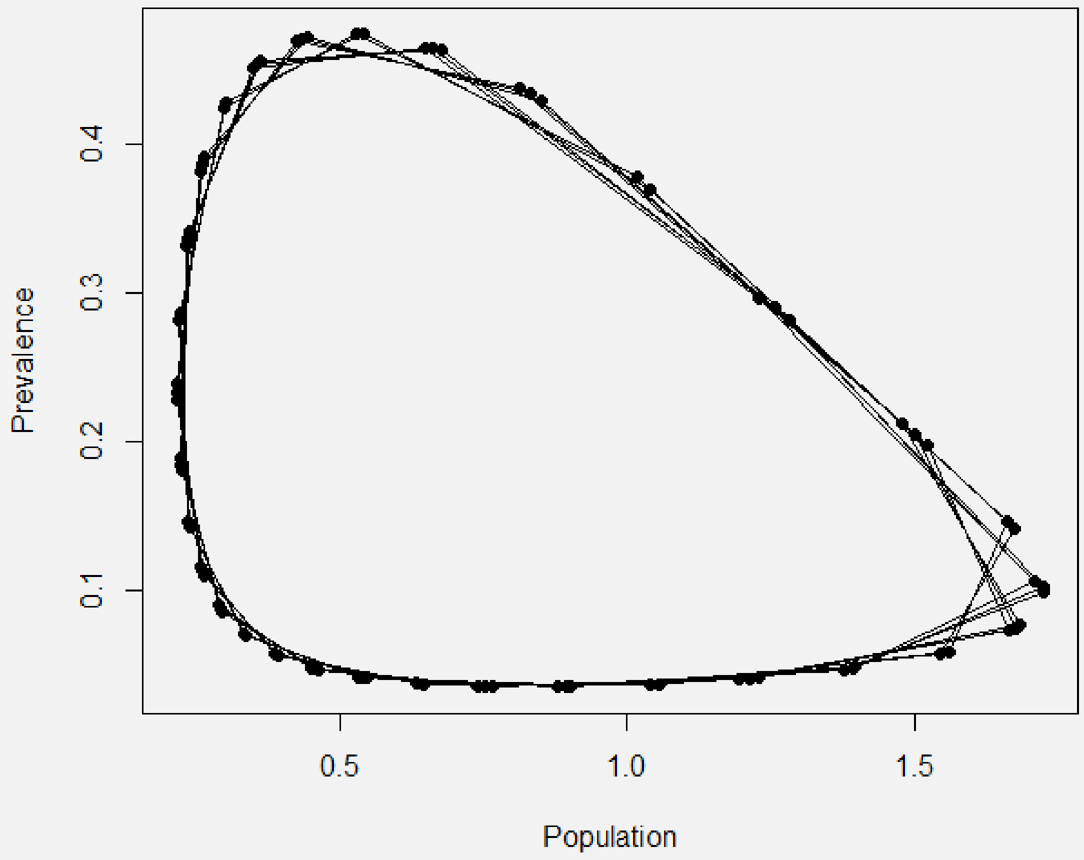
- Model due to

Hilker, Sun, Allen, Hamelin (2020). Separate seasons of infection and reproduction can lead to multi-year population cycles. *Journal of theoretical biology*.

Host parasitoid model – discrete time



« limit cycle » in discrete time

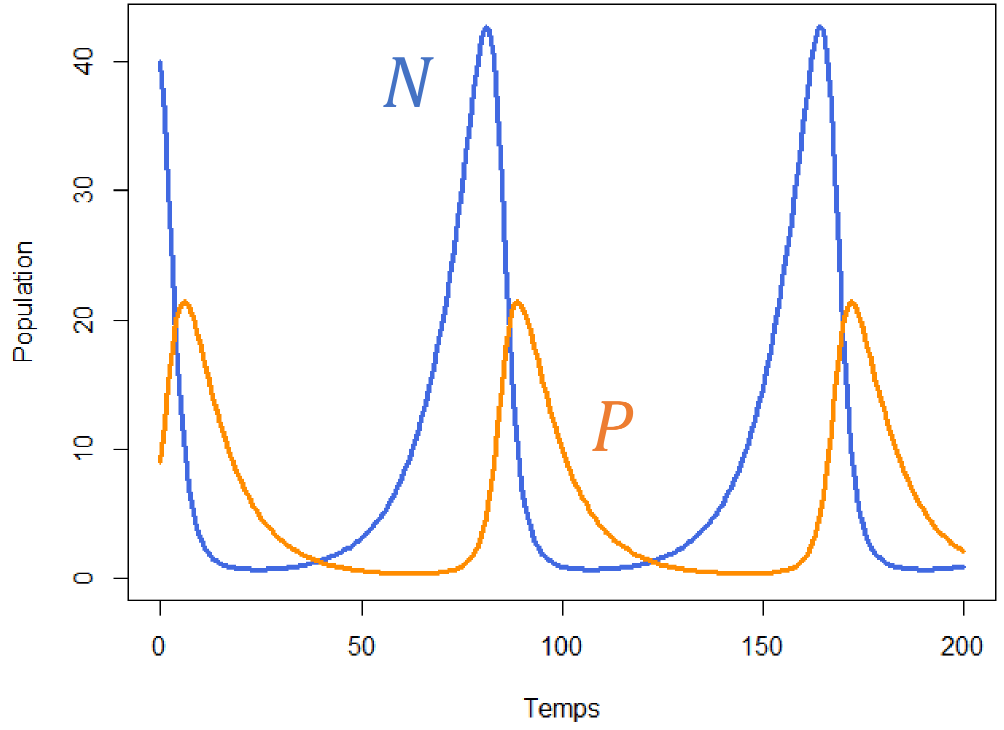


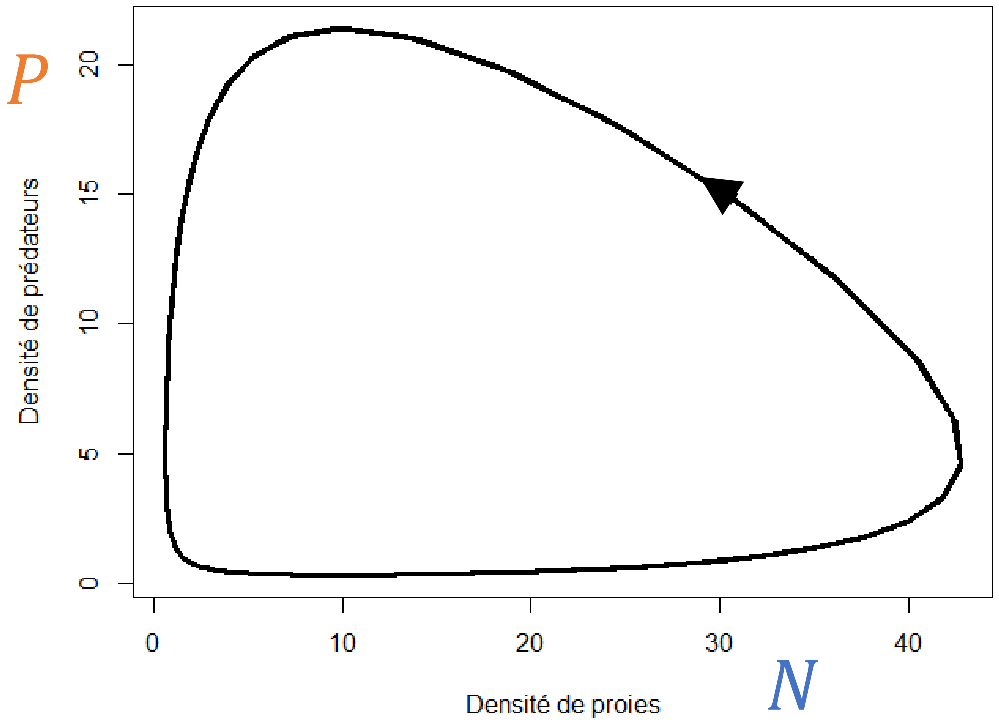
Hilker, Sun, Allen, Hamelin (2020). Separate seasons of infection and reproduction can lead to multi-year population cycles. *Journal of theoretical biology*.

Summary of the 2-body problem (2 species)

Periodic oscillations can occur in continuous-time

(We already knew it was possible in discrete-time for 1 species)





3. The three-body problem (three species)

3-species competition

- Species densities: N_1, N_2, N_3
- Intrinsic growth rate: r
- Carrying capacity: K
- Competition coefficients: α, β
- Rock-paper-scissor type competition:

$$\begin{bmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{bmatrix}$$

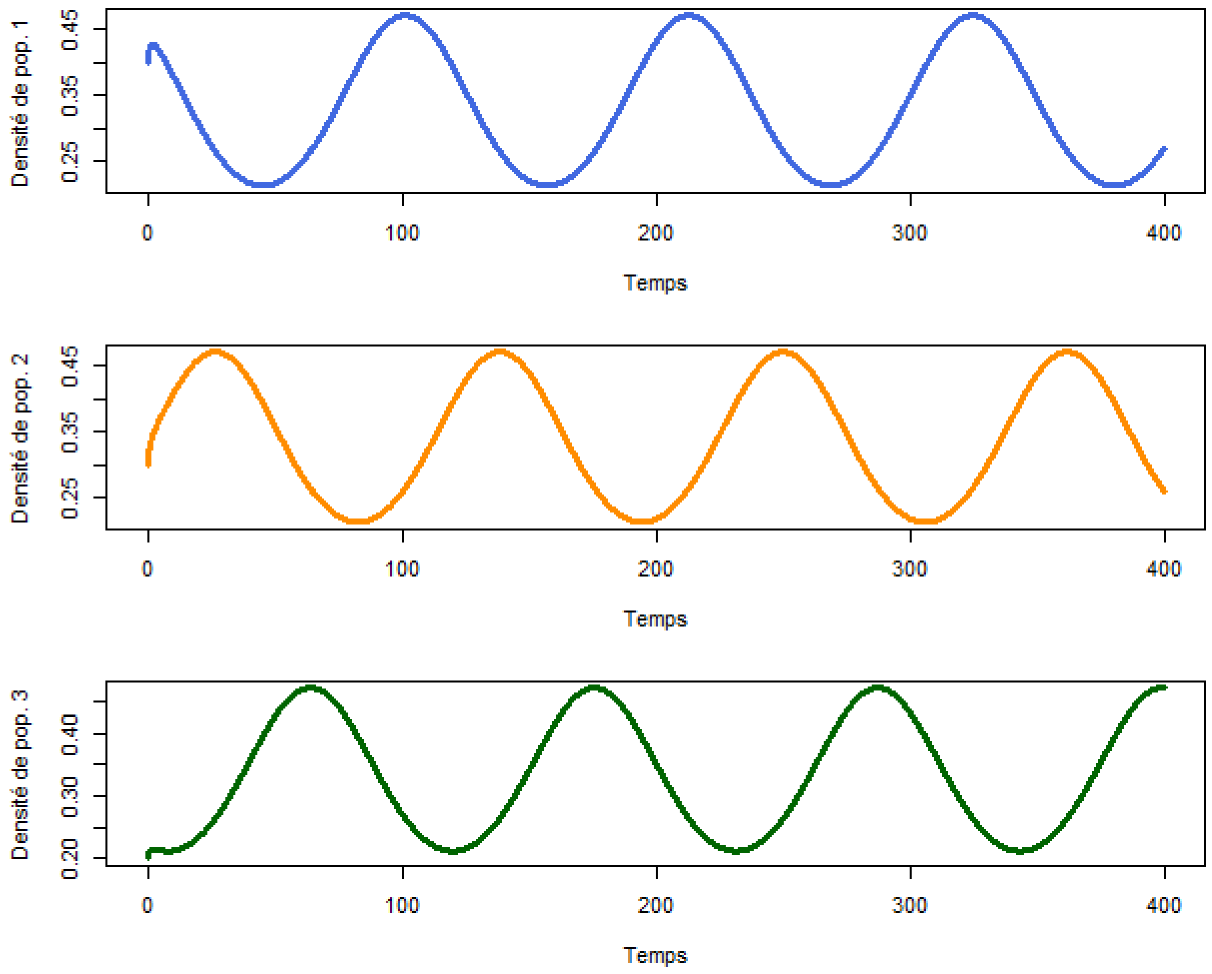
- Differential eq. system:

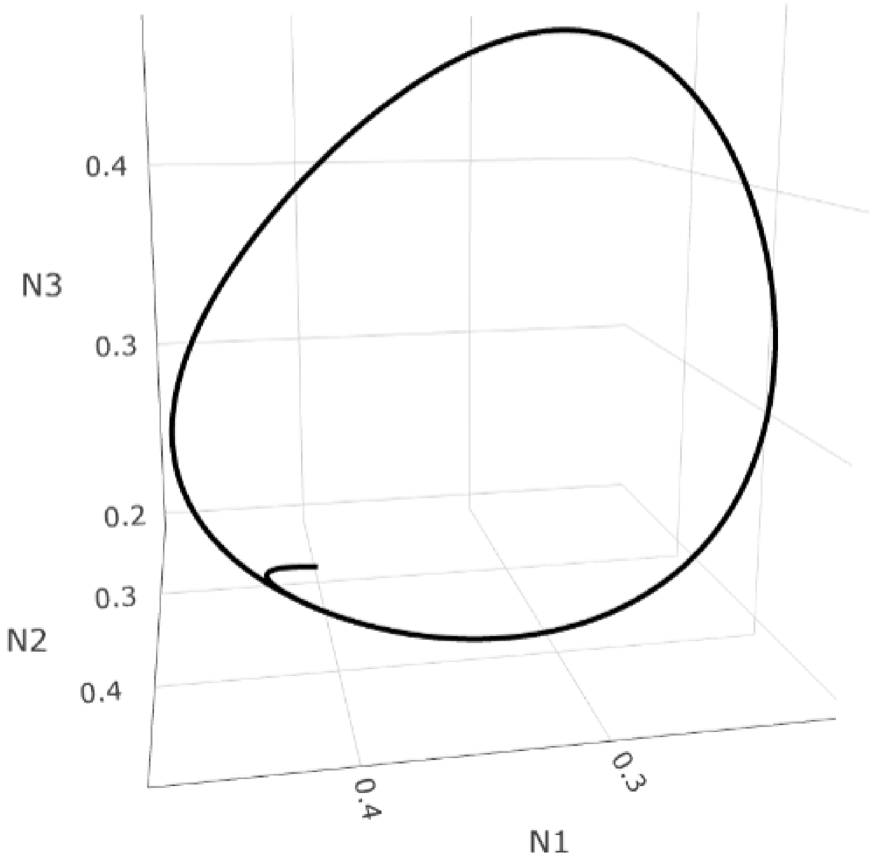
$$\begin{cases} \dfrac{dN_1}{dt} = rN_1\left(1 - \dfrac{N_1 + \alpha N_2 + \beta N_3}{K}\right) \\ \dfrac{dN_2}{dt} = rN_2\left(1 - \dfrac{\beta N_1 + N_2 + \alpha N_3}{K}\right) \\ \dfrac{dN_3}{dt} = rN_3\left(1 - \dfrac{\alpha N_1 + \beta N_2 + N_3}{K}\right) \end{cases}$$

- Model due to

May & Leonard (1975). Nonlinear aspects of competition between three species. *SIAM journal on applied mathematics*

Rock-paper-scissor type dynamics





3-species trophic chain

- Prey density: N
- Predator density: P
- Super-predator density: S
- Prey reproductive rate: r
- Prey carrying capacity: K
- Predation: $\frac{a_1 RC}{1+b_1 R}$
- Super-predation: $\frac{a_2 CP}{1+b_2 C}$
- Mortality of P, S : d_1, d_2

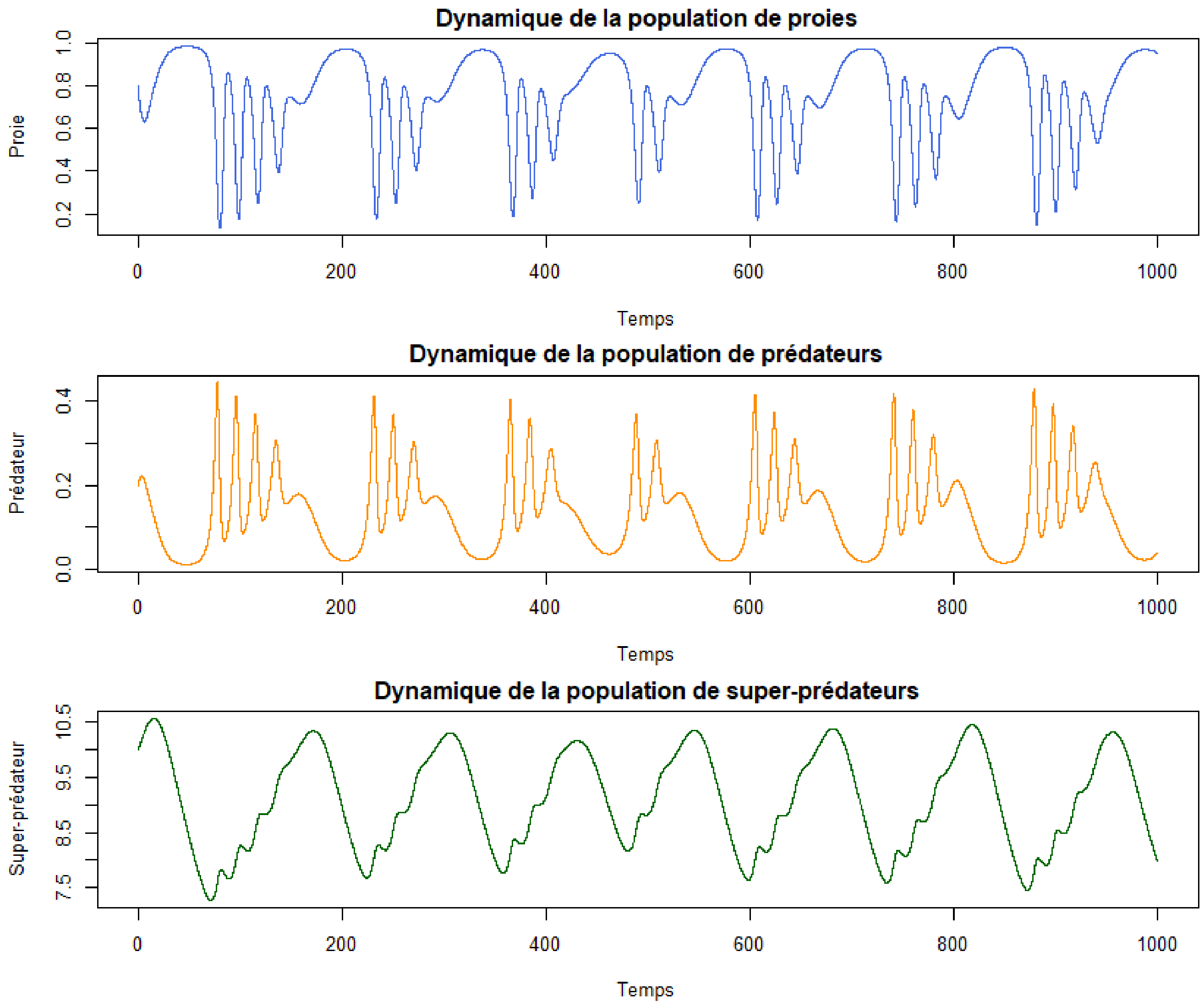
- Differential eq. system:

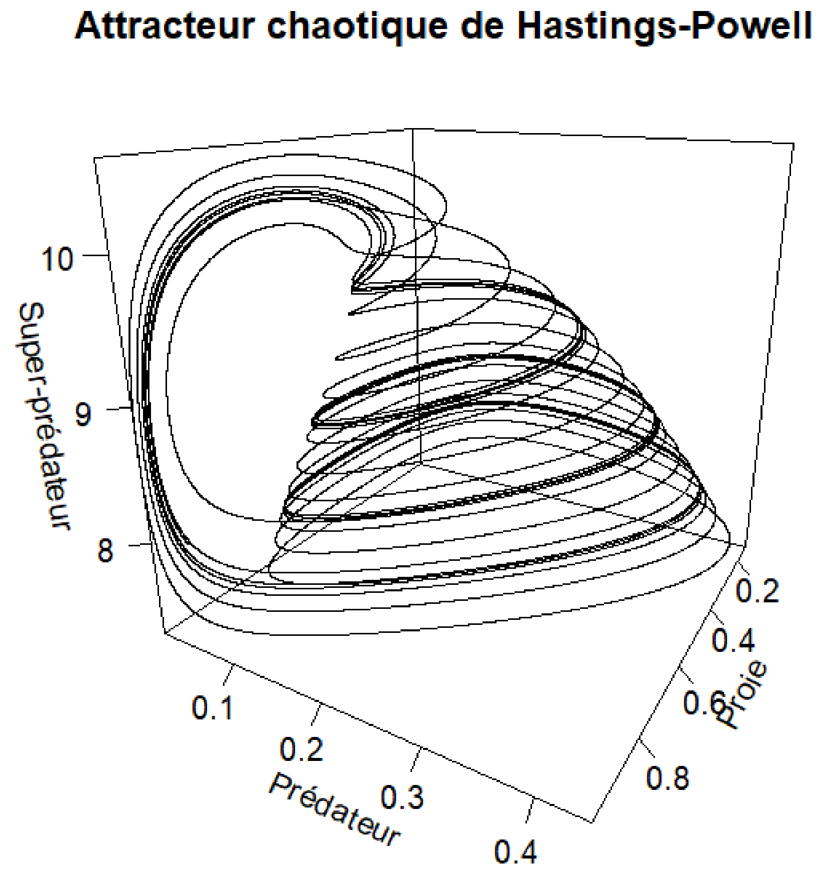
$$\begin{cases} \frac{dN}{dt} = rR\left(1 - \frac{R}{K}\right) - \frac{a_1 NP}{1 + b_1 N} \\ \frac{dP}{dt} = c_1 \frac{a_1 NP}{1 + b_1 N} - \frac{a_2 PS}{1 + b_2 P} - d_1 P \\ \frac{dS}{dt} = c_2 \frac{a_2 PS}{1 + b_2 P} - d_2 S \end{cases}$$

- Model due to

Hastings & Powell (1991) Chaos in a three-species food chain. *Ecology*.

Prey-predator-superpredator dynamics

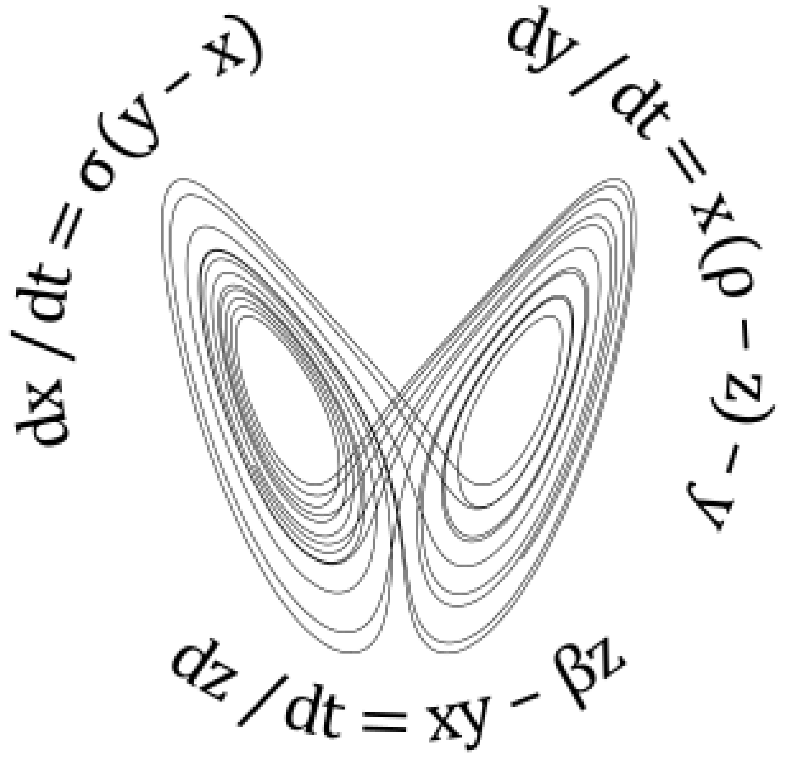




Summary of the 3-body problem (3 species)

Chaotic fluctuations can occur in continuous-time

(We knew that was possible in discrete-time already for 1 species)



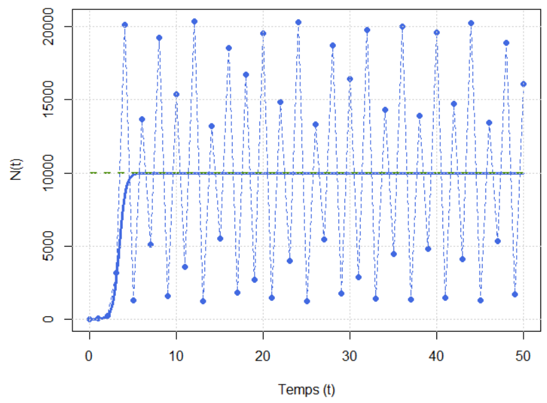
Strange attractor

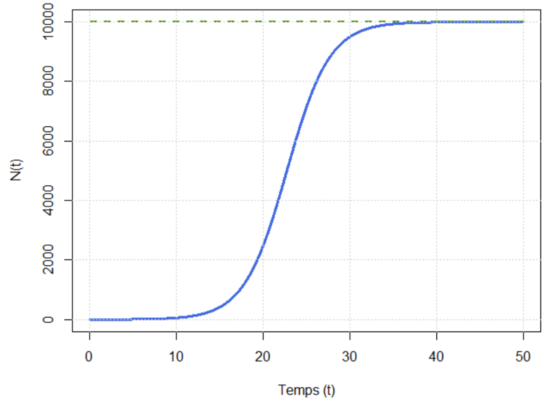
Butterfly effect : great sensitivity to initial conditions

Ecological dynamics impossible to predict

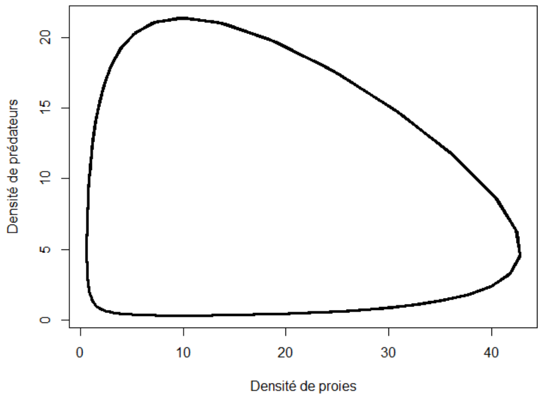
Summary

- In discrete-time (non-overlapping generations), dynamics can be unpredictable (chaotic) from dimension 1
- In continuous-time (overlapping generations), dynamics can be unpredictable (chaotic) from dimension 3

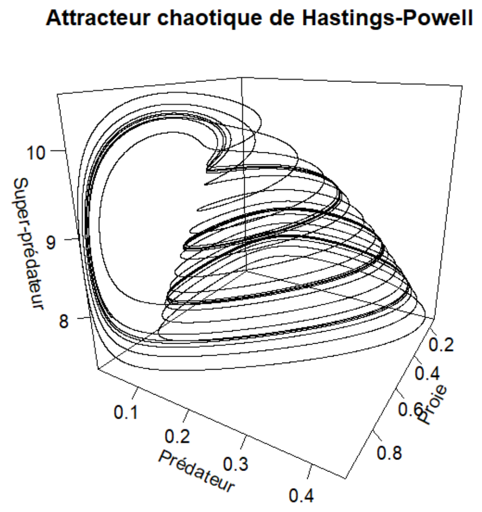




1D

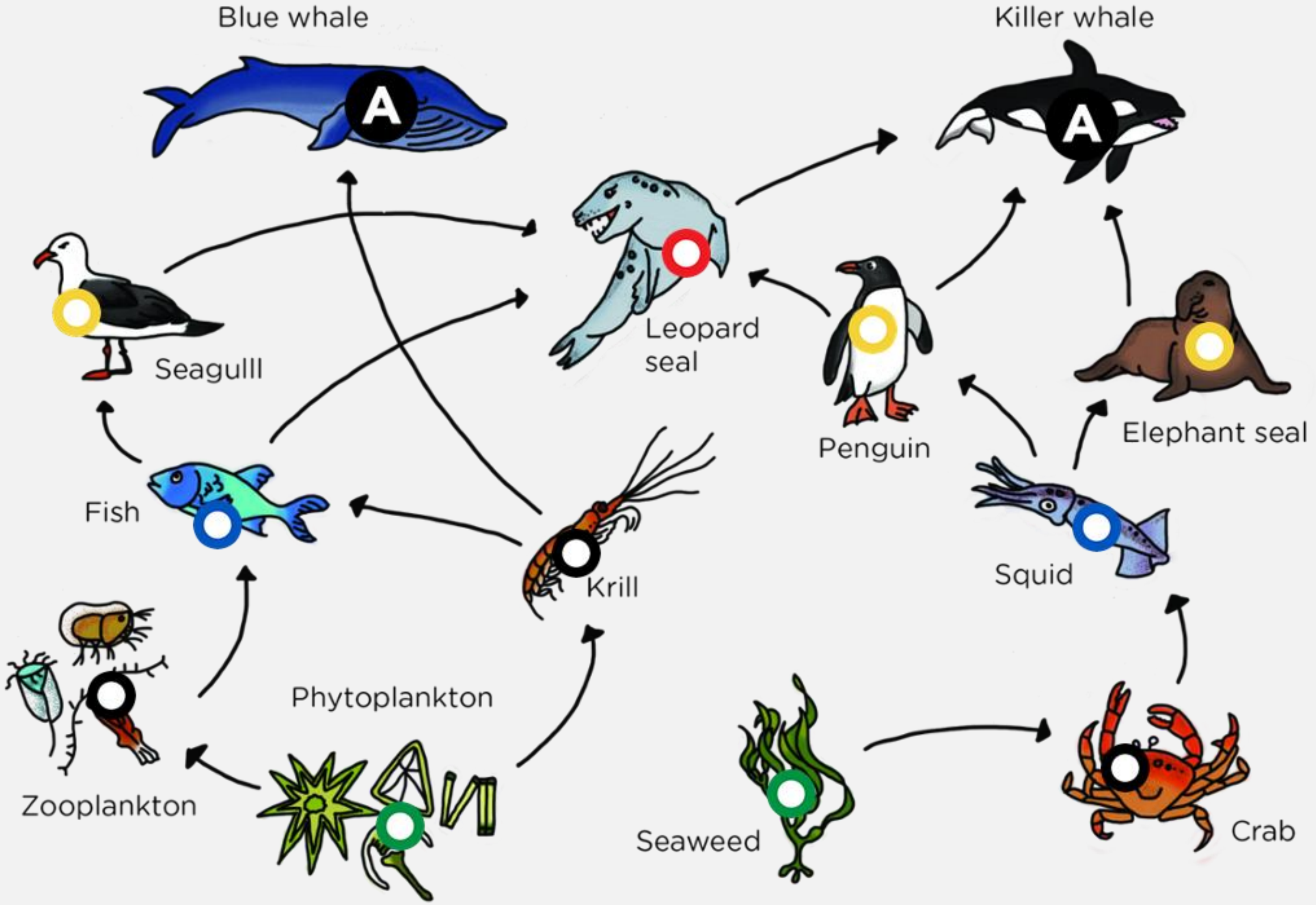


2D



3D

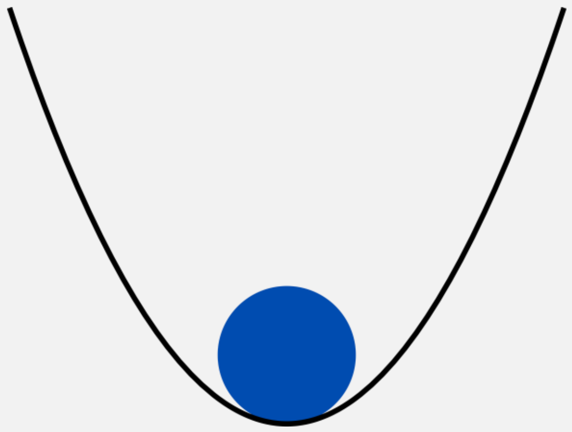
In ecology, dimension 3 is relatively low

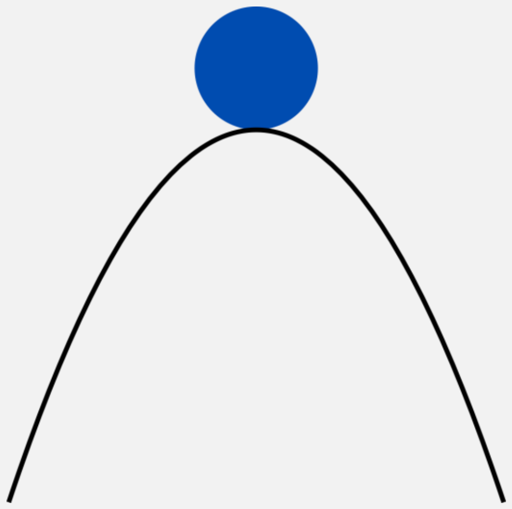


Notions of equilibrium and stability

Equilibrium

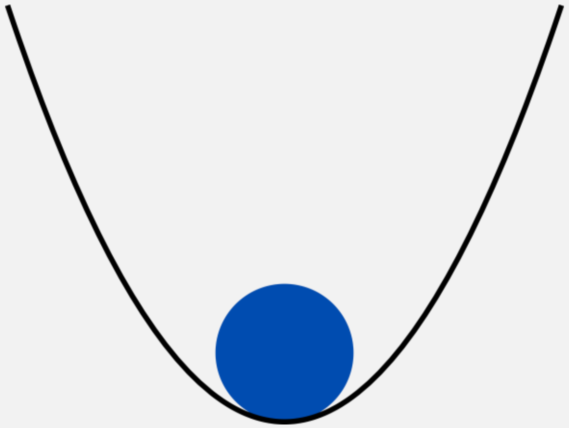
If starting from that state the dynamics stay in that state

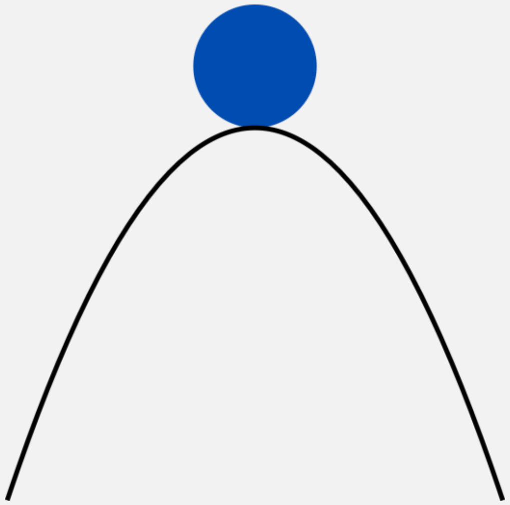




Stability

Stability of an equilibrium: the fact that the dynamics get back to equilibrium after a small perturbation





Unstability of an equilibrium: the fact that the dynamics goes away from that equilibrium after a small pertubation

1. Dimension 1

Equilibrium – dimension 1 – continuous time

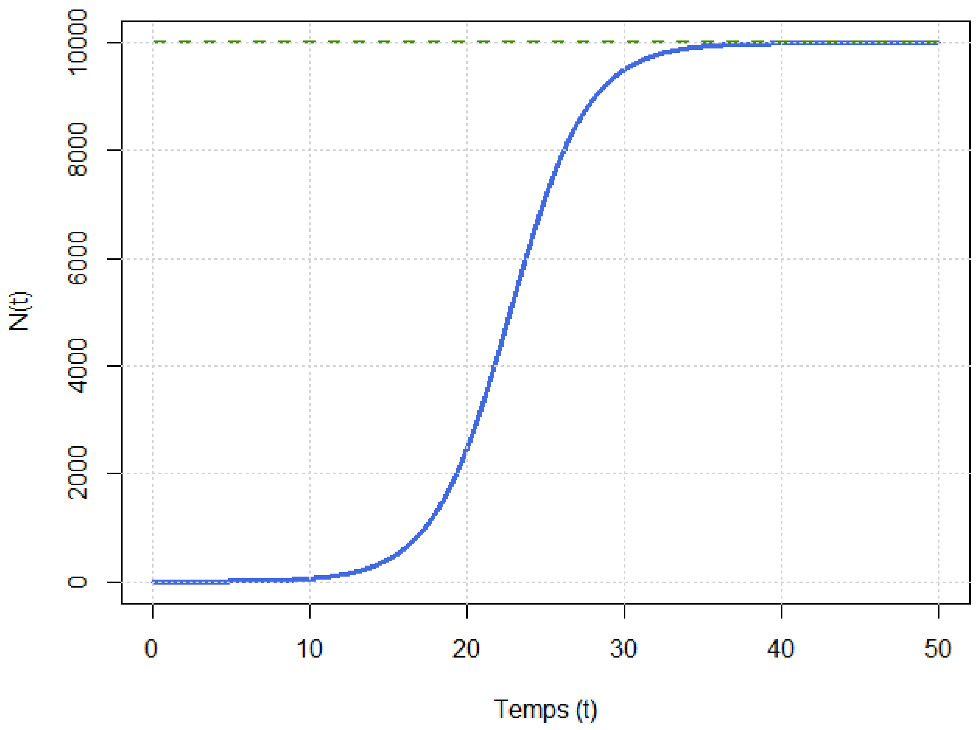
- General form of pop. dyn.:

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

- **Equilibrium**: any pop. size $\bar{N}$ for which pop. size does not vary:

$$\frac{dN}{dt} = f(\bar{N}) = 0$$

- In words: if pop. has size $\bar{N}$, it remains of size $\bar{N}$

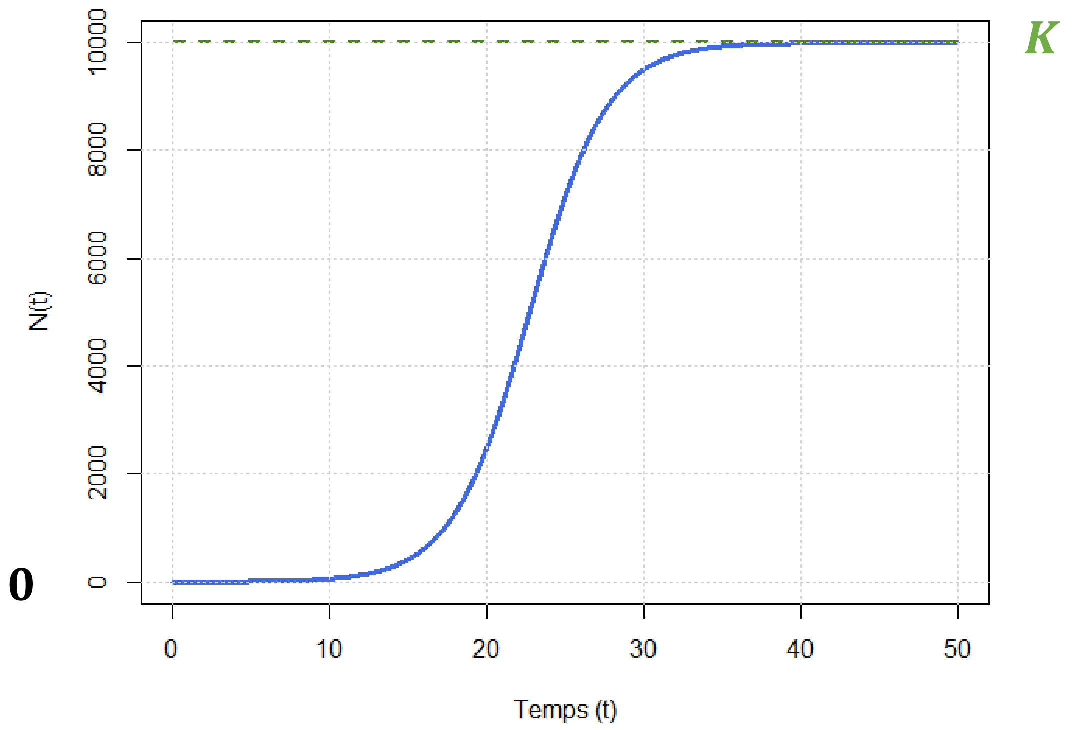


Equilibrim – dimension 1 – continuous time

- Ex.: logistic model

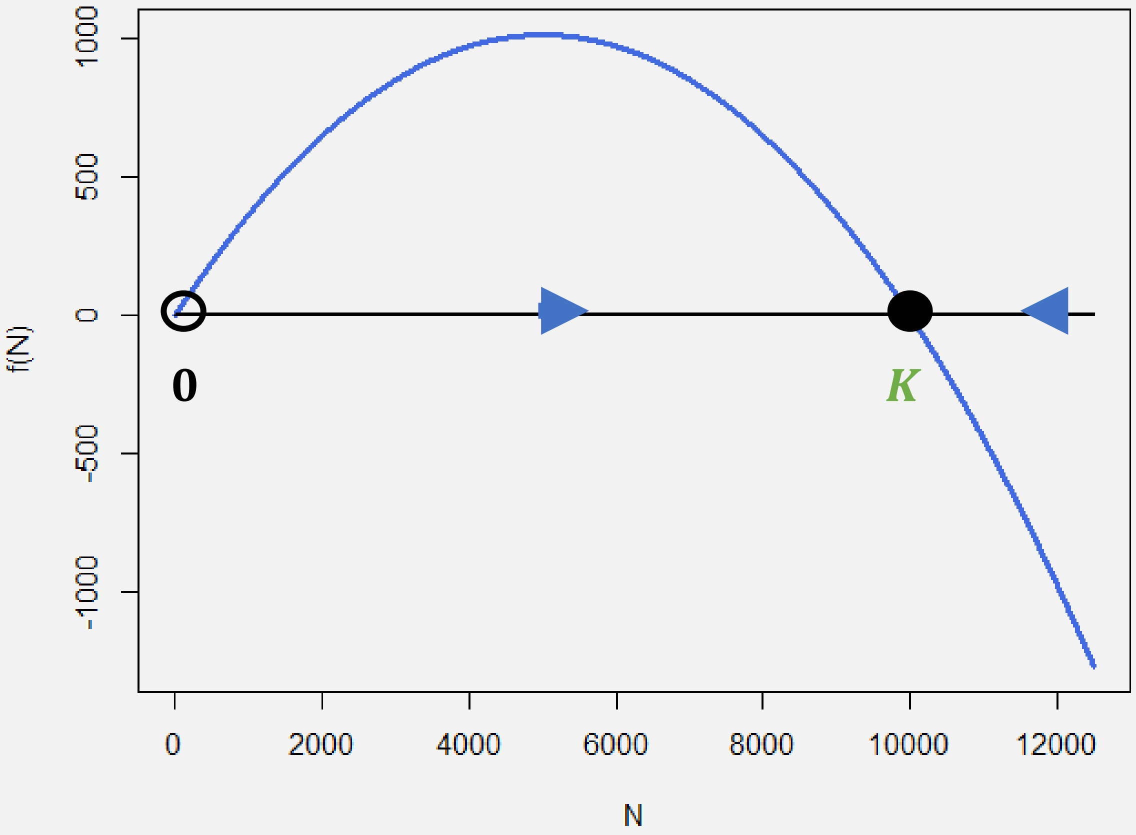
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

- **Two equilibria:**
  - Species absent: $\bar{N} = 0$
  - Sp. at carrying capacity: $\bar{N} = K$
- Remark: $N = 0$ is always an équilibrium in Biology (no spontaneous generation)



Stability of equilibria – 1D – continuous time

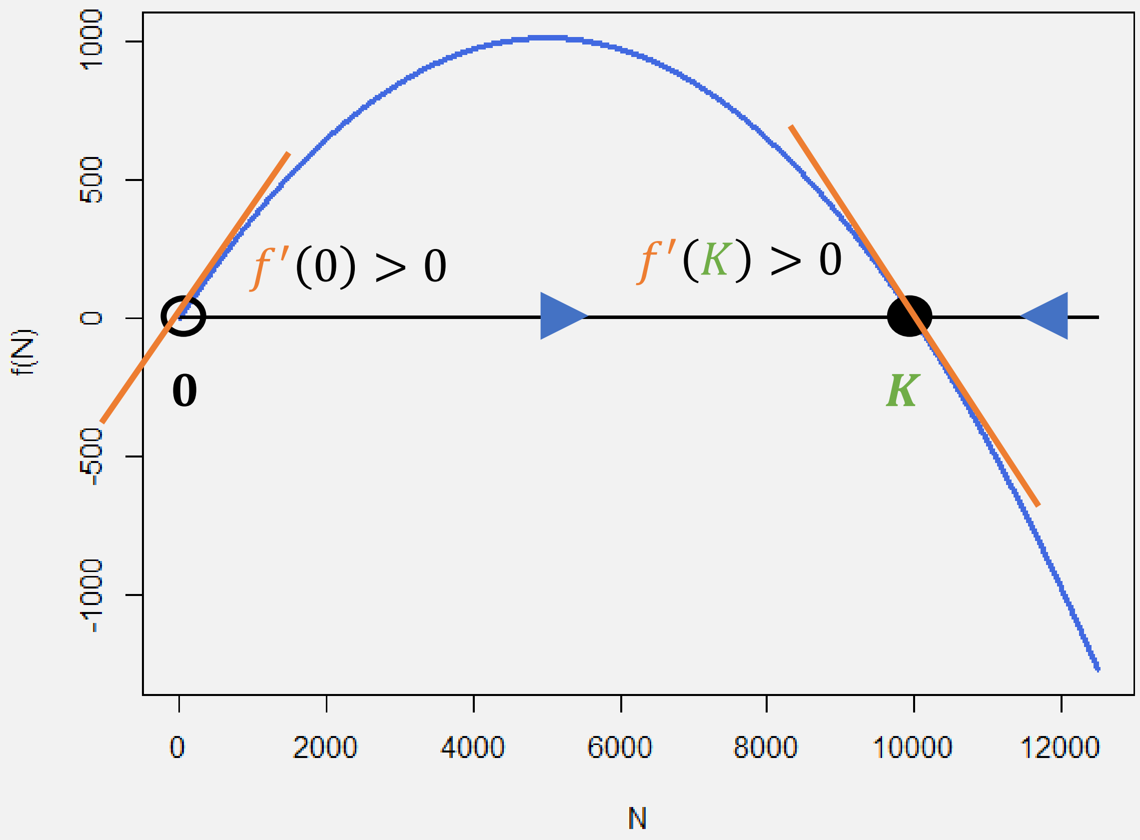
- Logistic model example: $\frac{dN}{dt} = f(N) = rN\left(1 - \frac{N}{K}\right)$



- Equilibrium $\bar{N} = 0$ is stable : if the species is introduced it does not go extinct
- Equilibrium $\bar{N} = K$ is stable : if pop. size deviates from K it gets back to K

Stability of equilibria – 1D – continuous time

- Logistic model example: $\frac{dN}{dt} = f(N) = rN\left(1 - \frac{N}{K}\right)$



Mathematically, the stability of equilibrium $\bar{N}$ is given by differentiating $f(N)$ around $\bar{N}$:

- $f'(\bar{N}) > 0$: unstable eq.
- $f'(\bar{N}) < 0$: stable eq.

Equilibrium – dimension 1 – discrete time

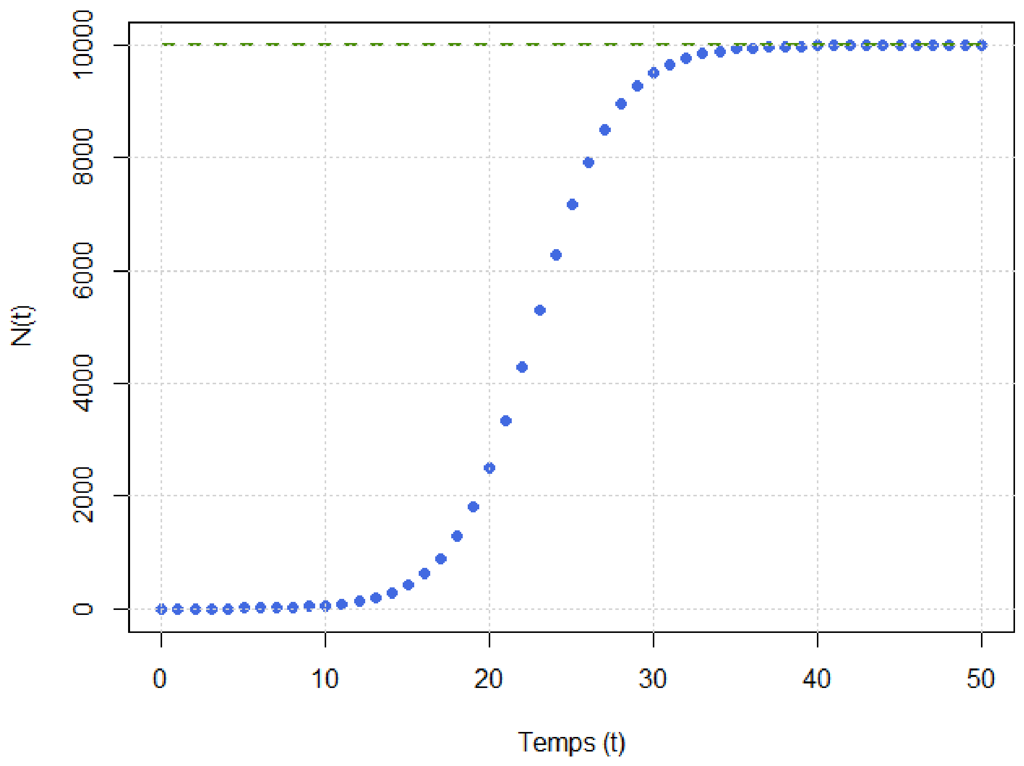
- General form of pop. dyn.:

$$N(t+1) = F(N(t))$$

- **Equilibrium**: any pop. size $\bar{N}$ for which pop. size does not vary:

$$\bar{N} = F(\bar{N})$$

- In words: if pop. has size $\bar{N}$, it remains of size $\bar{N}$

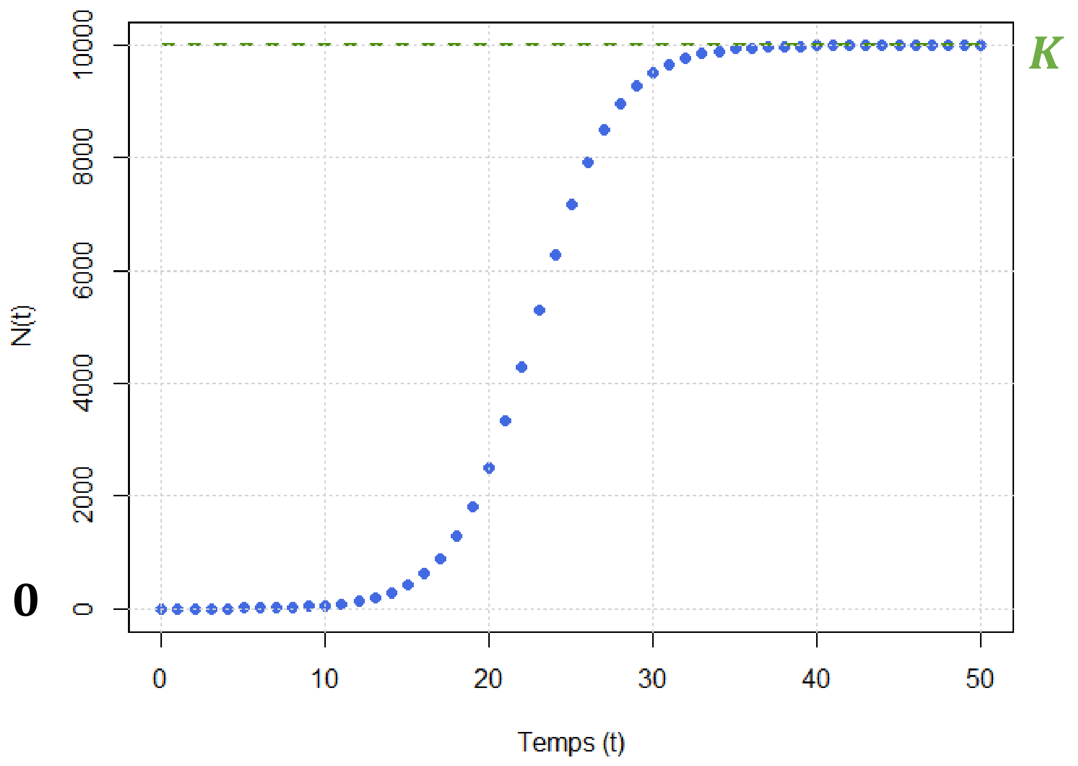


Equilibrium – dimension 1 – discrete time

- Ex.: Beverton-Holt model

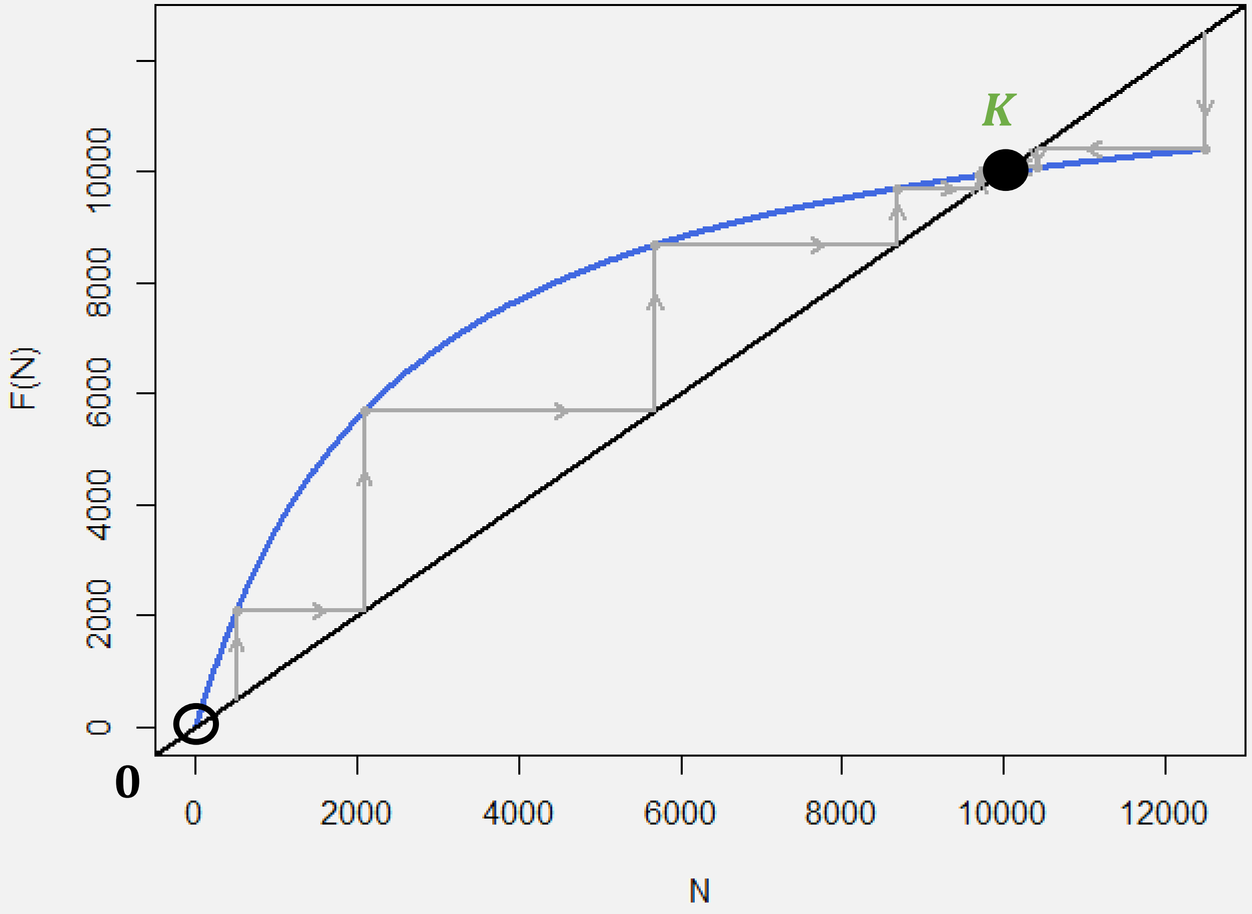
$$N(t+1) = \frac{RN(t)}{1 + \frac{N(t)}{K}(R-1)}$$

- **2 equilibria:**
  - Species absent: $\bar{N} = 0$
  - Sp. at carrying capacity: $\bar{N} = K$
- Remark: $N = 0$ is always an équilibrium in Biology (no spontaneous generation)



Stability of equilibria – 1D – discrete time

- Beverton-Holt model example: $N(t+1) = F(N) = \frac{RN(t)}{1+\frac{N(t)}{K}(R-1)}$

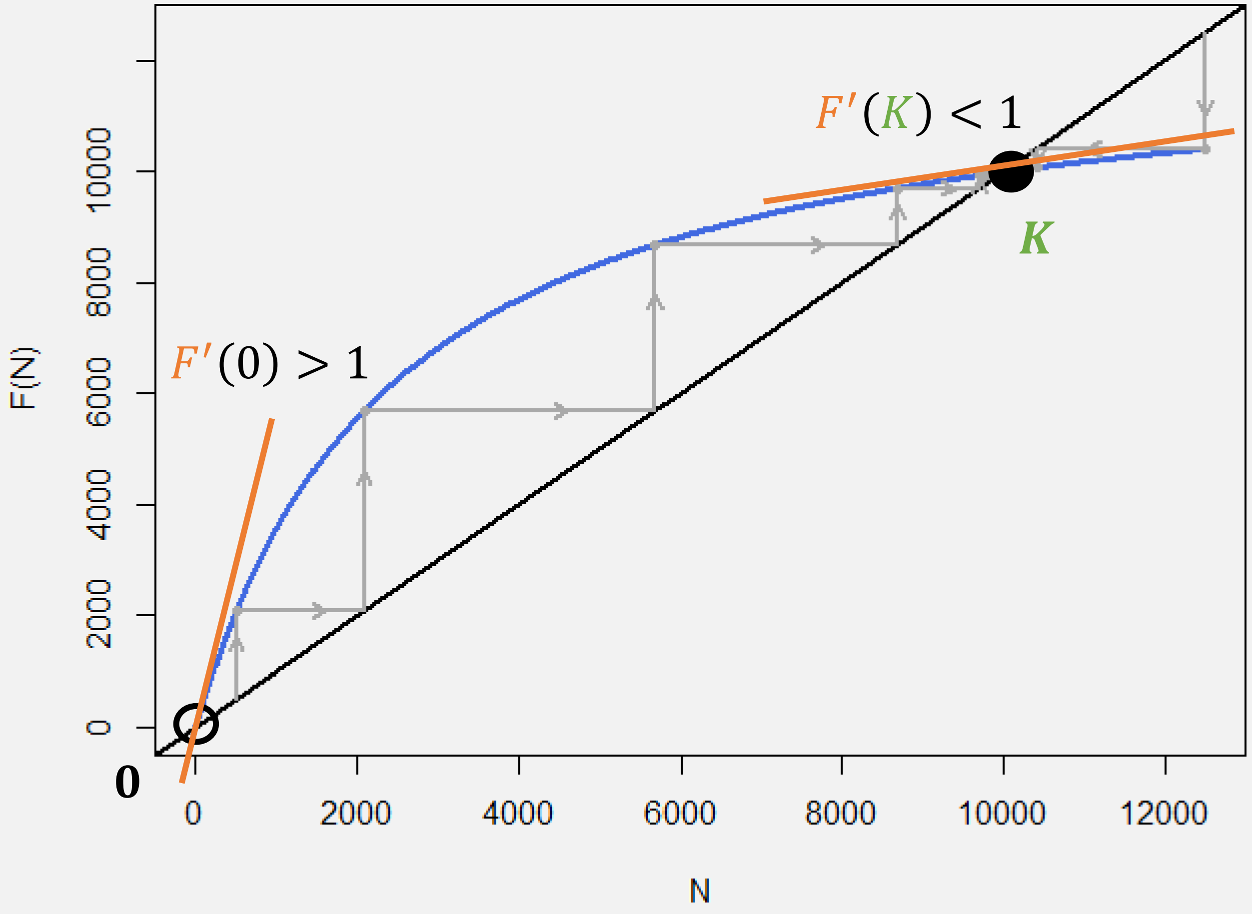


- Equilibrium $\bar{N} = 0$ is unstable: if the species is introduced it does no go extinct

- Equilibrium $\bar{N} = K$ is stable: if pop. size deviates from K it gets back to K

Stability of equilibria – 1D – discrete time

- Beverton-Holt model example: $N(t+1) = F(N) = \frac{RN(t)}{1+\frac{N(t)}{K}(R-1)}$

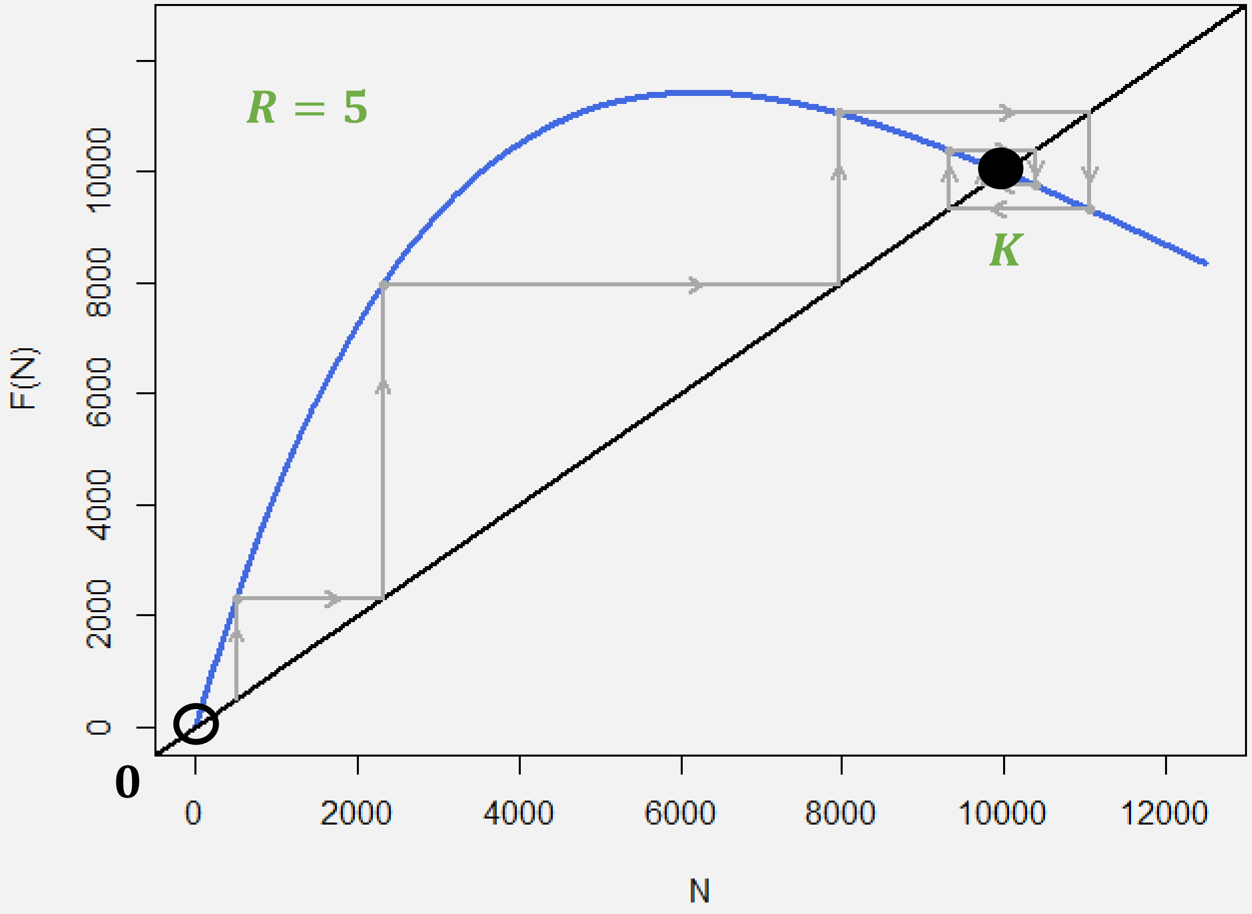


Mathematically, the stability of equilibrium $\bar{N}$ is given by differentiating $F(N)$ around $\bar{N}$:

- $|F'(\bar{N})| > 1$: unstable eq.
- $|F'(\bar{N})| < 1$: stable eq.

Stability of equilibria – 1D – discrete time

- Ricker model example: $N(t+1) = F(N) = R^{\left(1-\frac{N(t)}{K}\right)} N(t)$

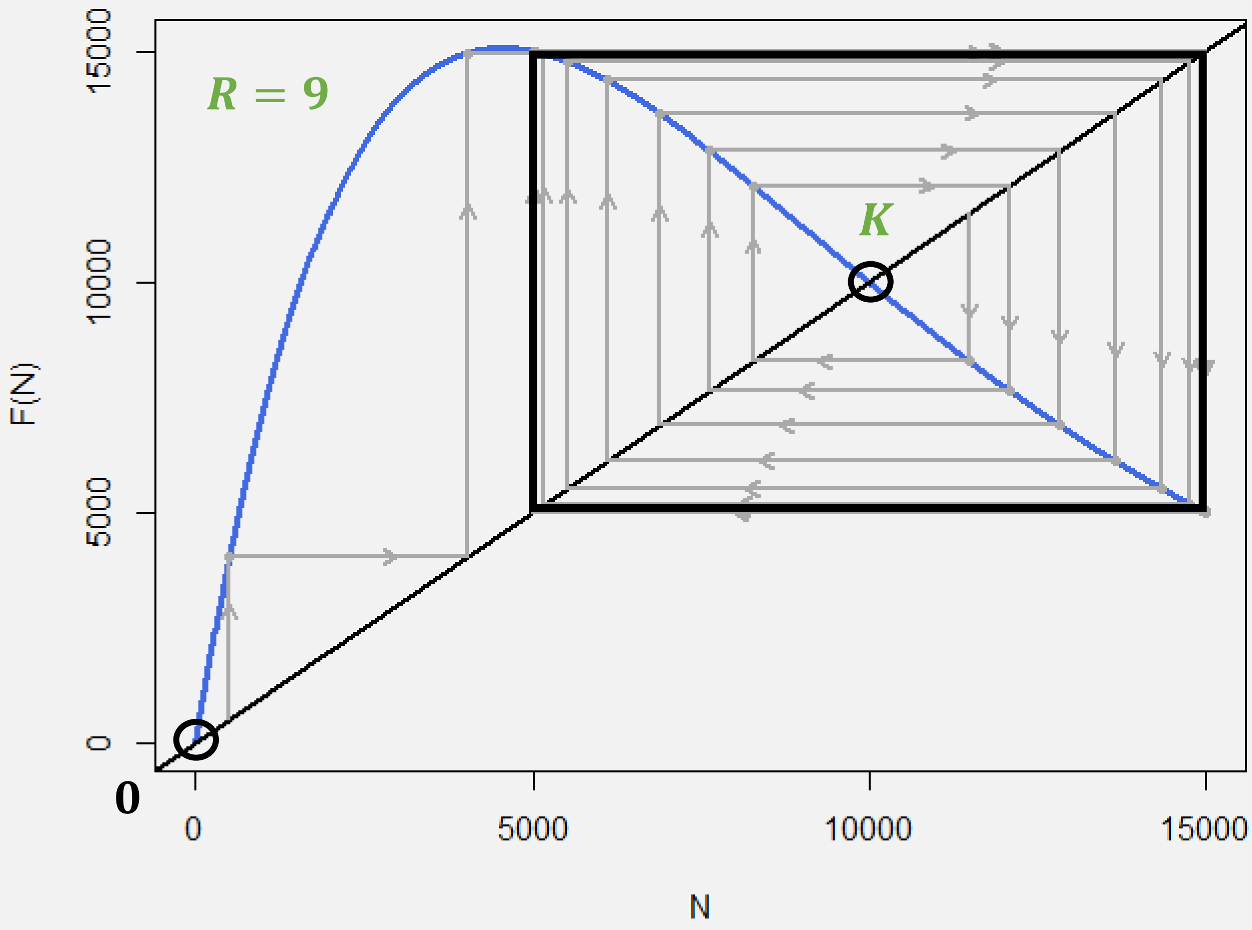


- Equilibrium $\bar{N} = 0$ is unstable: if the species is introduced it does not go extinct

- Equilibrium $\bar{N} = K$ is stable: if pop. size deviates from K it gets back to K

Stability of equilibria – 1D – discrete time

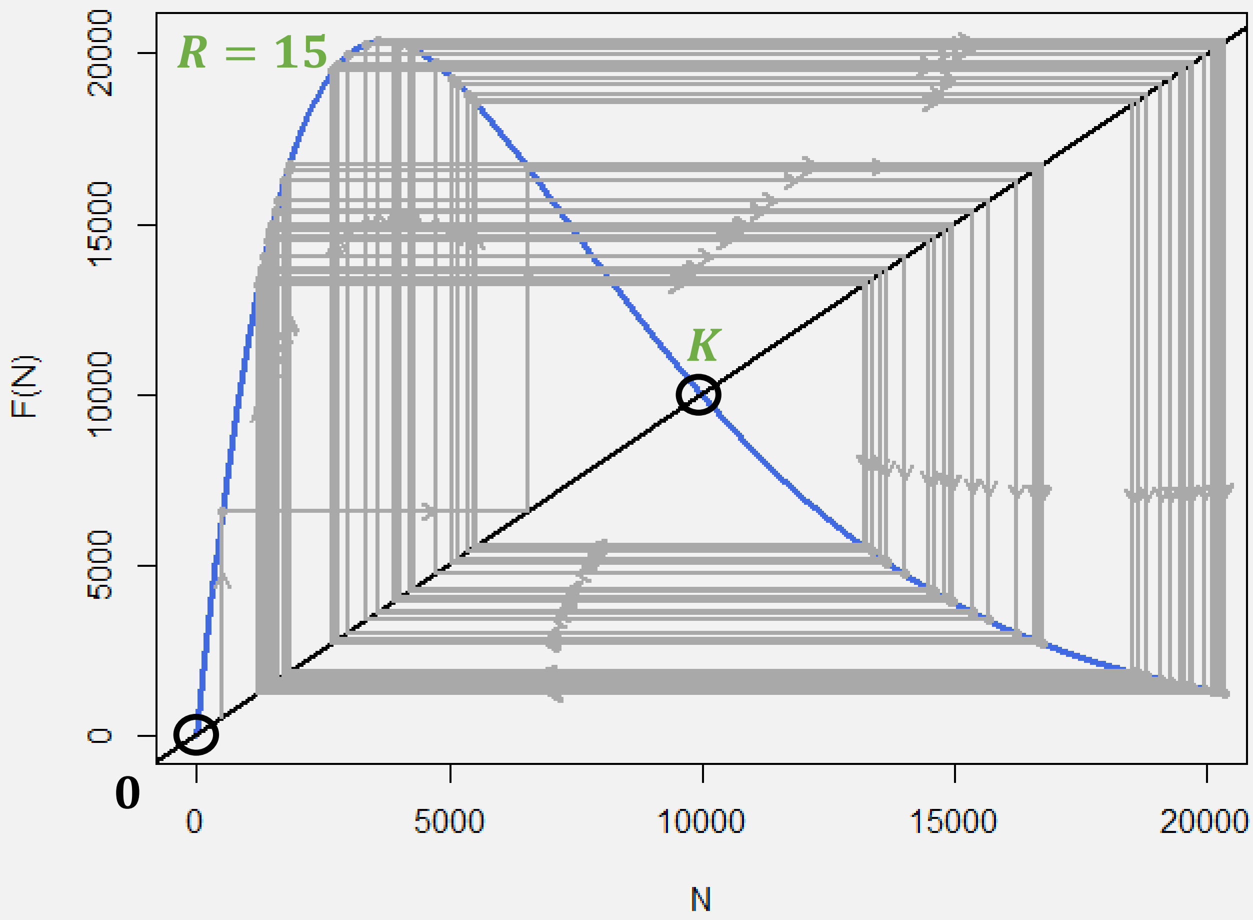
- Ricker model example: $N(t+1) = F(N) = R^{\left(1-\frac{N(t)}{K}\right)} N(t)$



- Equilibrium $\bar{N} = 0$ is unstable: if the species is introduced it does not go extinct
- Equilibrium $\bar{N} = K$ is **un**stable: if pop. size. deviates from K it goes away from K
- Stable limit cycle (periodic oscillations)

Stability of equilibria – 1D – discrete time

- Ricker model example: $N(t+1) = F(N) = R^{\left(1-\frac{N(t)}{K}\right)} N(t)$



- Equilibrium $\bar{N} = 0$ is unstable: if the species is introduced it does not go extinct

- Equilibrium $\bar{N} = K$ is **un**stable: if pop. size. deviates from K it goes away from K

- Chaotic fluctuations

2. Dimension 2

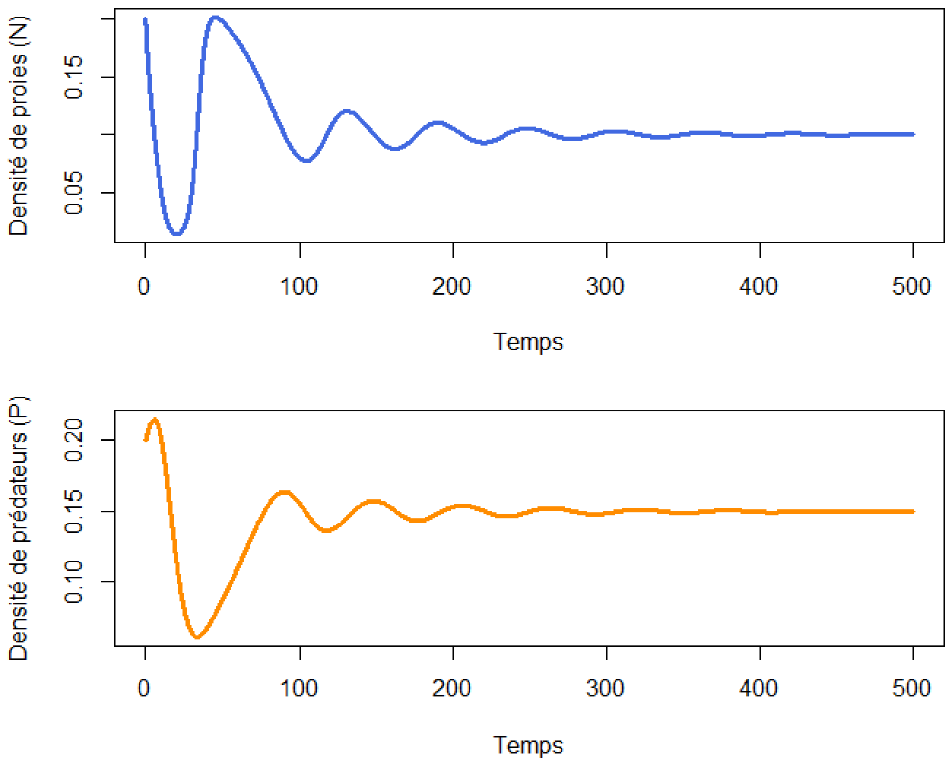
Equilibrium – dimension 2 – continuous time

- General form of the pop. dyn.:

$$\begin{cases} \frac{dN_1}{dt} = f(N_1, N_2) \\ \frac{dN_2}{dt} = g(N_1, N_2) \end{cases}$$

- **Equilibrium**: any pair $(\bar{N}_1, \bar{N}_2)$ s.t.:

$$\begin{cases} 0 = f(\bar{N}_1, \bar{N}_2) \\ 0 = g(\bar{N}_1, \bar{N}_2) \end{cases}$$



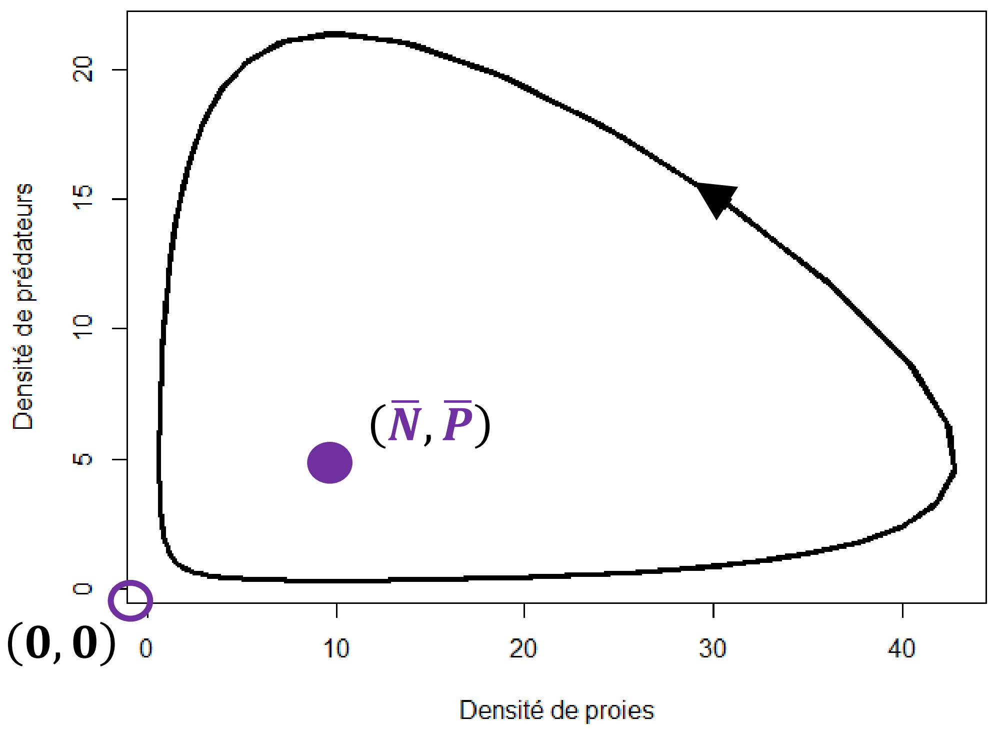
Equilibrium – dimension 2 – continuous time

- Ex.: Prey-predator model

$$\begin{cases} \frac{dN}{dt}(t) = rN(t) - aP(t)N(t) \\ \frac{dP}{dt}(t) = bP(t)N(t) - mP(t) \end{cases}$$

- **Equilibria**:
  - Both species absent: $(\bar{N}, \bar{P}) = (0,0)$
  - Both species present:

$$(\bar{N}, \bar{P}) = \left(\frac{m}{b}, \frac{r}{a}\right)$$



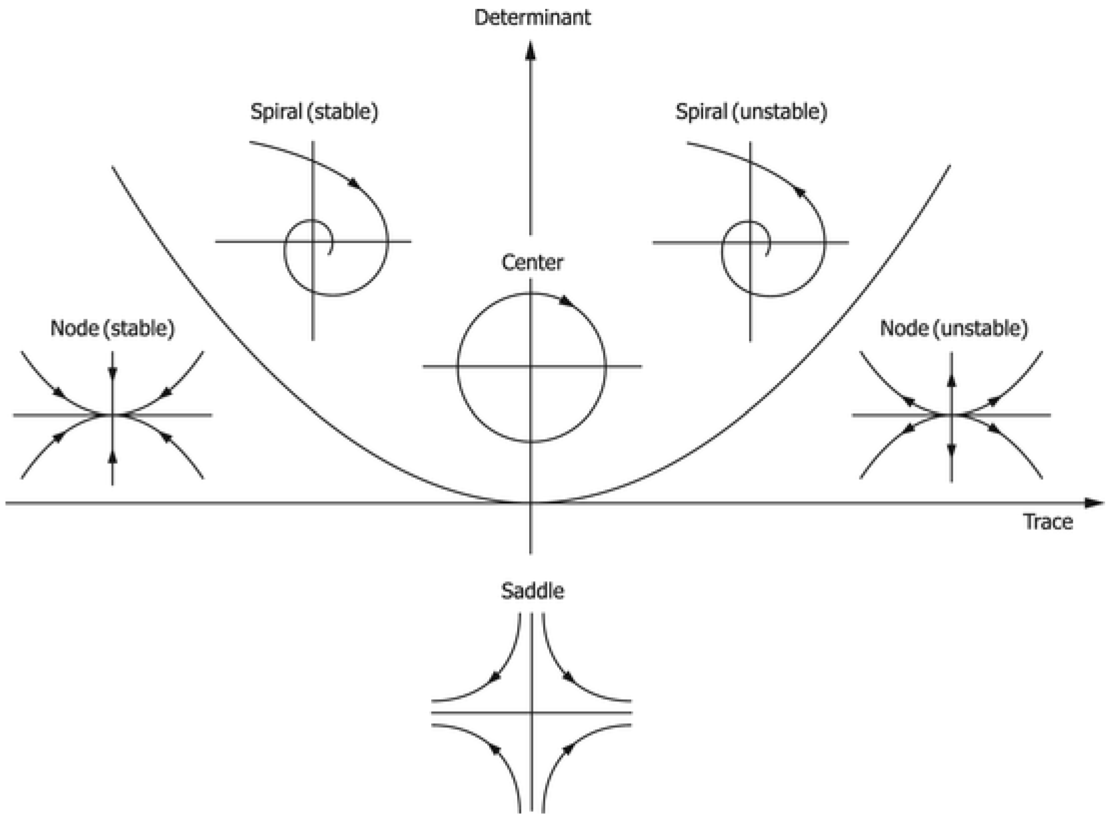
Stability – dimension 2 – continuous time

- General form of the dynamics:

$$\begin{cases} \dfrac{dN_1}{dt} = f(N_1, N_2) \\ \dfrac{dN_2}{dt} = g(N_1, N_2) \end{cases}$$

- **Jacobian matrix**:

$$J = \begin{bmatrix} \dfrac{\partial f}{\partial N_1} & \dfrac{\partial f}{\partial N_2} \\ \dfrac{\partial g}{\partial N_1} & \dfrac{\partial g}{\partial N_2} \end{bmatrix}$$



Stability – dimension 2 – continuous time

- Ex.: prey-predator model

$$\begin{cases} f(N,P) = rN(t) - aP(t)N(t) \\ g(N,P) = bP(t)N(t) - mP(t) \end{cases}$$

- Jacobian matrix:

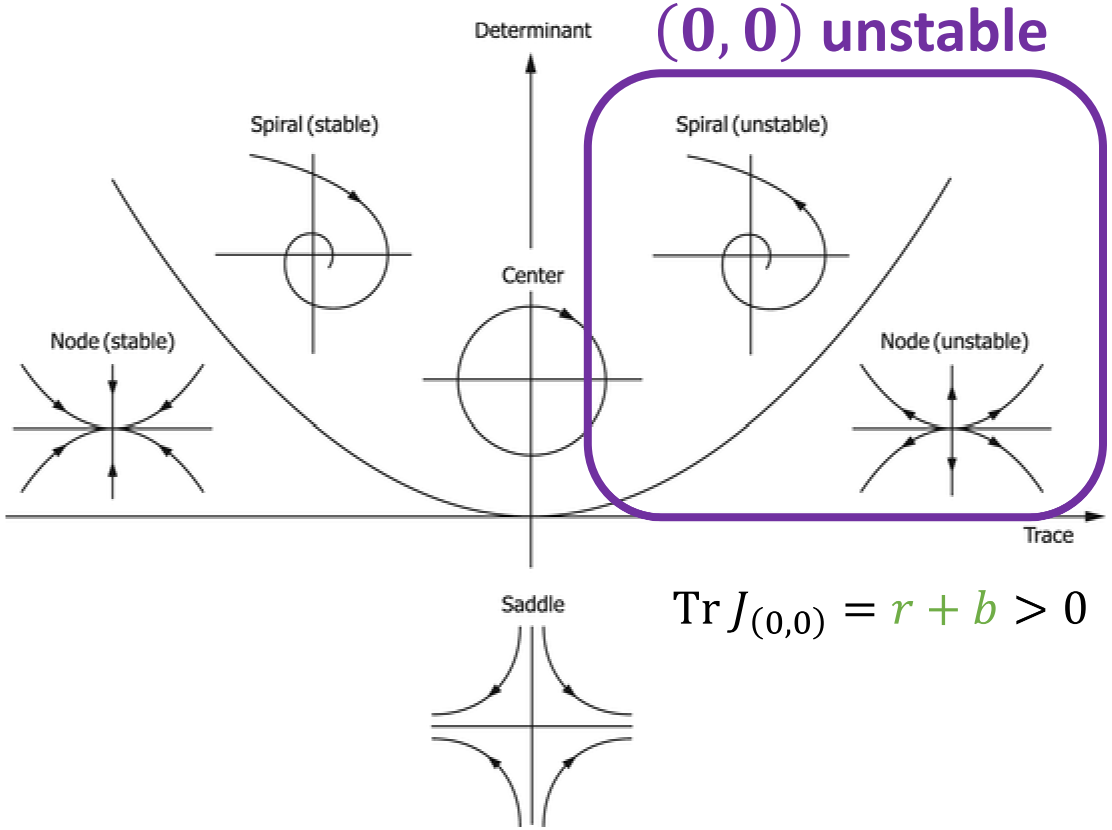
$$J = \begin{bmatrix} \frac{\partial f}{\partial N} & \frac{\partial f}{\partial P} \\ \frac{\partial g}{\partial N} & \frac{\partial g}{\partial P} \end{bmatrix} = \begin{bmatrix} r - aP & -aN \\ bP & b - mP \end{bmatrix}$$

- Evaluated around $(\bar{N}, \bar{P}) = (0,0)$:

$$J_{(0,0)} = \begin{bmatrix} r & 0 \\ 0 & b \end{bmatrix}$$

$\text{Det}\, J_{(0,0)} = rb > 0$

$(0,0)$ unstable



$\text{Tr}\, J_{(0,0)} = r + b > 0$

Stability – dimension 2 – continuous time

- Ex.: Prey-predator example

$$\begin{cases} f(N,P) = rN(t) - aP(t)N(t) \\ g(N,P) = bP(t)N(t) - mP(t) \end{cases}$$

- Jacobian matrix:

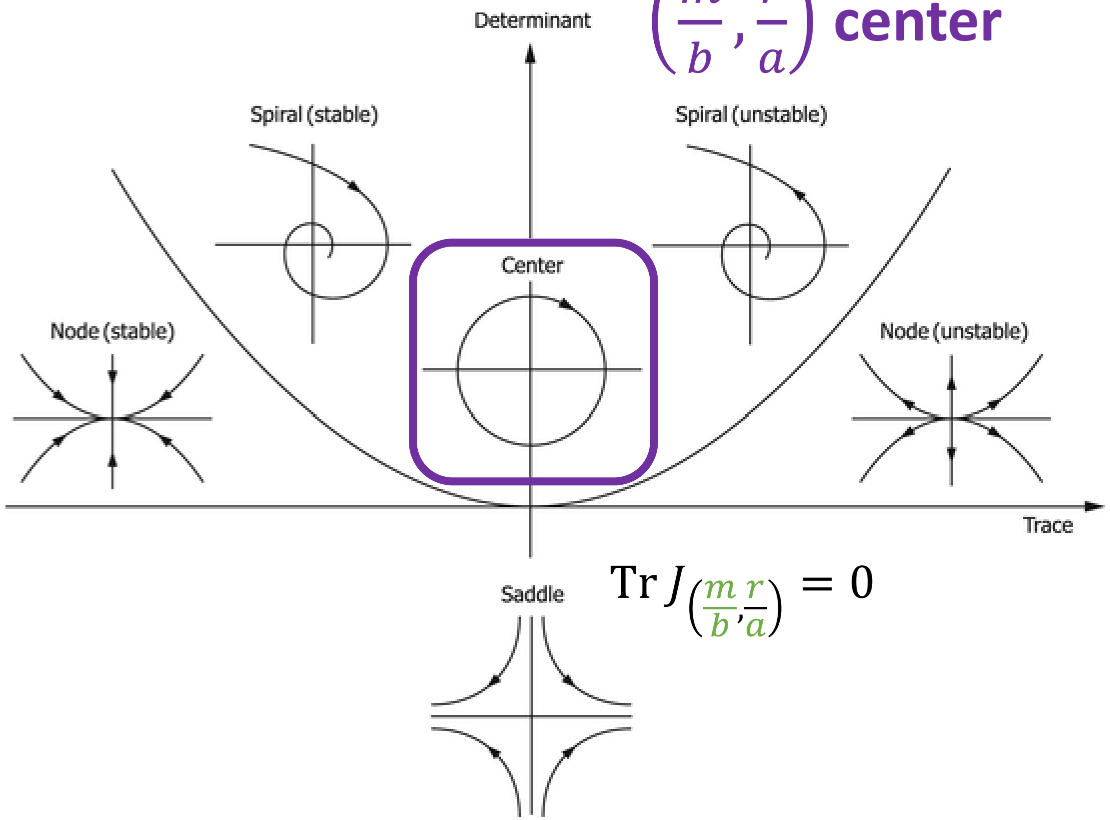
$$J = \begin{bmatrix} \frac{\partial f}{\partial N} & \frac{\partial f}{\partial P} \\ \frac{\partial g}{\partial N} & \frac{\partial g}{\partial P} \end{bmatrix} = \begin{bmatrix} r - aP & -aN \\ bP & bN - m \end{bmatrix}$$

- Evaluated around $(\bar{N}, \bar{P}) = \left(\frac{m}{b}, \frac{r}{a}\right)$:

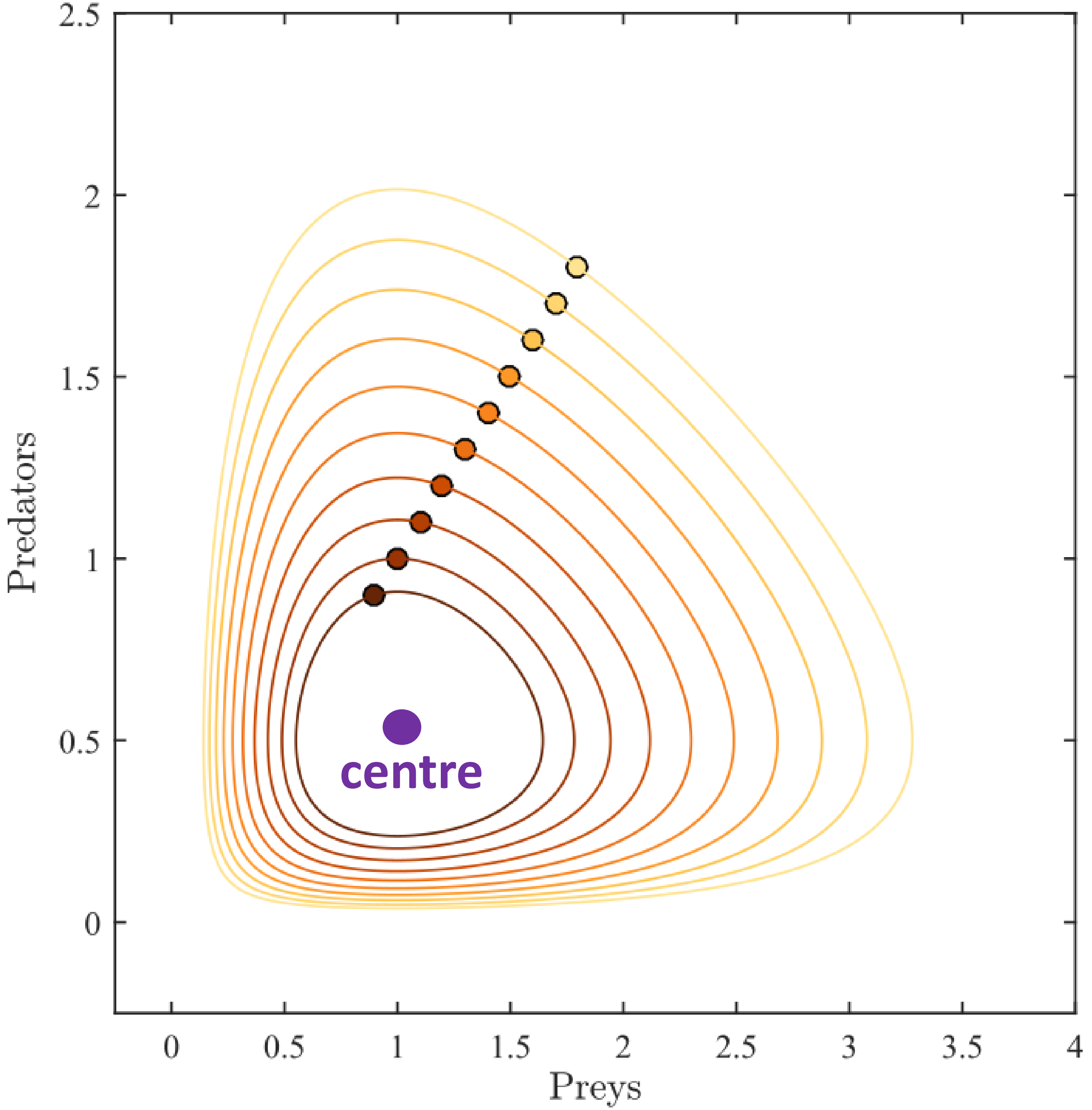
$$J_{\left(\frac{m}{b},\frac{r}{a}\right)} = \begin{bmatrix} 0 & -a\frac{m}{b} \\ b\frac{r}{a} & 0 \end{bmatrix}$$

$\mathrm{Det}\, J_{\left(\frac{m}{b},\frac{r}{a}\right)} = rm > 0$

$\left(\frac{m}{b}, \frac{r}{a}\right)$ **center**



$\mathrm{Tr}\, J_{\left(\frac{m}{b},\frac{r}{a}\right)} = 0$



The Lotka-Volterra predator-prey model generates an infinite number of possible cycles, as a function of initial conditions

This behavior is not robust to slight model variations. For instance, if the prey grows logistically in the absence of predator, the dynamics spiral towards a stable equilibrium

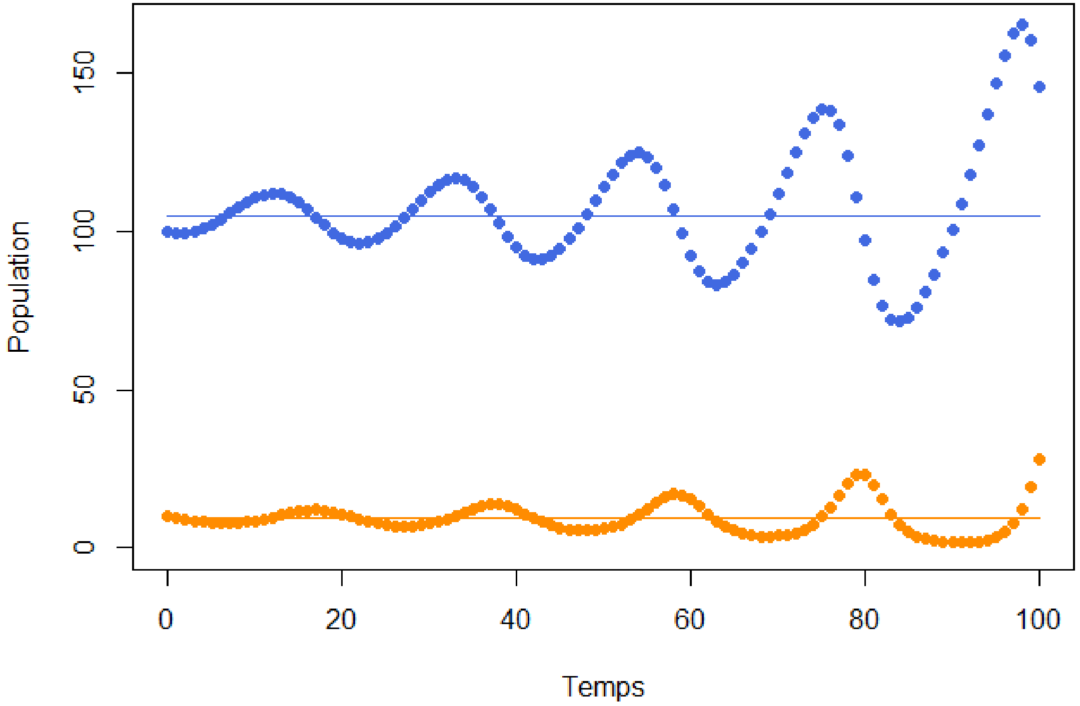
Equilibrium – dimension 2 – discrete time

- General form of the dynamics:

$$\begin{cases} N_1(t+1) = F(N_1, N_2) \\ N_2(t+1) = G(N_1, N_2) \end{cases}$$

- **Equilibrium**: any pair $(\bar{N}_1, \bar{N}_2)$ s.t.:

$$\begin{cases} \bar{N}_1 = F(\bar{N}_1, \bar{N}_2) \\ \bar{N}_2 = G(\bar{N}_1, \bar{N}_2) \end{cases}$$



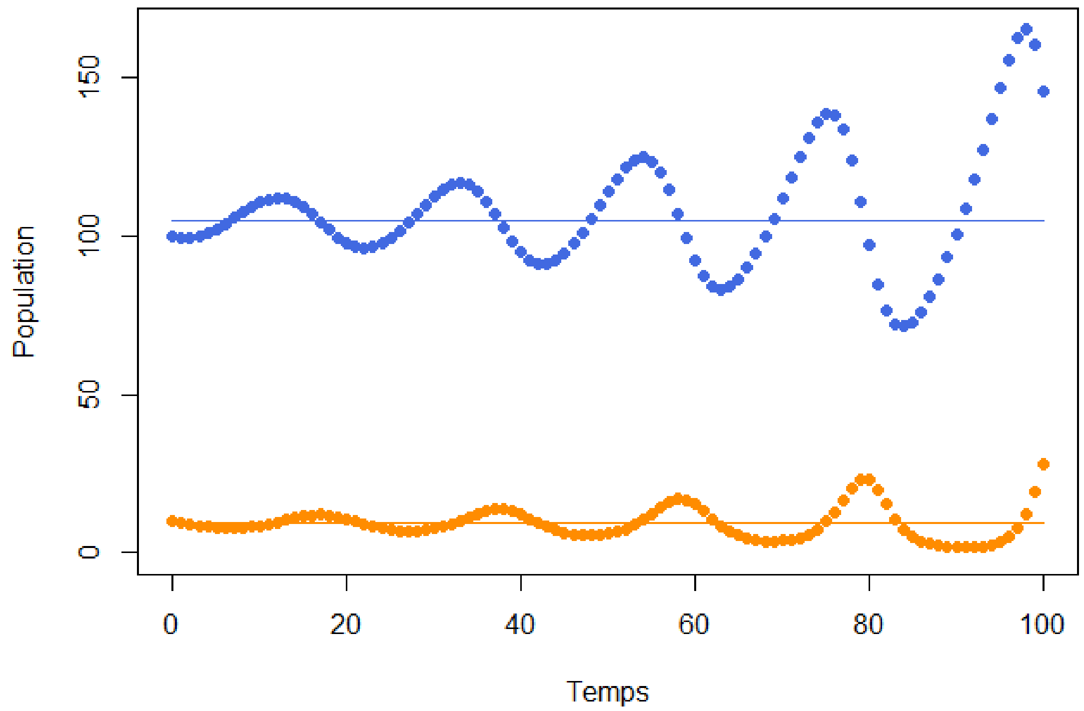
Equilibrium – dimension 2 – discrete time

- Ex.: Nicholson-Bailey model

$$\begin{cases} N(t+1) = RNe^{-aP} \\ P(t+1) = bN\left(1 - e^{-aP}\right) \end{cases}$$

- **Equilibria**:
  - Both species absent: $(\bar{N}, \bar{P}) = (0,0)$
  - Both species present:

$$(\bar{N}, \bar{P}) = \left(\frac{R}{R-1}\frac{\ln R}{ab}, \frac{\ln R}{a}\right)$$



Stability – dimension 2 – discrete time

- General form of the dynamics:

$$\begin{cases} F(N_1, N_2) = f(N_1, N_2) \\ G(N_1, N_2) = g(N_1, N_2) \end{cases}$$

- **Jacobian matrix**:

$$J = \begin{bmatrix} \frac{\partial f}{\partial N_1} & \frac{\partial f}{\partial N_2} \\ \frac{\partial g}{\partial N_1} & \frac{\partial g}{\partial N_2} \end{bmatrix}$$

- Let

$$A = 1 - \mathrm{Det}\, J$$
$$B = \mathrm{Det}\, J - \mathrm{Tr}\, J + 1$$
$$C = \mathrm{Det}\, J + \mathrm{Tr}\, \mathrm{J} + 1$$

- The stability of an equilibrium is given by the following necessary and sufficient conditions:

$$A, B, C > 0$$

Stability – dimension 2 – discrete time

- Ex.: Nicholson-Bailey model

$$\begin{cases} F(N,P) = RNe^{-aP} \\ G(N,P) = bN\,(1-e^{-aP}) \end{cases}$$

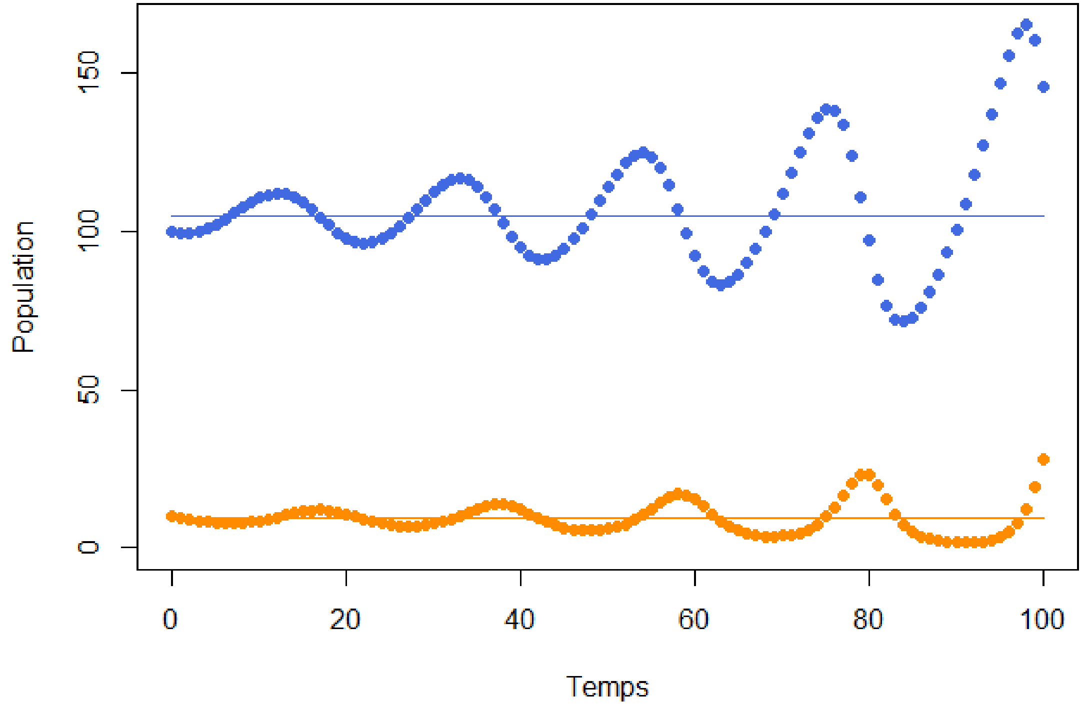
- Jacobian matrix:

$$J = \begin{bmatrix} \frac{\partial f}{\partial N} & \frac{\partial f}{\partial P} \\ \frac{\partial g}{\partial N} & \frac{\partial g}{\partial P} \end{bmatrix} = \begin{bmatrix} Re^{-aP} & -aRNe^{-aP} \\ b(1-e^{-aP}) & -abNe^{-aP} \end{bmatrix}$$

- Evaluated around $(\bar{N},\bar{P}) = (0,0)$:

$$J_{(0,0)} = \begin{bmatrix} R & 0 \\ 0 & 0 \end{bmatrix}$$

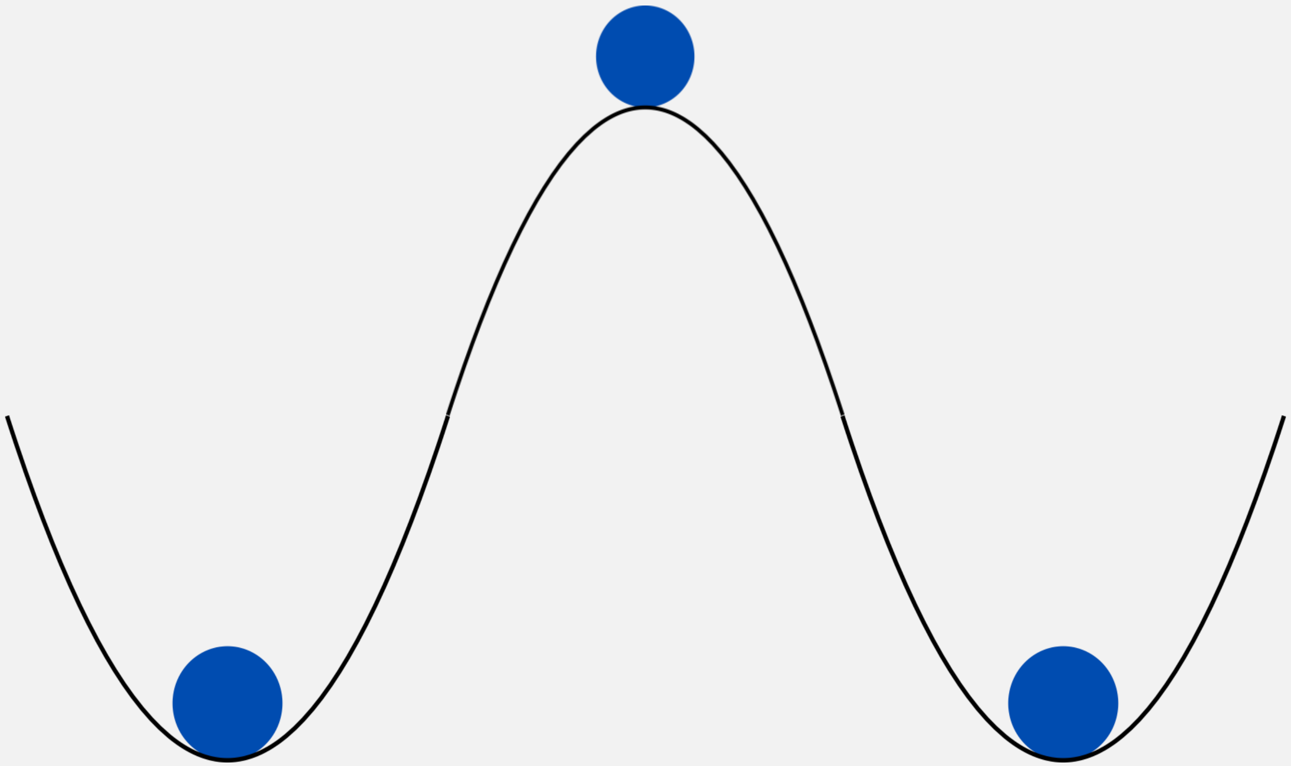
- Since $B = \mathrm{Det}\,J - \mathrm{Tr}\,J = 1 - R < 0$, the $(0,0)$ equilibrium is unstable (since $R > 1$)



End of the mathematically simple examples

Notion of bi-stability

Bi-stability: which equilibrium the dynamics converge to depends on the initial condition

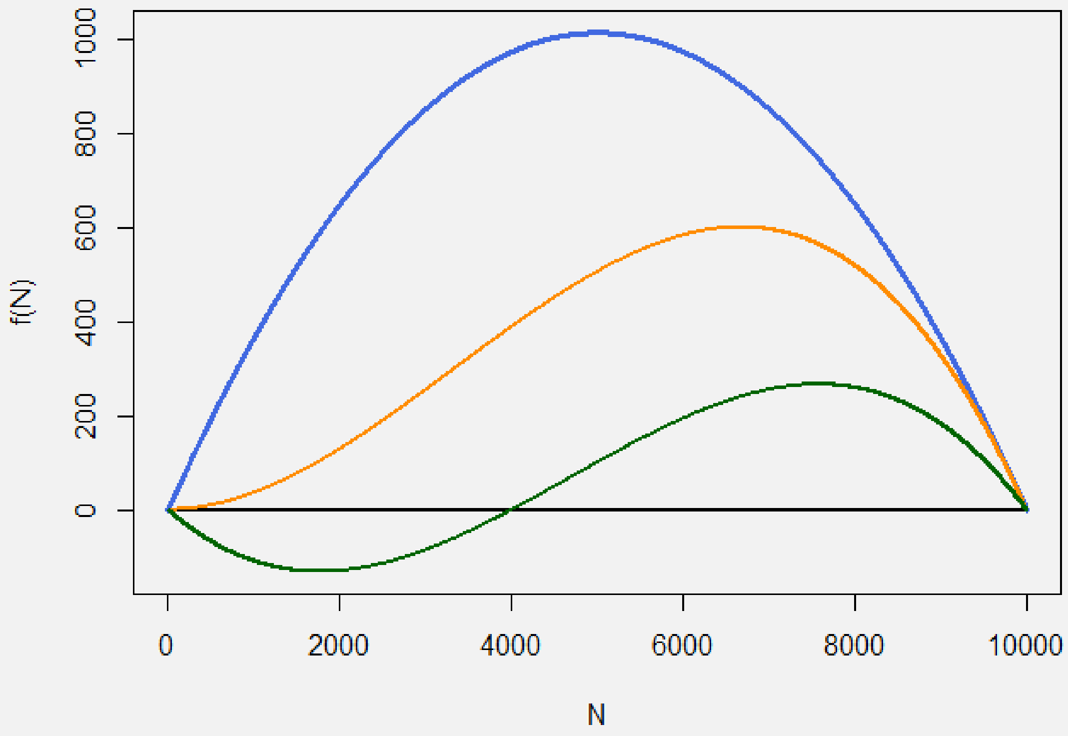


Allee effect

- Lower growth rate at low pop. density
- Ex.: logistic model with Allee effect :

$$\frac{dN}{dt} = f(N) = rN\left(1 - \frac{N}{K}\right)\left(\frac{N - A}{K}\right)$$

- $A = 0$: weak Allee effect
- $A > 0$: strong Allee effect (threshold)

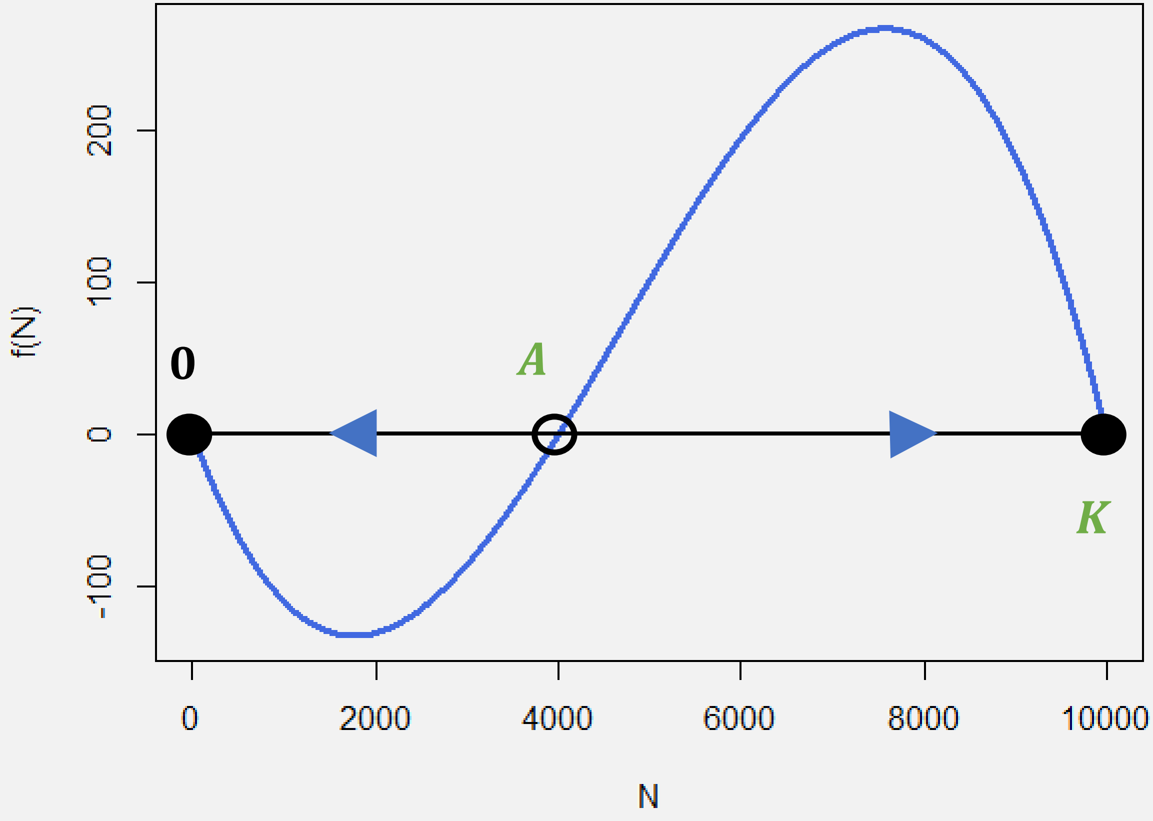


Strong Allee effect

- Ex.: logistic model with Allee effect:

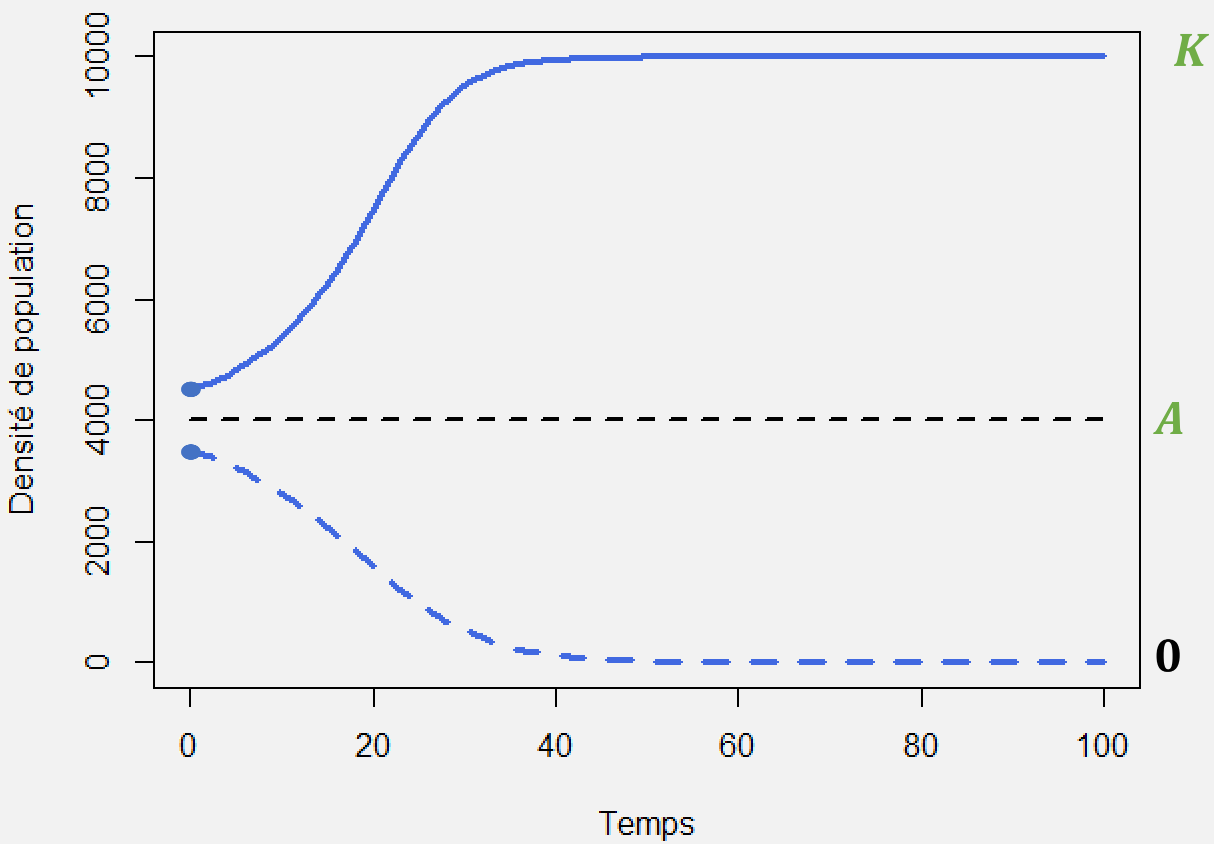
$$\frac{dN}{dt} = f(N) = rN\left(1 - \frac{N}{K}\right)\left(\frac{N - A}{K}\right)$$

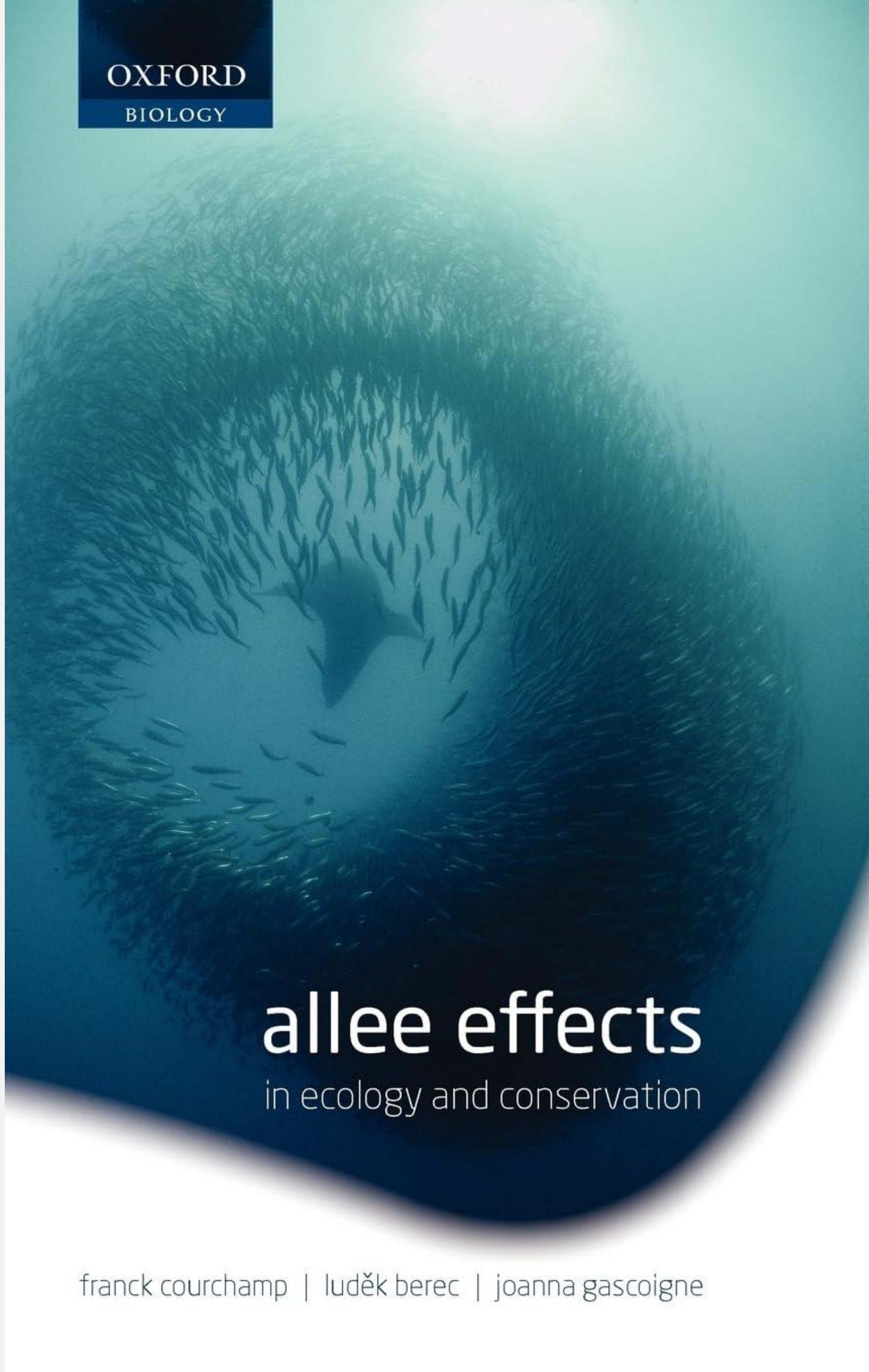
- 3 equilibria:
  - Species absent: $\bar{N} = 0$ (**stable**)
  - Allee threshold: $\bar{N} = A$ (unstable)
  - Carrying capacity: $\bar{N} = K$ (stable)
- **Bi-stability**: which equilibrium the dynamics converge to depends on initial conditions



Bi-stability

- Which equilibrium the dynamics converge to depends on initial conditions





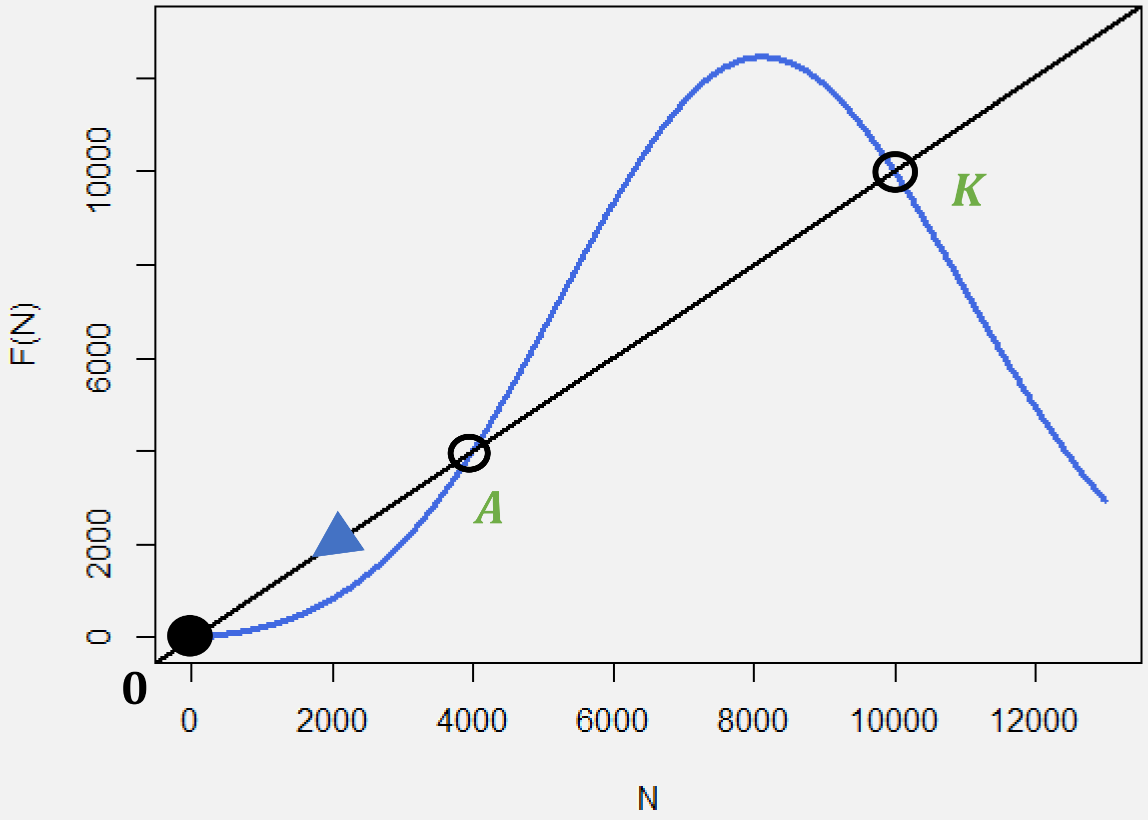
Notion of transient dynamics

Ricker model with Allee effect

- Example:

$$N(t+1) = R^{rN\left(1-\frac{N}{K}\right)\left(\frac{N-A}{K}\right)} N(t)$$

- 3 équilibria:
  - Species absent: $\bar{N} = 0$ (stable)
  - Allee threshold: $\bar{N} = A$ (unstable)
  - Carrying capacity: $\bar{N} = K$ (unstable)
- Extinction ($\bar{N} = 0$) is globally asymptotically stable (for this parameter set)



Ricker model with Allee effect

- Example:

$$N(t+1) = R^{rN\left(1-\frac{N}{K}\right)\left(\frac{N-A}{K}\right)} N(t)$$

- 3 équilibria:
  - Species absent: $\bar{N} = 0$ (stable)
  - Allee threshold: $\bar{N} = A$ (unstable)
  - Carrying capacity: $\bar{N} = K$ (unstable)
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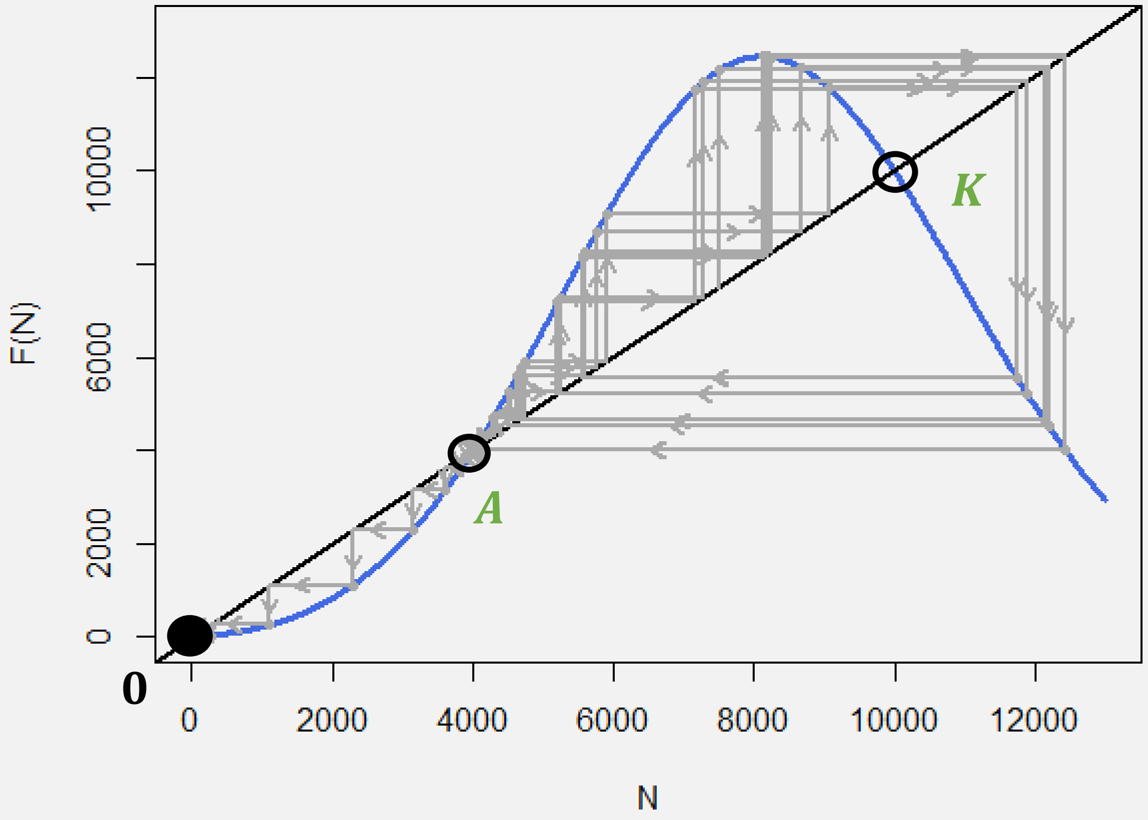


Schreiber (2001). Chaos and population disappearances in simple ecological models. *Journal of Mathematical Biology*

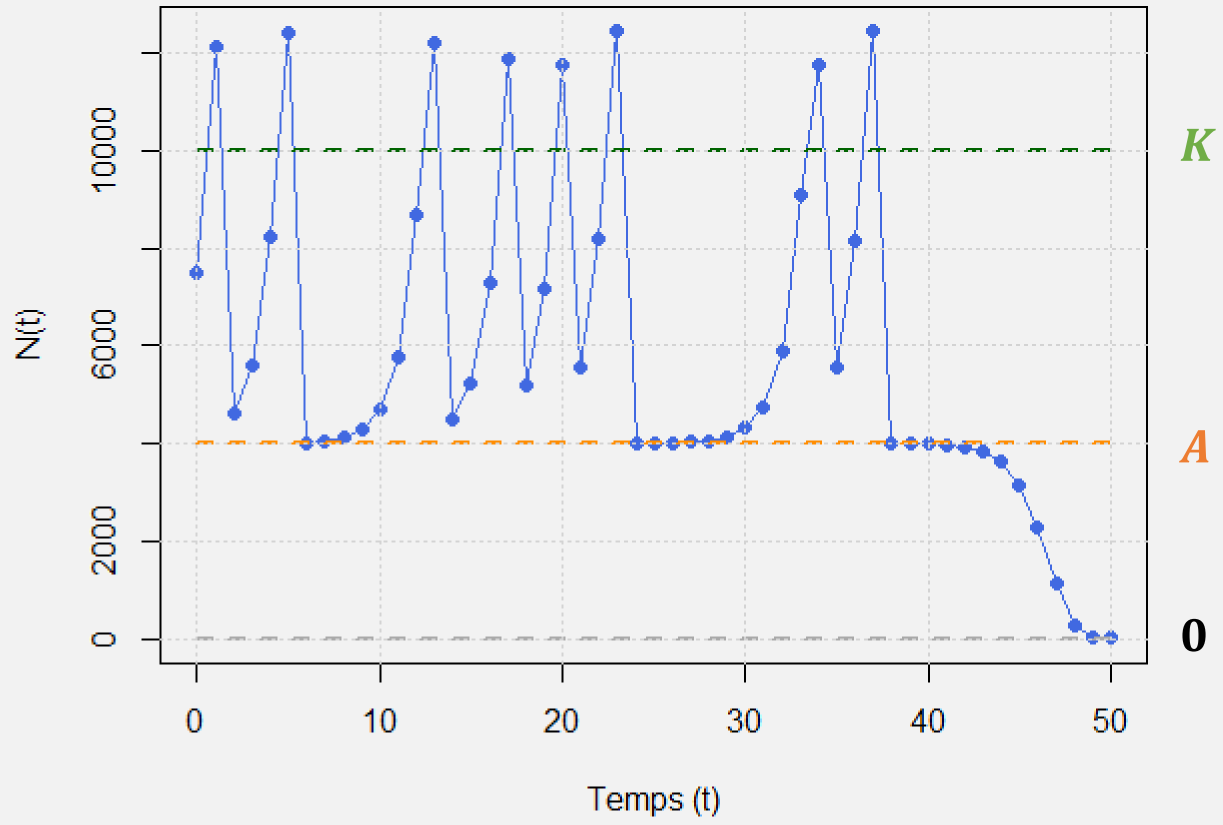
Ricker model with Allee effect

- Example:

$$N(t+1) = R^{rN\left(1-\frac{N}{K}\right)\left(\frac{N-A}{K}\right)} N(t)$$

- 3 équilibria:
  - Species absent: $\bar{N} = 0$ (stable)
  - Allee threshold: $\bar{N} = A$ (unstable)
  - Carrying capacity: $\bar{N} = K$ (unstable)
- Extinction ($\bar{N} = 0$) is globally asymptotically stable (for this parameter set)

Transient dynamics and extinction




PAR LES CRÉATEURS DE GAME OF THRONES
UNE SÉRIE NETFLIX
LE PROBLÈME
À 3 CORPS
SEULEMENT SUR NETFLIX | LE 21 MARS