

La relation *Ressource - Consommateur*

IV - Arditi - Ginzburg

Claude Lobry,
Université de Nice et INRIA Modemic
Septembre 2015

Interaction Ressource-Consommateur

$$\dot{x} = f(x) - \frac{1}{Y} \mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

Modèle canonique

$$\dot{x} = f(x) - \frac{1}{Y} \mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

$$\dot{x} = f(x) - \frac{1}{Y}\mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

L-V 1925

$$1. f(x) = r$$

$$2. \mu(x, y) = \mu \cdot x$$

$$3. \nu(y) = m$$

Gause 1936

$$1. f(x) = r$$

$$2. \mu(x, y) = \mu \cdot \frac{x}{e+x}$$

si $x > \alpha$ 0 sinon

$$3. \nu(y) = m$$

Rosenzweig-MacArthur 1963

$$1. f(x) = r \cdot x - \alpha \cdot x^2$$

$$2. \mu(x, y) = \mu \cdot \frac{x}{e+x}$$

$$3. \nu(y) = m$$


Rosenzweig-MacArthur

$$\dot{x} = f(x) - \frac{1}{Y} \mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

- $f(x) = r \cdot x \left(1 - \frac{x}{K}\right)$ $x \mapsto f(x)$ nulle en 0, croissante puis décroissante nulle en $x = K$
- $\mu(x, y) = \frac{\mu \cdot x}{e + x}$ $x \mapsto \mu(x)$ nulle en 0, croissante bornée (concave)
- $\nu(y) = m$

Pas obligatoire mais...



Critiques de Rosenzweig-MacArthur

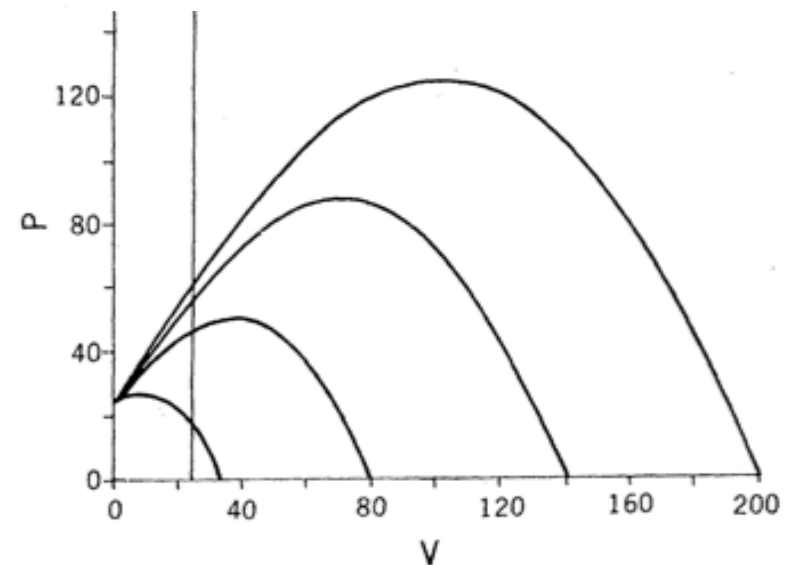
1. Le problème Atto - Fox
2. Paradoxe de l'enrichissement
3. Réponse d'une chaîne trophique
4. Paradoxe du plankton (Exclusion compétitive)

Critiques de Rosenzweig-MacArthur

Paradoxe de l'enrichissement Rosenzweig Science 1971

Paradox of Enrichment: Destabilization of Exploitation Ecosystems in Ecological Time

Abstract. Six reasonable models of trophic exploitation in a two-species ecosystem whose exploiters compete only by depleting each other's resource supply are presented. In each case, increasing the supply of limiting nutrients or energy tends to destroy the steady state. Thus man must be very careful in attempting to enrich an ecosystem in order to increase its food yield. There is a real chance that such activity may result in decimation of the food species that are wanted in greater abundance.



Réponse d'une chaîne trophique

$$\begin{aligned}(1) \quad \dot{x} &= U - \mu_1(x) \cdot y_1 \\(2) \quad \dot{y}_1 &= \mu_1(x) \cdot y_1 - \mu_2(y_1) \cdot y_2 \\(3) \quad \dot{y}_2 &= \mu_2(y_1) \cdot y_2 - \mu_3(y_2) \cdot y_3 \\(4) \quad \dot{y}_3 &= \mu_3(y_2) \cdot y_3 - m \cdot y_3\end{aligned}$$

$$\begin{aligned}(1) \quad 0 &= U - \mu_1(x) \cdot y_1 \\(2) \quad 0 &= \mu_1(x) \cdot y_1 - \mu_2(y_1) \cdot y_2 \\(3) \quad 0 &= \mu_2(y_1) \cdot y_2 - \mu_3(y_2) \cdot y_3 \\(4) \quad 0 &= \mu_3(y_2) \cdot y_3 - m \cdot y_3\end{aligned}$$

Critiques de Rosenzweig-MacArthur


$$\begin{array}{rcl} (1) & 0 & = U - \mu_1(x) \cdot y_1 \\ (2) & 0 & = \mu_1(x) \cdot y_1 - \mu_2(y_1) \cdot y_2 \\ \longrightarrow (3) & 0 & = \mu_2(y_1) \cdot y_2 - \mu_3(y_2) \cdot y_3 \\ (4) & 0 & = \mu_3(y_2) \cdot y_3 - m \cdot y_3 \end{array}$$


$$(4) \implies y_2 = \mu_3^{-1}(m)$$

Critiques de Rosenzweig-MacArthur

$$(1) \quad 0 = U - \mu_1(x) \cdot y_1$$

$$(2) \quad 0 = \mu_1(x) \cdot y_1 - \mu_2(y_1) \cdot y_2$$


$$(3) \quad 0 = \mu_2(y_1) \cdot y_2 - \mu_3(y_2) \cdot y_3$$


$$(4) \quad 0 = \mu_3(y_2) \cdot y_3 - m \cdot y_3$$

$$(4) \implies y_2 = \mu_3^{-1}(m)$$

$$(1 + 2 + 3 + 4) \implies \{U - m \cdot y_3 = 0\} \implies y_3 = U/m$$

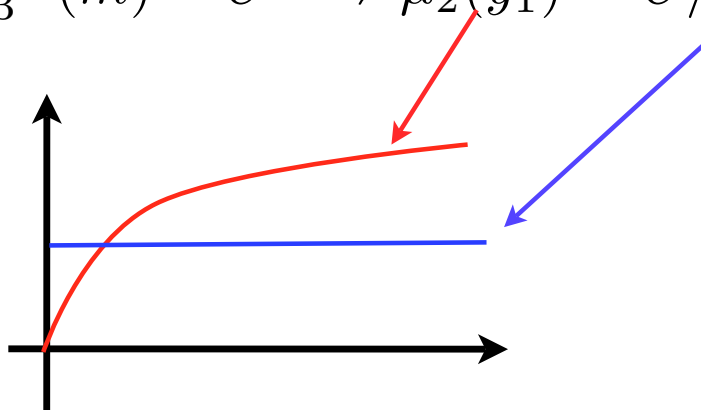
Critiques de Rosenzweig-MacArthur

$$\begin{array}{ll}
 \begin{array}{c} \nearrow \\ \longrightarrow \\ \nearrow \end{array} & \begin{array}{l} (1) \quad 0 = U - \mu_1(x) \cdot y_1 \\ (2) \quad 0 = \mu_1(x) \cdot y_1 - \mu_2(y_1) \cdot y_2 \\ (3) \quad 0 = \mu_2(y_1) \cdot y_2 - \mu_3(y_2) \cdot y_3 \\ (4) \quad 0 = \mu_3(y_2) \cdot y_3 - m \cdot y_3 \end{array}
 \end{array}$$

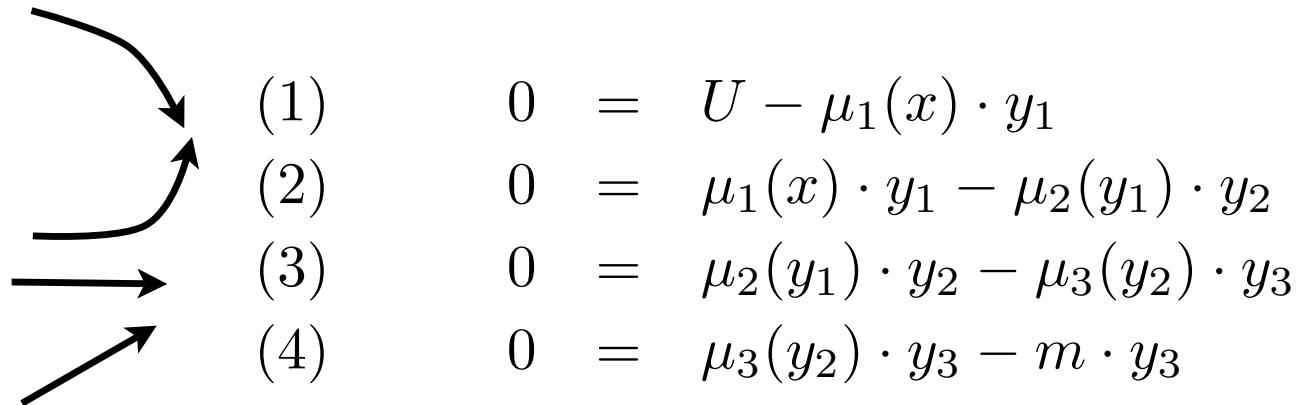
$$(4) \implies y_2 = \mu_3^{-1}(m)$$

$$(1 + 2 + 3 + 4) \implies \{U - m \cdot y_3 = 0\} \implies y_3 = U/m$$

$$(3) \implies \mu_2(y_1) \cdot \mu_3^{-1}(m) - U \implies \mu_2(y_1) = U/\mu_3^{-1}(m)$$



Critiques de Rosenzweig-MacArthur

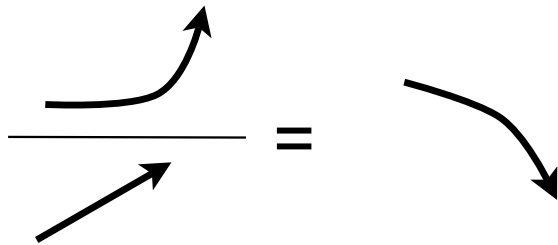


$$(4) \implies y_2 = \mu_3^{-1}(m)$$

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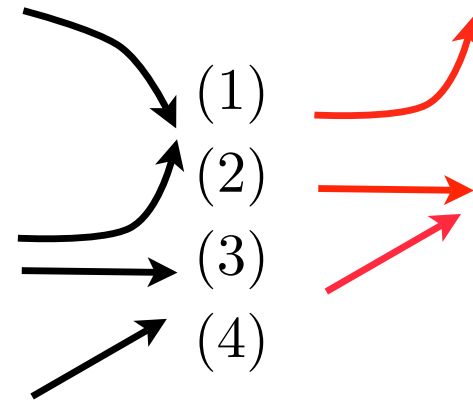
$$(3) \implies \mu_2(y_1) \cdot \mu_3^{-1}(m) - U \implies \mu_2(y_1) = U/\mu_3^{-1}(m)$$

$$(1) \implies \mu_1(x) = U/y_1$$



Critiques de Rosenzweig-MacArthur

Avec seulement 3



$$(1) \quad 0 = U - \mu_1(x) \cdot y_1$$

$$(2) \quad 0 = \mu_1(x) \cdot y_1 - \mu_2(y_1) \cdot y_2$$

$$(3) \quad 0 = \mu_2(y_1) \cdot y_2 - m \cdot y_2$$

Top down

$$(3) \implies \mu_2(y_1) = m \implies y_1 = \mu_2^{-1}(m)$$

$$(1 + 2 + 3) \implies U - m \cdot y_2 = 0 \implies y_2 = U/m$$

$$(1) \implies U - \mu_1(x) \cdot y_1 = 0 \implies x = \mu_1^{-1}(U/y_1)$$

Critiques de Rosenzweig-MacArthur

Paradoxe du plancton

$$\dot{x} = f(x) - \frac{1}{Y} \mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

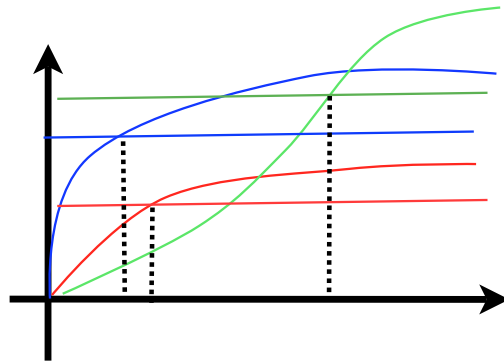
$$\dot{x} = f(x) - \sum_{i=1}^n \mu_i(x_i)$$

$$\dot{y}_i = (\varepsilon_i \mu_i(x) - m_i) \cdot y_i \quad i = 1 \dots n$$

$$(\varepsilon_i \mu_i(x) - m_i) \cdot y_i = 0$$

$$\mu_i(x) = m_i$$

$$\forall j \neq i : y_j = 0$$



Généralisation :
si p ressources alors p espèces

Paradoxe du plancton Hutchinson 1903-1991

Vol. XCV, No. 882

The American Naturalist

May-June, 1961

THE PARADOX OF THE PLANKTON*

G. E. HUTCHINSON

Osborn Zoological Laboratory, New Haven, Connecticut

Paradoxe du plancton

The problem that is presented by the phytoplankton is essentially how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials. The problem is particularly acute because there is adequate evidence from enrichment experiments that natural waters, at least in the summer, present an environment of striking nutrient deficiency, so that competition is likely to be extremely severe.

According to the principle of *competitive exclusion* (Hardin, 1960) known by many names and developed over a long period of time by many investigators (see Rand, 1952; Udvardy, 1959; and Hardin, 1960, for historic reviews), we should expect that one species alone would outcompete all the others so that in a final equilibrium situation the assemblage would reduce to a population of a single species.

Modèle Ratio-dépendant

$$\dot{x} = f(x) - \frac{1}{Y} \mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

$\frac{1}{Y} \mu(x, y) =$ Quantité de ressource prélevée par $\left\{ \begin{array}{l} \text{par consommateur} \\ \text{unite' de temps} \end{array} \right.$

1. Fonction de la "quantité des ressource" uniquement :

$$x \mapsto \mu(x) \quad \textbf{(R-MA)}$$

2. Fonction de la "quantité de ressource par consommateur":

$$x \mapsto \mu(x/y) \quad \textbf{(A-G)}$$

Modèle Ratio-dépendant



Journal of Theoretical Biology

Volume 139, Issue 3, 9 August 1989, Pages 311-326



Coupling in predator-prey dynamics: Ratio-Dependence

Roger Arditi [†], Lev R. Ginzburg [‡]

$$\begin{cases} \dot{x} &= f(x) - \frac{1}{Y} \mu(x/y) \cdot y \\ \dot{y} &= \mu(x/y) \cdot y - m \cdot y \end{cases}$$

Modèle Ratio-dépendant

(Parenthèse)

Monod (Ratio-dep) = Contois

$$\frac{\mu \cdot (x/y)}{e + (x/y)} = \frac{\mu \cdot x}{e \cdot y + x}$$

Modèle Ratio-dépendant

(Parenthèse)

40

CONTOIS, D. E. (1959). *J. gen. Microbiol.* **21**, 40–50

Kinetics of Bacterial Growth: Relationship between Population Density and Specific Growth Rate of Continuous Cultures

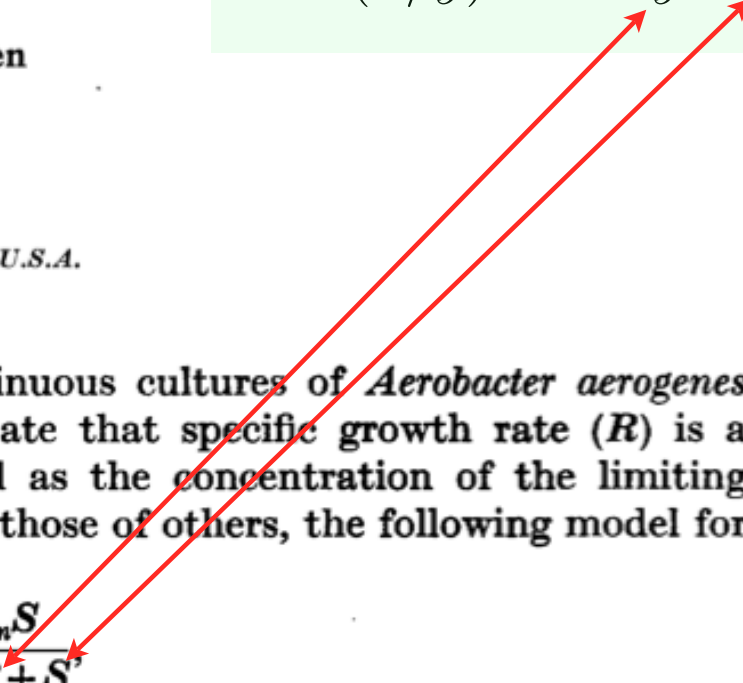
By D. E. CONTOIS*

Department of Marine Biology, University of California, La Jolla, California, U.S.A.

SUMMARY: Results from studies of continuous cultures of *Aerobacter aerogenes* growing in chemically defined media indicate that specific growth rate (R) is a function of population density (P) as well as the concentration of the limiting nutrient (S). From these observations, and those of others, the following model for bacterial growth is derived:

$$R = \frac{u_m S}{BP + S}$$

where u_m and B are growth parameters that are constants under defined conditions. This model is believed to have general applicability and to account for bacterial growth in both batch and continuous cultures.

$$\frac{\mu \cdot (x/y)}{e + (x/y)} = \frac{\mu \cdot x}{e \cdot y + x}$$


Modèle Ratio-dépendant

(Parenthèse)

$$\frac{\mu \cdot (x/y)}{e + (x/y)} = \frac{\mu \cdot x}{e \cdot y + x}$$

FORUM
FORUM
FORUM

FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

Predator-prey theory: hidden twins in ecology and microbiology

*Christian Jost, Institut national agronomique Paris-Grignon, Ecologie des populations et communautés,
16, rue Claude Bernard, F-75231 Paris cedex 05, France (christian.jost@inapg.inra.fr).*

OIKOS 90:1 (2000)

Modèle Ratio-dépendant

(Parenthèse)

$$\frac{\mu \cdot (x/y)}{e + (x/y)} = \frac{\mu \cdot x}{e \cdot y + x}$$

functional response or growth rate	reference in ecology	reference in microbiology
$\begin{cases} as & s \leq s_b \\ as_m & s \geq s_b \end{cases}$	Holling (1959) type I with added upper limit	Blackman (1905)
$\frac{as}{1+ahs} = \mu_{\max} \frac{s}{K_s+s}$	Holling (1959) type II	Monod (1942)
$a(1-e^{-cs})$	Ivlev (1961)	Teissier (1936)
$\frac{as^m}{1+ahs^m}$	Real (1977)	Moser (1958)
$\frac{\alpha s/x}{1+\alpha hs/x} = \frac{\alpha s}{x+\alpha hs}$	Arditi and Ginzburg (1989), Arditi and Akçakaya (1990)	Contois (1959)
$\mu_{\max} \frac{s}{K_s+s} \frac{1}{x}$	Hassell and Rogers (1972) (special case)	Ashby (1976)
$\mu_{\max} \frac{s}{K_s+s+cx}$	Beddington (1975), DeAngelis et al. (1975)	Roques et al. (1982) (special case)

Modèle Ratio-dépendant

Qu'est-ce-que ça
change ?

$$\begin{cases} \dot{x} &= f(x) - \frac{1}{Y} \mu(x/y) \cdot y \\ \dot{y} &= \mu(x/y) \cdot y - m \cdot y \end{cases}$$

- $Y = 1$
- $f(x) = r \cdot x \cdot (1 - x)$
- $\mu(U) = \frac{\mu \cdot U}{e + U}$

Isocline de x

$$r \cdot x \cdot (1 - x) - \frac{x}{e \cdot y + x} y = 0$$

Modèle Ratio-dépendant

Qu'est-ce-que ça
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Isocline de x

$$r \cdot x \cdot (1 - x) - \frac{\mu x}{e \cdot y + x} y = 0$$

- $x = 0$

ou

- $y = \frac{r \cdot x \cdot (1 - x)}{(\mu - r \cdot e) + r \cdot e \cdot x}$

Modèle Ratio-dépendant

Qu'est-ce-que ça
change ?

$$\begin{cases} \dot{x} &= f(x) - \frac{1}{Y} \mu(x/y) \cdot y \\ \dot{y} &= \mu(x/y) \cdot y - m \cdot y \end{cases}$$

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Complicé

Modèle Ratio-dépendant

Qu'est-ce-que ça change ?

$$\begin{cases} \dot{x} &= f(x) - \frac{1}{Y} \mu(x/y) \cdot y \\ \dot{y} &= \mu(x/y) \cdot y - m \cdot y \end{cases}$$

- $Y = 1$
- $f(x) = r \cdot x \cdot (1 - x)$
- $\mu(U) = \frac{\mu \cdot U}{e + U}$

Isocline de x

$$r \cdot x \cdot (1 - x) - \frac{x}{e \cdot y + x} y = 0$$

- $x = 0$

ou

Complicé

- $y = \frac{r \cdot x \cdot (1 - x)}{(\mu - r \cdot e) + r \cdot e \cdot x}$

Isocline de y

$$\frac{x}{y} = \frac{m \cdot e}{\mu - m} \iff y = \frac{\mu - m}{m \cdot e} \cdot x$$

C'est une droite qui passe par l'origine

Modèle Ratio-dépendant

Qu'est-ce-que ça change ?

$$\begin{cases} \dot{x} &= f(x) - \frac{1}{Y} \mu(x/y) \cdot y \\ \dot{y} &= \mu(x/y) \cdot y - m \cdot y \end{cases}$$

- $Y = 1$

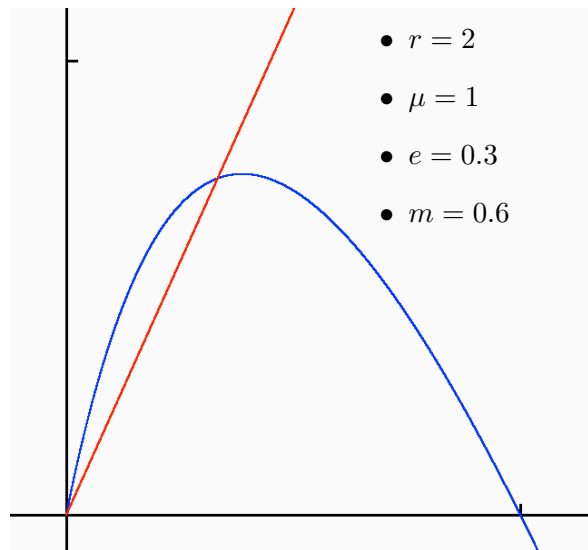
- $f(x) = r \cdot x \cdot (1 - x)$

- $\mu(U) = \frac{\mu \cdot U}{e + U}$

- $y = \frac{r \cdot x \cdot (1 - x)}{(\mu - r \cdot e) + r \cdot e \cdot x}$

Bleu : isocline de x

Rouge : isocline de y



Modèle Ratio-dépendant

Qu'est-ce-que ça change ?

$$\begin{cases} \dot{x} &= f(x) - \frac{1}{Y} \mu(x/y) \cdot y \\ \dot{y} &= \mu(x/y) \cdot y - m \cdot y \end{cases}$$

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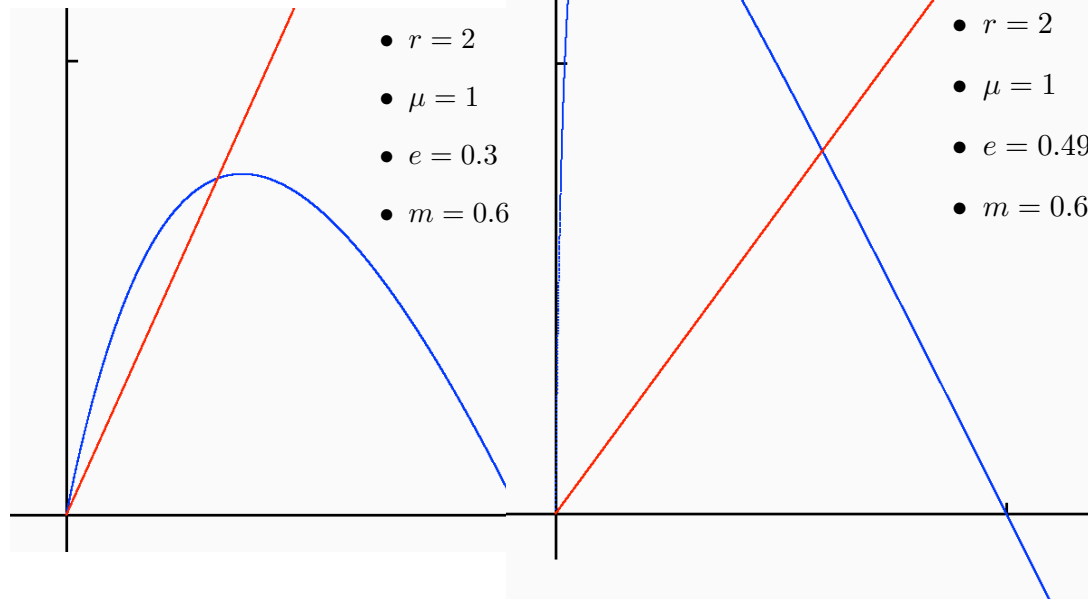
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Bleu : isocline de x

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Modèle Ratio-dépendant

Qu'est-ce-que ça change ?

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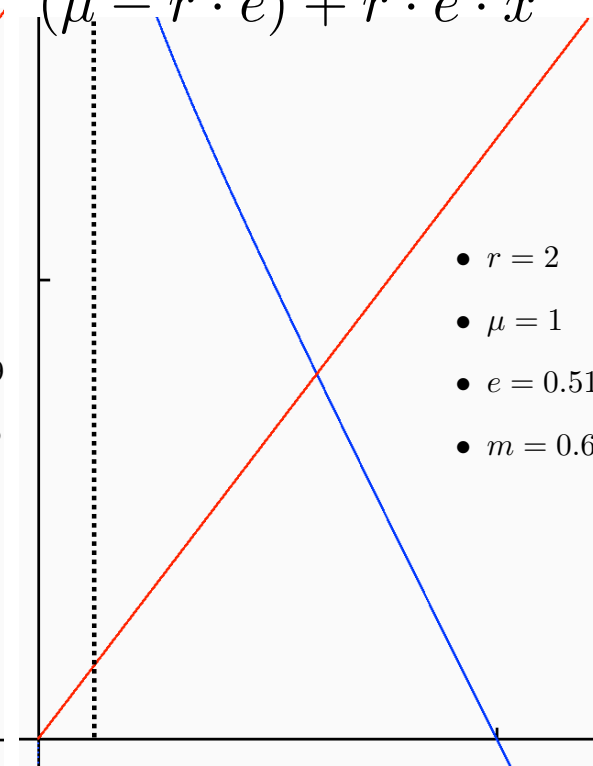
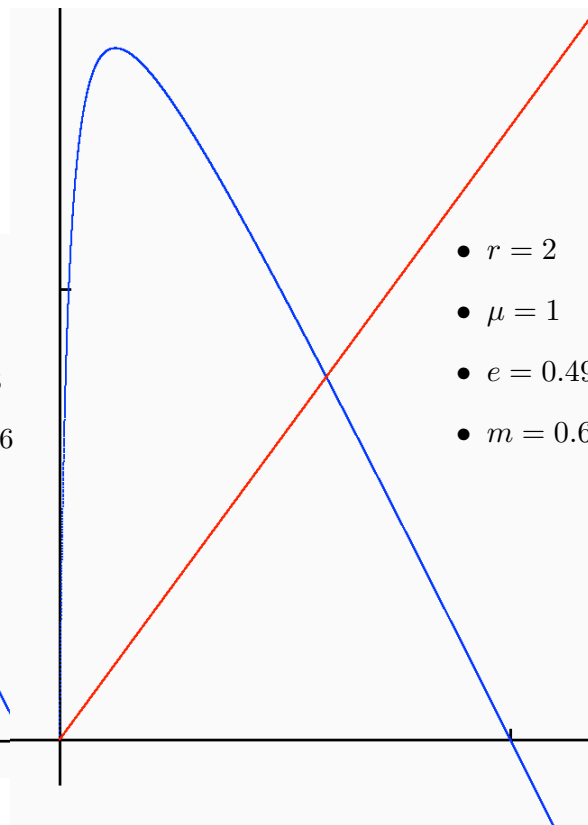
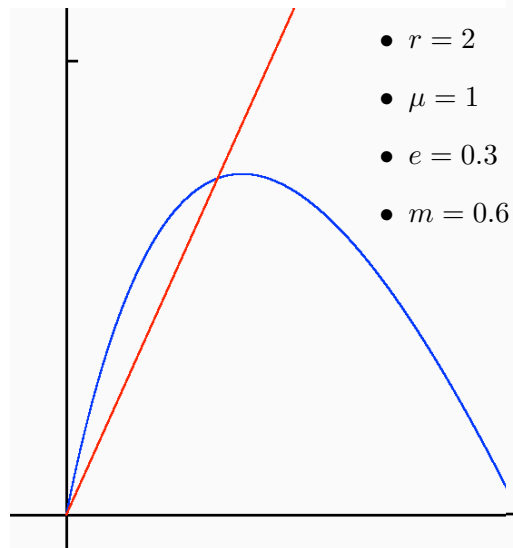
- $f(x) = r \cdot x \cdot (1 - x)$

- $\mu(U) = \frac{\mu \cdot U}{e + U}$

- $y = \frac{r \cdot x \cdot (1 - x)}{(\mu - r \cdot e) + r \cdot e \cdot x}$

Bleu : isocline de x

Rouge : isocline de y



Modèle Ratio-dépendant

Qu'est-ce-que ça change ?

$$\dot{x} = f(x) - \mu(x) \cdot y \qquad \dot{x} = f(x) - \mu(x/y) \cdot y$$

$$\dot{y} = (\mu(x) - m) \cdot y \qquad \dot{y} = (\mu(x/y) - m) \cdot y$$

$$g(x, y) = \mu(x/y)$$

$$h(x, y) = g(x, y) y$$

avec μ nulle en 0 ($\mu' > 0$) croissante bornée **concave** ($\mu'' < 0$)

- $g'_x(x, y) = \mu'(x/y) \frac{1}{y} > 0$
- $g'_y(x, y) = \mu'(x/y) \cdot \left(-\frac{x}{y^2}\right) < 0$
- $h'_x(x, y) = g'_x(x, y) y > 0$
- $h'_y(x, y) = \mu(x/y) - \frac{x}{y} \mu'(x/y)$ **Signe ?**

Modèle Ratio-dépendant

Qu'est-ce-que ça
change ?

avec μ nulle en 0 ($\mu' > 0$) croissante bornée concave ($\mu'' < 0$)

- $h'_y(x, y) = \mu(x/y) - \frac{x}{y}\mu'(x/y)$ **Signe ?**

1. $u = \frac{x}{y} \in [0; \infty)$

2. $u \mapsto \varphi(u) = \mu(u) - u\mu'(u)$

3. $\varphi(0) = 0$

4. $\varphi'(u) = \mu'(u) - \mu'(u) - u\mu''(u) > 0$

5. Donc $\varphi(u) > 0$ C.Q.F.D.

Modèle Ratio-dépendant

Qu'est-ce-que ça
change ?

$$\dot{x} = f(x) - \mu(x) \cdot y \qquad \dot{x} = f(x) - \mu(x/y) \cdot y$$

$$\dot{y} = (\mu(x) - m) \cdot y \qquad \dot{y} = (\mu(x/y) - m) \cdot y$$

$$g(x, y) = \mu(x/y)$$

$$h(x, y) = g(x, y) y$$

avec μ nulle en 0 ($\mu' > 0$) croissante bornée concave ($\mu'' < 0$)

- $g'_x(x, y) = \mu'(x/y) \frac{1}{y} > 0$
- $g'_y(x, y) = \mu'(x/y) \cdot \left(-\frac{x}{y^2}\right) < 0$
- $h'_x(x, y) = g'_x(x, y) y > 0$
- $h'_y(x, y) = \mu(x/y) - \frac{x}{y} \mu'(x/y) > 0$

Modèle Ratio-dépendant

Qu'est-ce-que ça change ?

$$g(x, y) = \mu(x/y)$$

$$h(x, y) = g(x, y) y$$

$$\bullet g'_x(x, y) = \mu'(x/y) \frac{1}{y} > 0$$

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$$\bullet h'_x(x, y) = g'_x(x, y) y > 0$$

$$\bullet h'_y(x, y) = \mu(x/y) - \frac{x}{y} \mu'(x/y) > 0$$

$$\begin{aligned} \dot{x} &= f(x) - \mu(x/y) \cdot y \\ \dot{y} &= (\mu(x/y) - m) \cdot y \end{aligned} \iff \begin{aligned} \dot{x} &= f(x) - h(x, y) \\ \dot{y} &= h(x, y) - m \cdot y \end{aligned}$$

$$\left(\begin{array}{c|c} \frac{f'(x_e) - h'_x(x_e, y_e)}{h'_x(x_e, y_e)} & \frac{-h'_y(x_e, y_e)}{h'_y(x_e, y_e) - m} \end{array} \right)$$

$$\left(\begin{array}{c|c} \frac{f'(x_e) - h'_x(x_e, y_e)}{h'_x(x_e, y_e)} & \frac{-h'_y(x_e, y_e)}{-(x/y)\mu'(x_e, y_e)} \end{array} \right)$$

$$\lambda^2 - (f' - h'_x - (x/y)\mu')\lambda + [(f' - h'_x)(-(x/y)\mu') + h'_x h'_y] = 0$$

Modèle Ratio-dépendant

Qu'est-ce-que ça change ?

$$g(x, y) = \mu(x/y)$$

$$h(x, y) = g(x, y) y$$

$$\bullet g'_x(x, y) = \mu'(x/y) \frac{1}{y} > 0$$

$$\bullet g'_y(x, y) = \mu'(x/y) \cdot \left(-\frac{x}{y^2}\right) < 0$$

$$\bullet h'_x(x, y) = g'_x(x, y) y > 0$$

$$\bullet h'_y(x, y) = \mu(x/y) - \frac{x}{y} \mu'(x/y) > 0$$

$$\lambda^2 - (f' - h'_x - (x/y)\mu')\lambda + [(f' - h'_x)(-(x/y)\mu') + h'_x h'_y] = 0$$

$$\Phi(x, y) = 0 \implies \Phi'_x dx + \Phi'_y dy = 0 \quad \text{Isocline des } x$$

$$f(x) - h(x, y) = 0 \implies (f' - h'_x)dx - h'_y dy = 0 \implies \frac{dy}{dx} = \frac{(f' - h'_x)}{h'_y}$$

$$\text{Pente négative} \implies (f' - h'_x) < 0$$

Modèle Ratio-dépendant

Qu'est-ce-que ça change ?

$$g(x, y) = \mu(x/y)$$

$$h(x, y) = g(x, y) y$$

$$\bullet g'_x(x, y) = \mu'(x/y) \frac{1}{y} > 0$$

$$\bullet g'_y(x, y) = \mu'(x/y) \cdot \left(-\frac{x}{y^2}\right) < 0$$

$$\bullet h'_x(x, y) = g'_x(x, y) y > 0$$

$$\bullet h'_y(x, y) = \mu(x/y) - \frac{x}{y} \mu'(x/y) > 0$$

$$\lambda^2 - (f' - h'_x - (x/y)\mu')\lambda + [(f' - h'_x)(-(x/y)\mu') + h'_x h'_y] = 0$$

< 0 > 0

$$\Phi(x, y) = 0 \implies \Phi'_x dx + \Phi'_y dy = 0$$

$$f(x) - h(x, y) = 0 \implies (f' - h'_x)dx - h'_y dy = 0 \implies \frac{dy}{dx} = \frac{(f' - h'_x)}{h'_y}$$

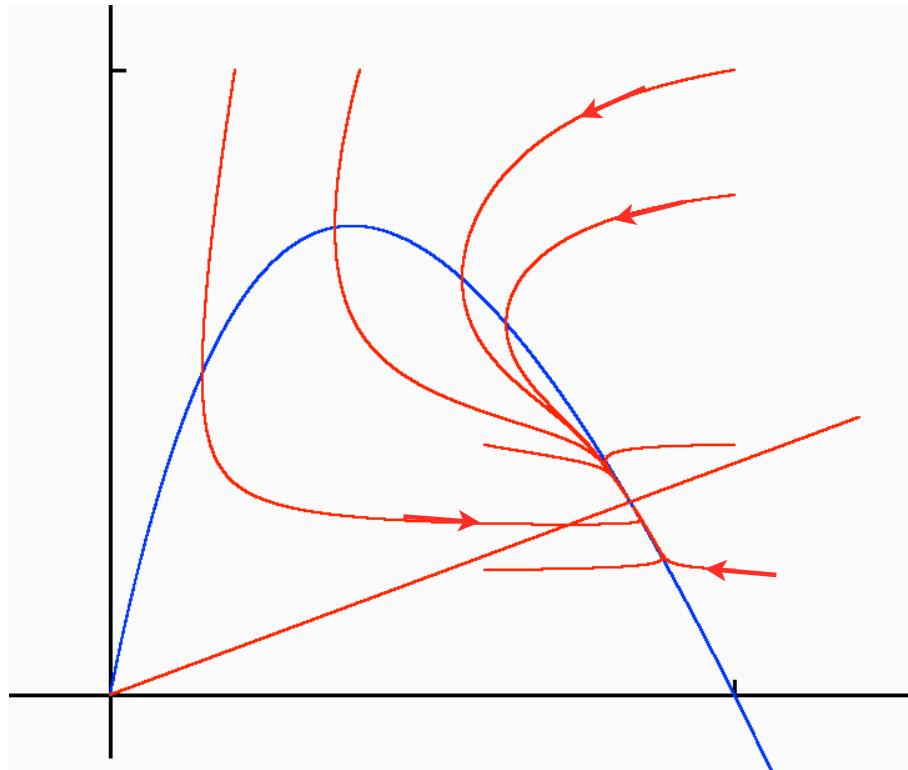
$$\text{Pente négative} \implies (f' - h'_x) < 0$$

Donc l'équilibre est stable en tous les points où l'isocline des x est de pente négative

Modèle Ratio-dépendant

Qu'est-ce-que ça
change ?

Donc l'équilibre est stable en tous les points où l'isocline des
x est de pente négative

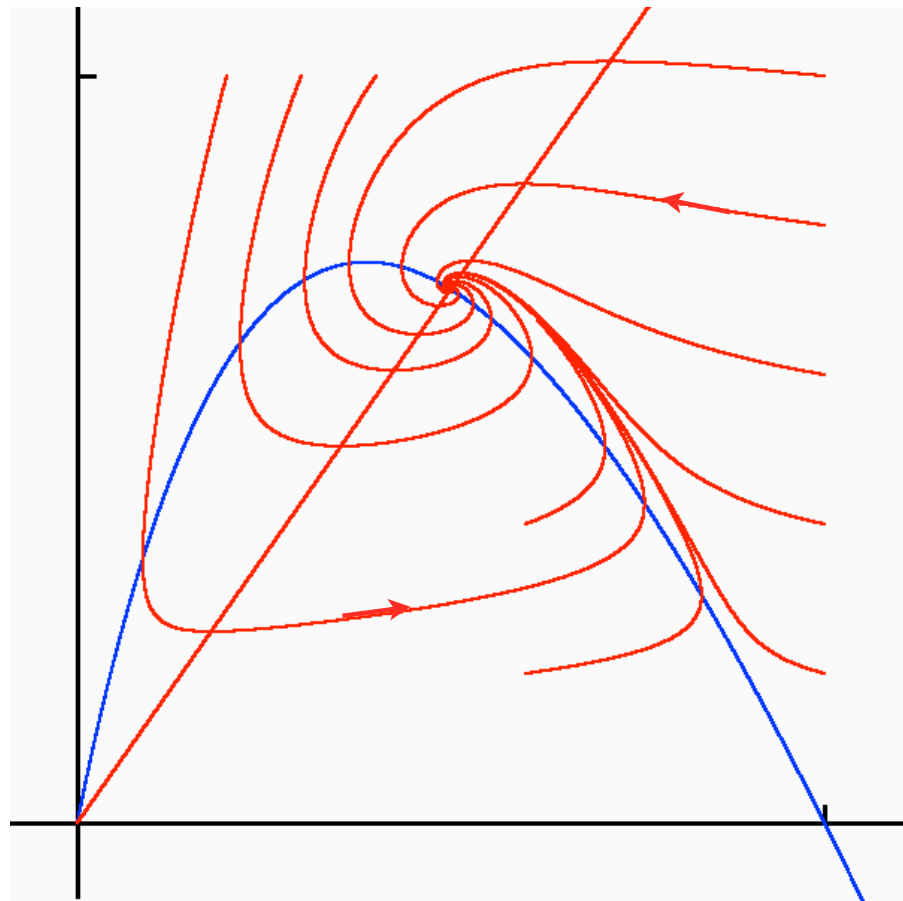


$$m = 0.9$$

Modèle Ratio-dépendant

Qu'est-ce-que ça
change ?

Donc l'équilibre est stable en tous les points où l'isocline des
x est de pente négative

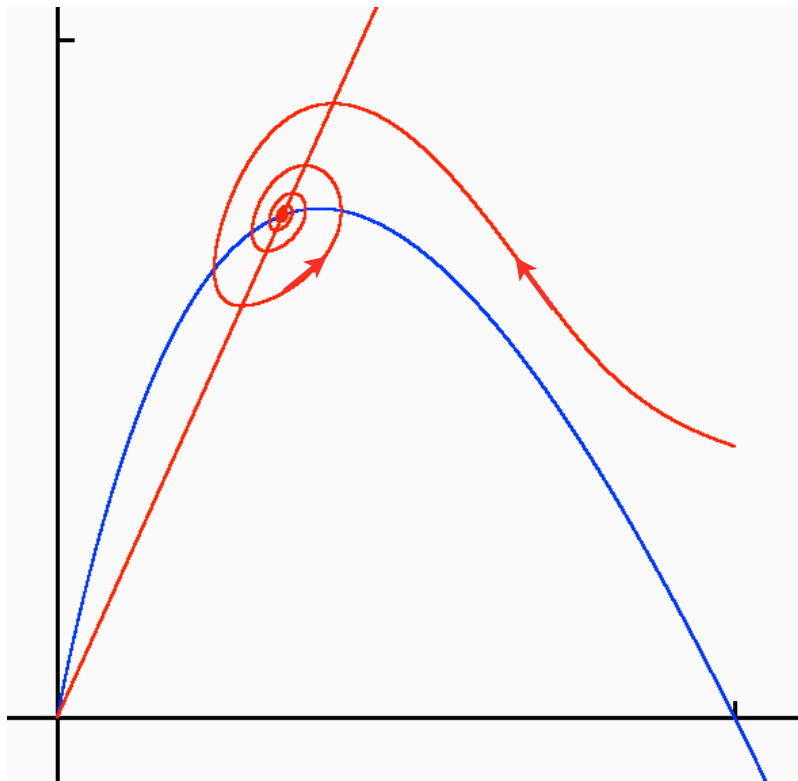


$$m = 0.7$$

Modèle Ratio-dépendant

Qu'est-ce-que ça
change ?

Donc l'équilibre est stable en tous les points où l'isocline des
x est de pente négative



$$m = 0.6$$

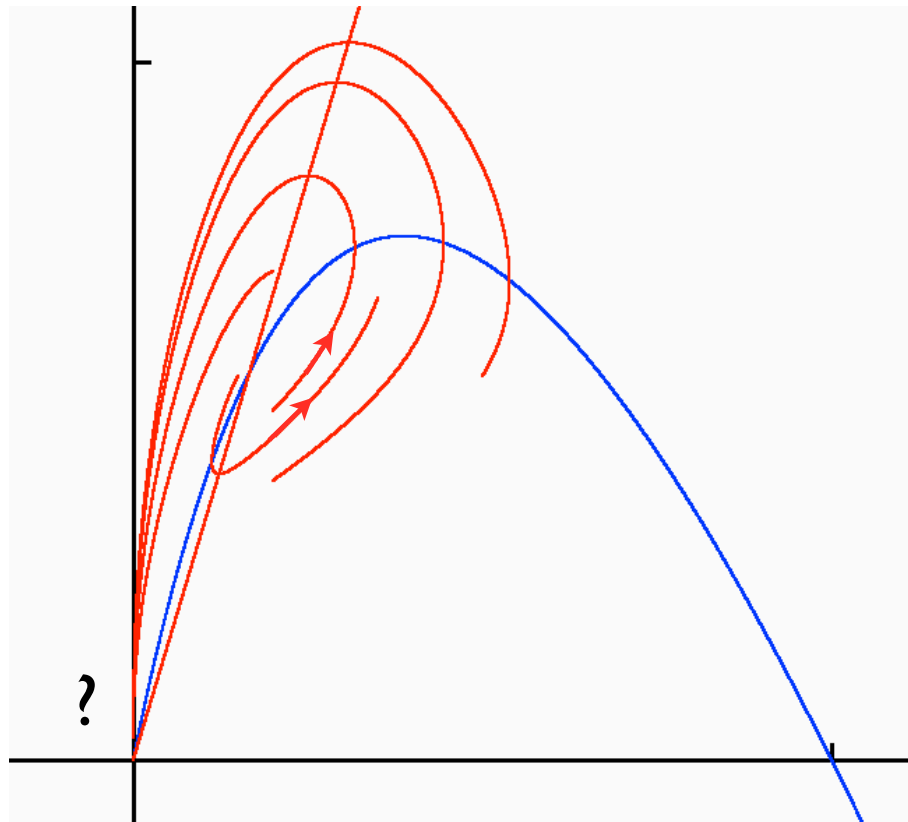
Pente positive mais
stable quand même

Modèle Ratio-dépendant

Qu'est-ce-que ça
change ?

Donc l'équilibre est stable en tous les points où l'isocline des
x est de pente négative

Et une partie de la portion de pente positive



$m = 0.5$

Instable

Modèle Ratio-dépendant

$$\dot{x} = f(x) - \mu(x) \cdot y$$

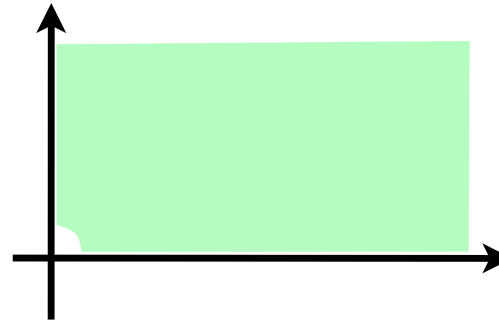
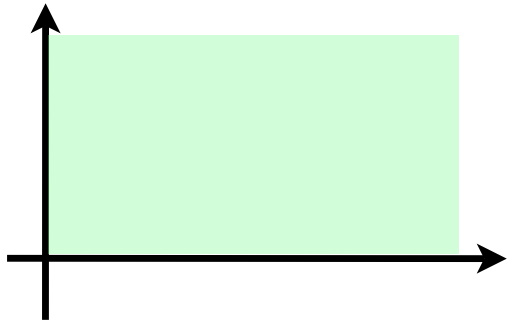
$$\dot{y} = (\mu(x) - m) \cdot y$$

$$\dot{x} = f(x) - \mu(x/y) \cdot y$$

$$\dot{y} = (\mu(x/y) - m) \cdot y$$

$\mu(0/0)$ pas défini

Modèle non défini en (0,0)



Modèle Ratio-dépendant

$$\dot{x} = f(x) - \mu(x) \cdot y$$

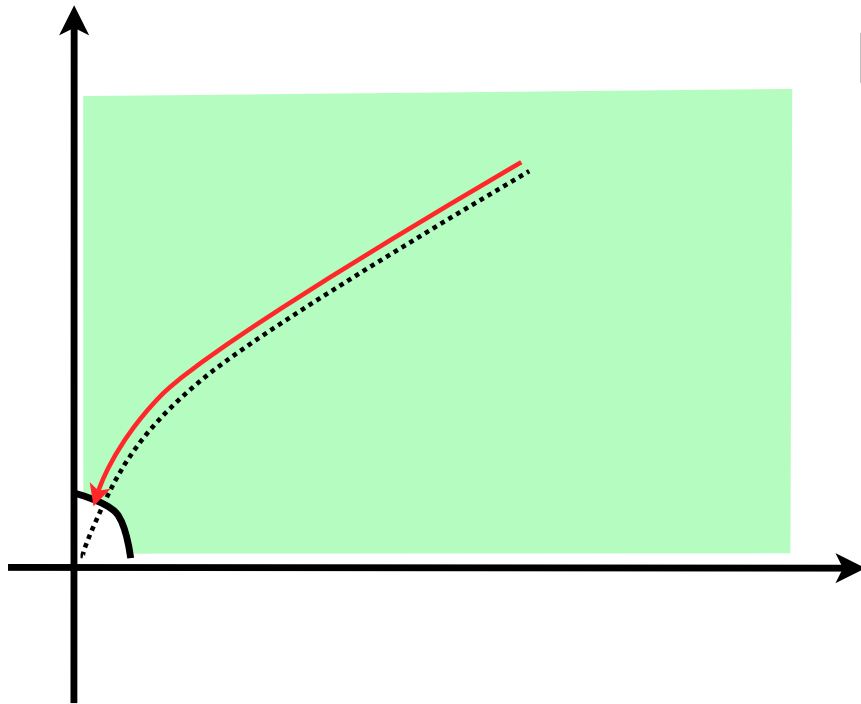
$$\dot{y} = (\mu(x) - m) \cdot y$$

$$\dot{x} = f(x) - \mu(x/y) \cdot y$$

$$\dot{y} = (\mu(x/y) - m) \cdot y$$

$\mu(0/0)$ pas défini

Modèle non défini en (0,0)



Que se passe-t-il à l'origine ?

Bulletin of Mathematical Biology (1999) **61**, 19–32
Article No. bulm.1998.0072
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About Deterministic Extinction in Ratio-dependent Predator–Prey Models

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Etude mathématique complexe

Que se passe-t-il à l'origine ?

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Extinction in Predator–Prey Models

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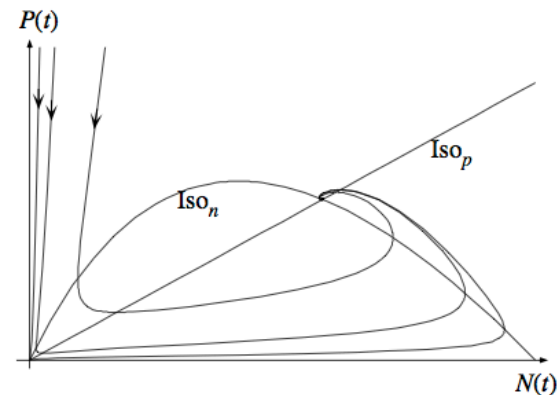


Figure 2. The non-trivial equilibrium is a global attractor and $(0, 0)$ behaves like a saddle point, $S < Q + R$. Parameter values are $R = 0.5$, $Q = 0.79$, $S = 1.0$.

Que se passe-t-il à l'origine ?

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C. Jost et al.

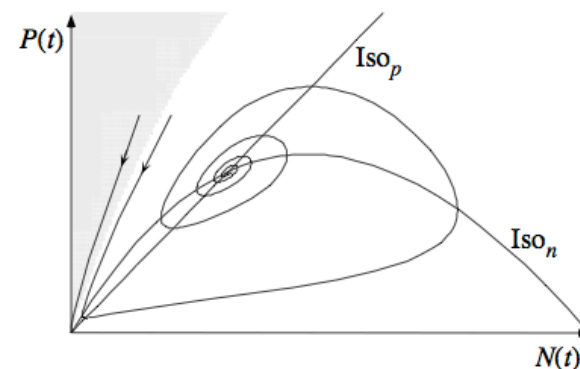


Figure 3. The non-trivial equilibrium is locally stable, but $(0, 0)$ becomes also attractive, $S > Q + R$. The white area is the basin of attraction of the non-trivial equilibrium, the gray area is the one of equilibrium $(0, 0)$. Parameter values are $R = 0.5$, $Q = 0.79$, $S = 1.66$.

Que se passe-t-il à l'origine ?

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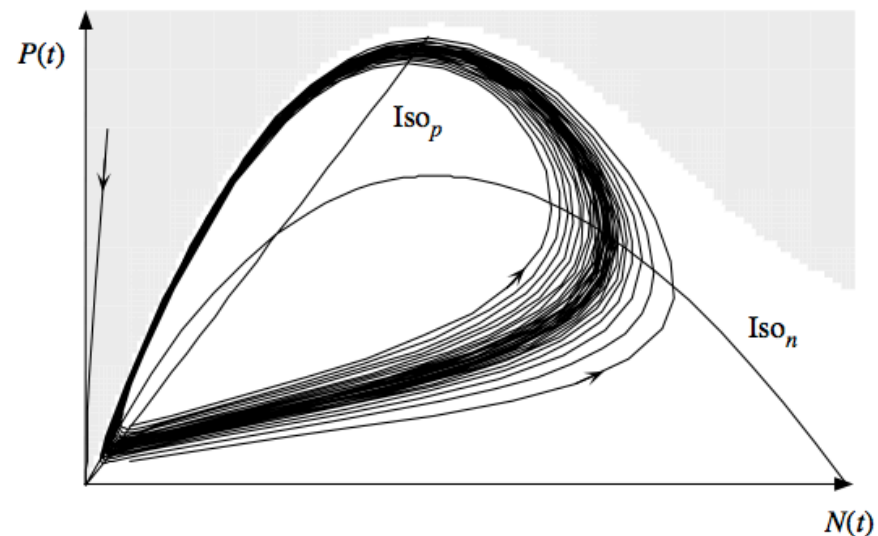


Figure 4. The non-trivial equilibrium is unstable and $(0, 0)$ becomes attractive, $S > Q + R$. There are two attractors, a stable limit cycle and $(0, 0)$. Parameter values are $R = 0.5$, $Q = 0.79$, $S = 1.78$.

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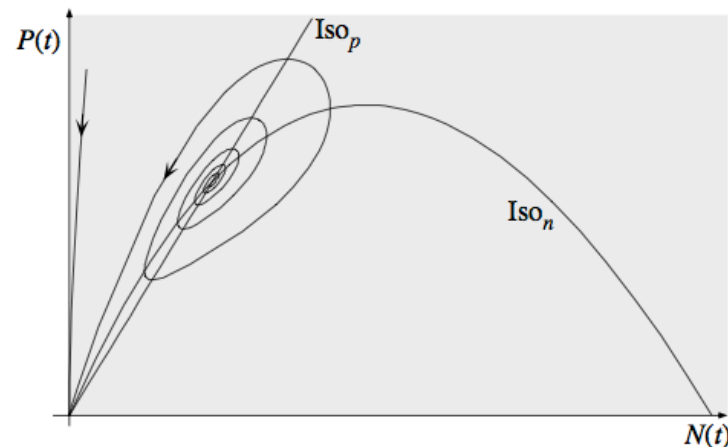
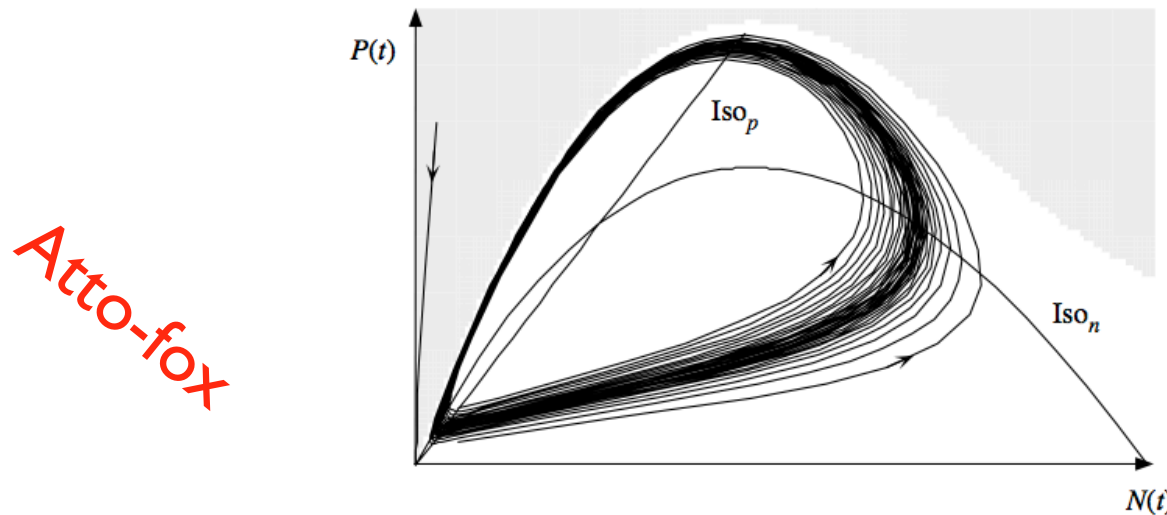


Figure 5. The equilibrium $(0, 0)$ is a global attractor, $S > Q + R$. Parameter values are $R = 0.5$, $Q = 0.79$, $S = 1.85$. There is no formal proof for the global attractivity.

Que se passe-t-il à l'origine ?

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C. Jost et al.



Atto-fox

Figure 4. The non-trivial equilibrium is unstable and $(0, 0)$ becomes attractive, $S > Q + R$. There are two attractors, a stable limit cycle and $(0, 0)$. Parameter values are $R = 0.5$, $Q = 0.79$, $S = 1.78$.

form of the separatrix. This figure also shows that the limit cycles will be very sensitive to stochastic influences: random perturbations to the populations occurring while the cycle is not far from the separatrix can bring the trajectory into the basin of attraction of $(0, 0)$, thereby causing extinction. Figure 5 shows the case when

Modèle Ratio-dépendant régulier en (0,0)

Hypothèses sur $g(x, y)$

$$\dot{x} = f(x) - g(x, y) \cdot y$$

$$\dot{y} = (g(x, y) - m) \cdot y$$

1. $g(0, y) = 0$

2. Croissante en x ($g'_x > 0$)

3. Décroissante en y ($g'_y < 0$)

4. $y \mapsto g(x, y) \cdot y$ est croissante

Satisfait par :

$$g(x, y) = \mu(x/(\alpha + y))$$

avec μ nulle en 0, croissante concave, $\alpha > 0$

Modèle Ratio-dépendant régulier en (0,0)

$$\dot{x} = f(x) - g(x, y) \cdot y$$

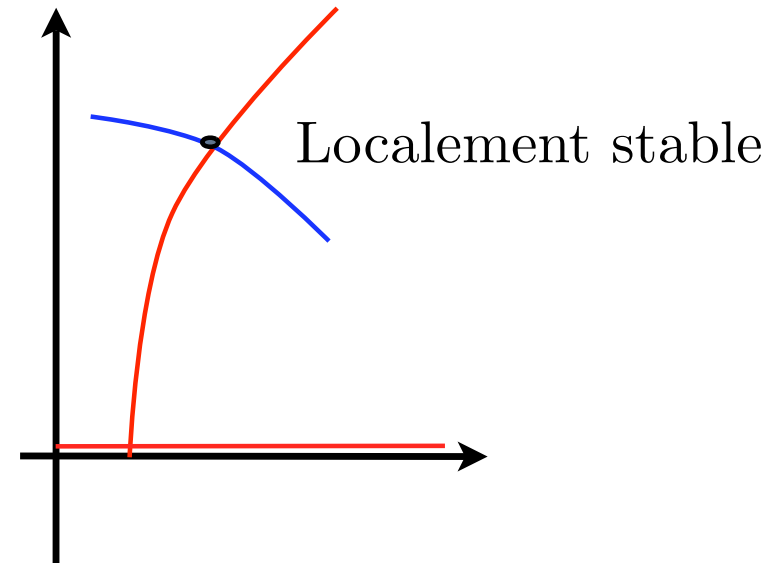
$$\dot{y} = (g(x, y) - m) \cdot y$$

Hypothèses sur $g(x, y)$

1. $g(0, y) = 0$
2. Croissante en x ($g'_x > 0$)
3. Décroissante en y ($g'_y < 0$)
4. $y \mapsto g(x, y) \cdot y$ est croissante

$$1 + 2 + 3 \implies$$

$$1 + 2 + 3 + 4 \implies$$



Modèle Ratio-dépendant régulier en (0,0)

$$\dot{x} = f(x) - g(x, y) \cdot y$$

$$\dot{y} = (g(x, y) - m) \cdot y$$

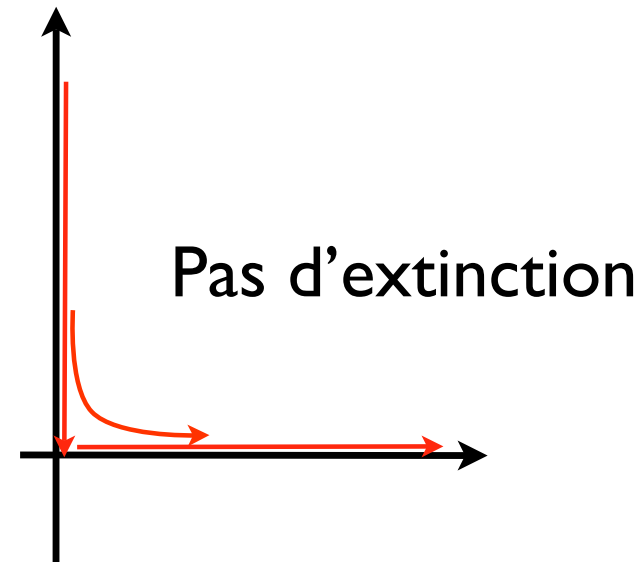
Hypothèses sur $g(x, y)$

1. $g(0, y) = 0$
2. Croissante en x ($g'_x > 0$)
3. Décroissante en y ($g'_y < 0$)
4. $y \mapsto g(x, y) \cdot y$ est croissante

$$1 + 2 + 3 \implies$$

$$1 + 2 + 3 + 4 \implies$$

$(0,0)$ est un col



Modèle Ratio-dépendant régulier en (0,0)
(simulations du)

$$\begin{cases} \dot{x} &= f(x) - \frac{1}{Y} \mu(x/y) \cdot y \\ \dot{y} &= \mu(x/y) \cdot y - m \cdot y \end{cases}$$

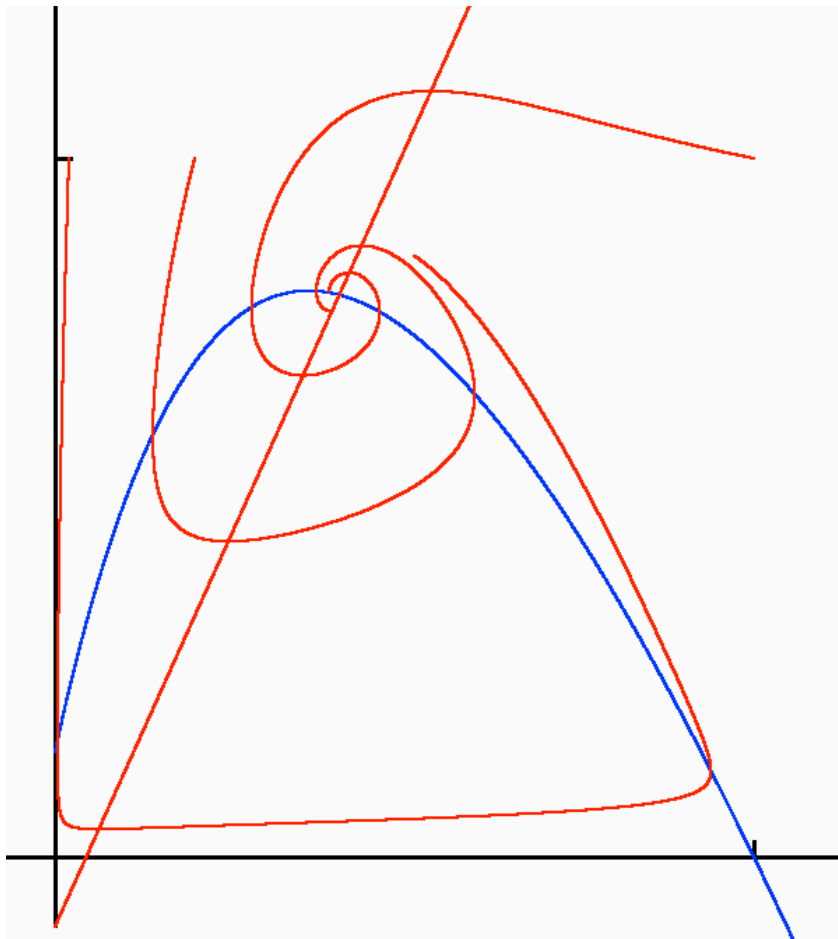
- $Y = 1$

- $f(x) = r \cdot x \cdot (1 - x)$

- $\mu(U) = \frac{\mu \cdot U}{e + U}$

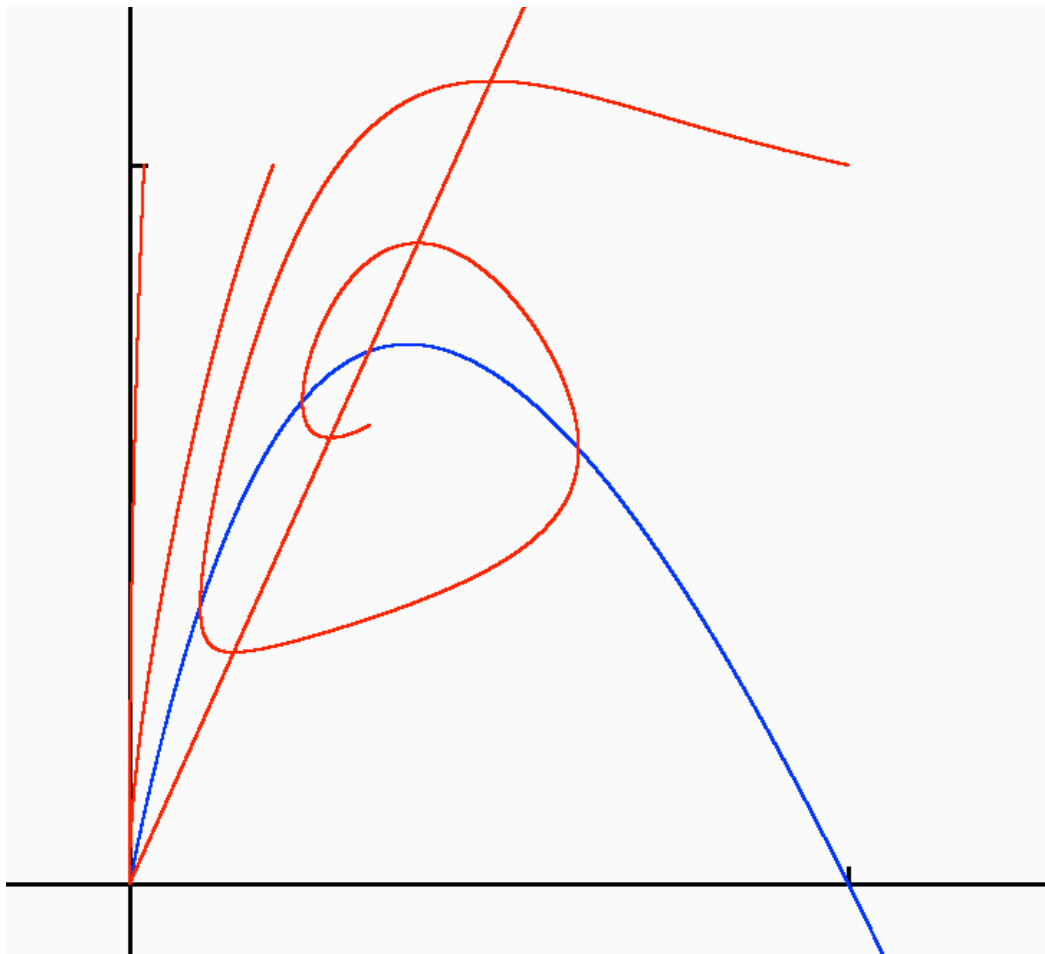
$x/y \leftarrow x/(\alpha + y)$ avec α petit.

Modèle Ratio-dépendant régulier en (0,0)
(simulations du)



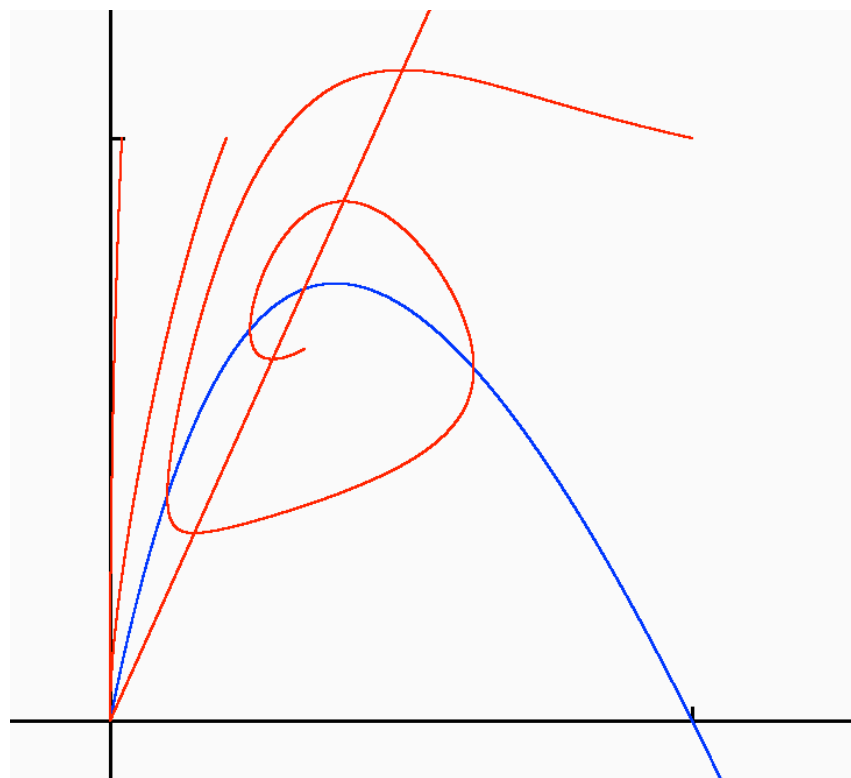
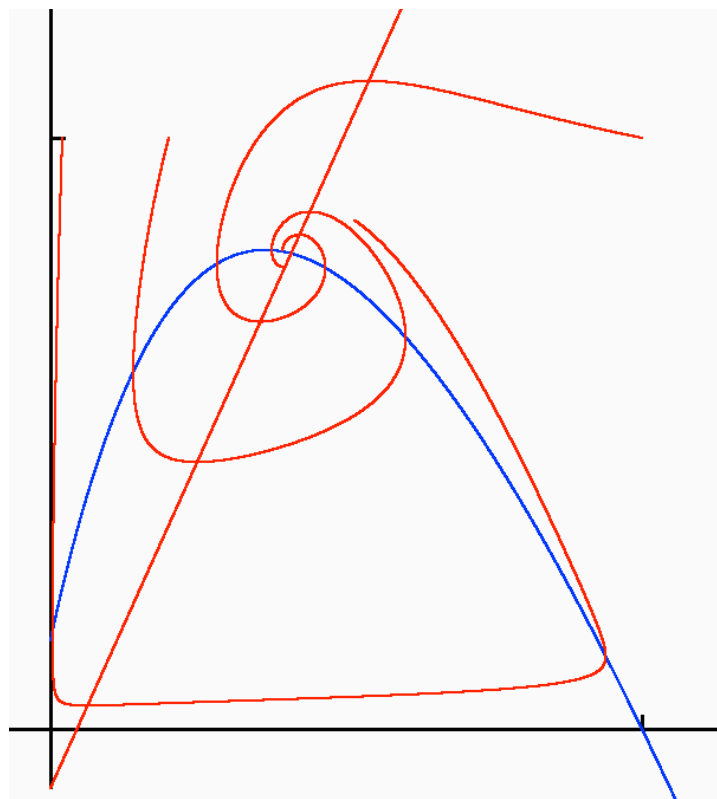
- $r = 2$
- $\mu = 1$
- $e = 0.3$
- $m = 0.6$
- $\alpha = 0.1$

Modèle Ratio-dépendant régulier en (0,0)
(simulations du)

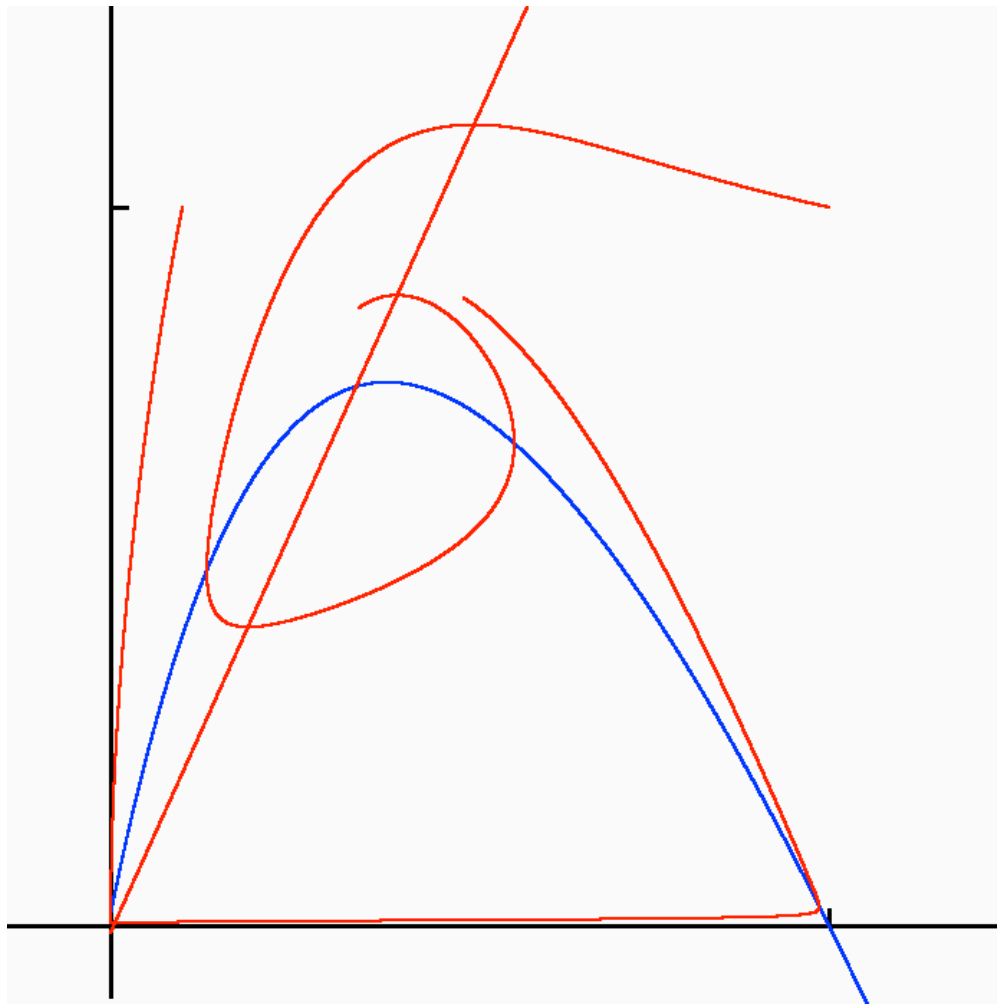


- $r = 2$
- $\mu = 1$
- $e = 0.3$
- $m = 0.6$
- $\alpha = 0$

Modèle Ratio-dépendant régulier en $(0,0)$
(simulations du)

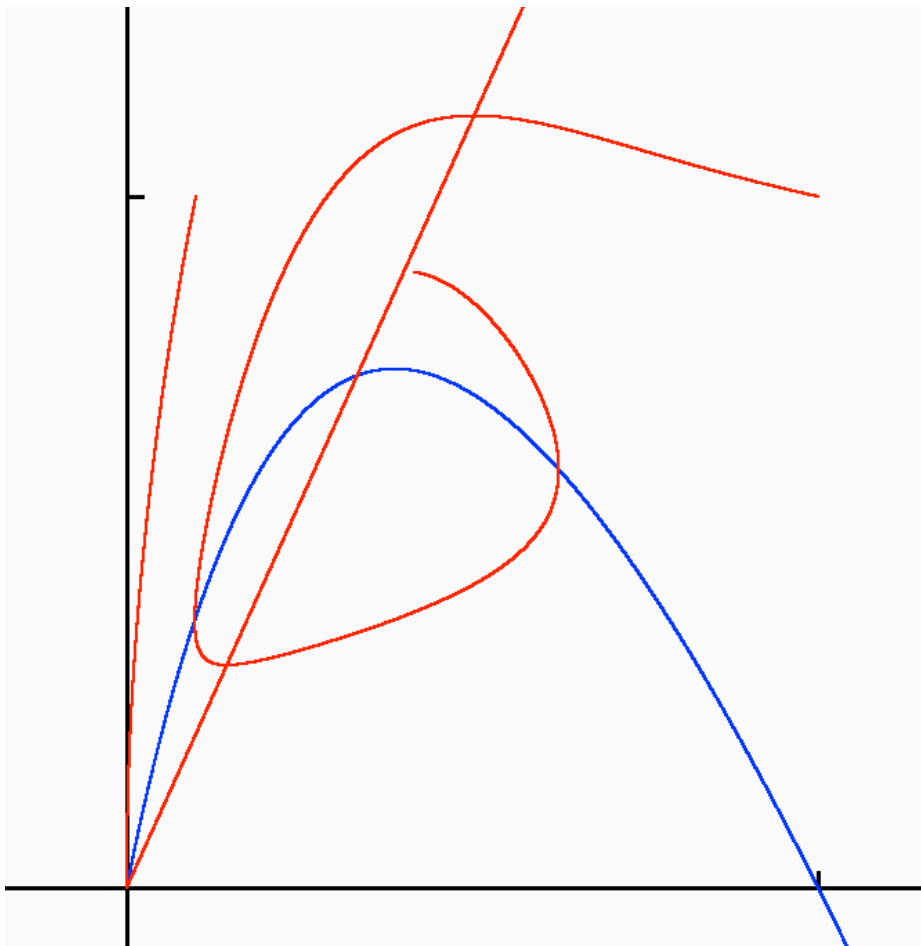


Modèle Ratio-dépendant régulier en (0,0)
(simulations du)



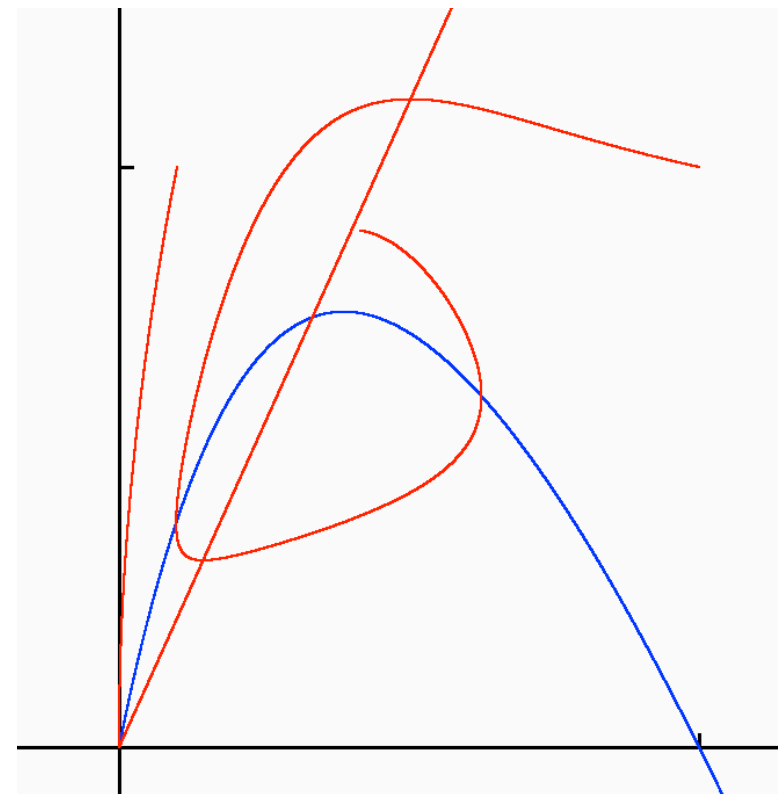
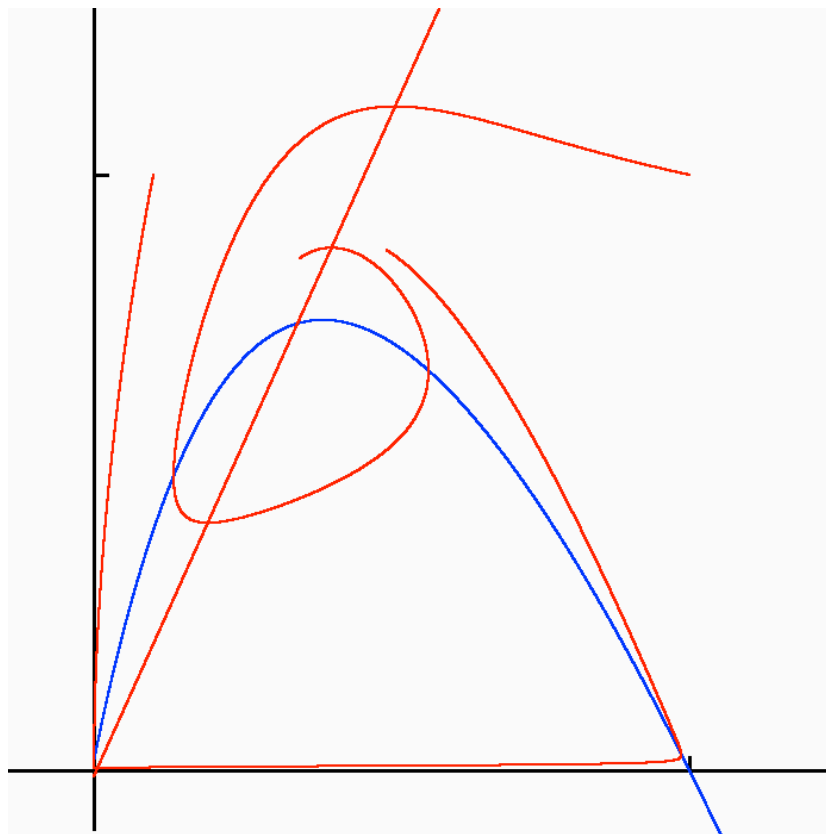
- $r = 2$
- $\mu = 1$
- $e = 0.3$
- $m = 0.6$
- $\alpha = 0.01$

Modèle Ratio-dépendant régulier en (0,0)
(simulations du)

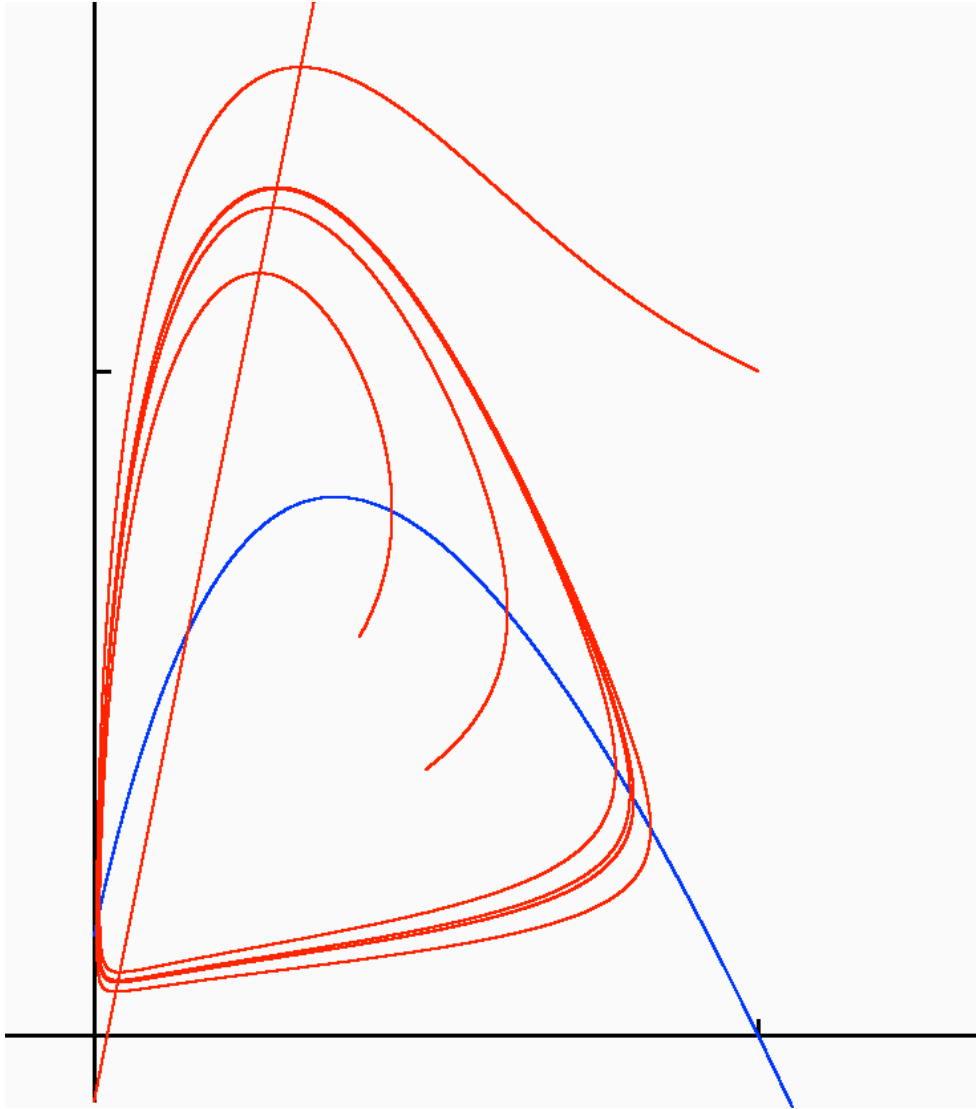


- $r = 2$
- $\mu = 1$
- $e = 0.3$
- $m = 0.6$
- $\alpha = 0$

Modèle Ratio-dépendant régulier en $(0,0)$
(simulations du)



Modèle Ratio-dépendant régulier en (0,0)
(simulations du)



- $r = 2$
- $\mu = 1$
- $e = 0.3$
- $m = 0.4$
- $\alpha = 0.1$

Modèle Ratio-dépendant
("Pur" ou "régulier")

Régulier plus simple

Le régulier ne présente pas d'extinction des proies...

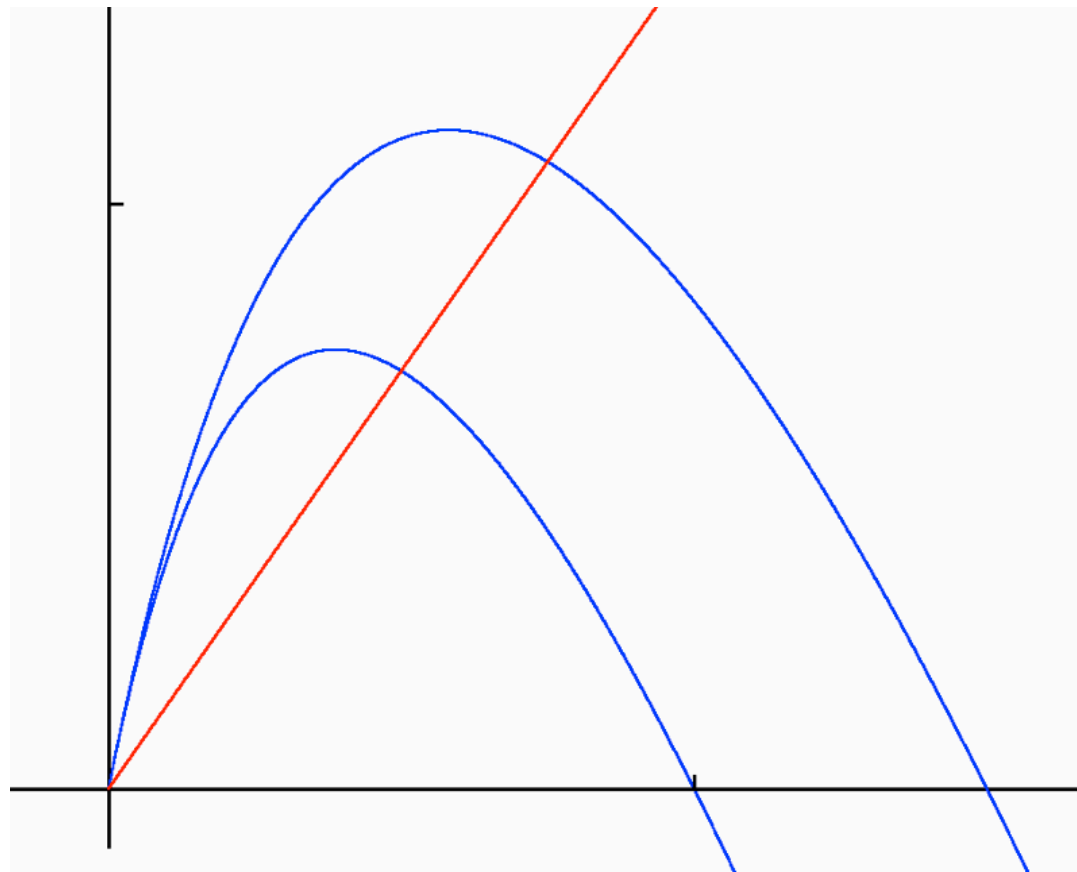
... Mais l'extinction des proies
est présente sous la forme d'atto-fox

A-G 1989

<<Thus the ratio-dependent model can describe the extinction of the system by complete prey exhaustion ; the prey-dependent model is unable to generate this outcome.>>

Modèle Ratio-dépendant

Paradoxe de l'enrichissement



$$\begin{aligned}
 \dot{x} &= U - \mu_1(x/y_1)y_1 \\
 \dot{y}_1 &= \mu_1(x/y_1)y_1 - \mu_2(y_1/y_2)y_2 \\
 \dot{y}_2 &= \mu_2(y_1/y_2)y_2 - \mu_3(y_2/y_3)y_3 \\
 \dot{y}_3 &= \mu_3(y_2/y_3)y_3 - m \cdot y_3
 \end{aligned}$$

Réponse d'une chaîne trophique ?

$$\begin{aligned}
(1) \quad & 0 = U - \mu_1(x/y_1)y_1 \\
(2) \quad & 0 = \mu_1(x/y_1)y_1 - \mu_2(y_1/y_2)y_2 \\
(3) \quad & 0 = \mu_2(y_1/y_2)y_2 - \mu_3(y_2/y_3)y_3 \\
(4) \quad & 0 = \mu_3(y_2/y_3)y_3 - m \cdot y_3
\end{aligned}$$

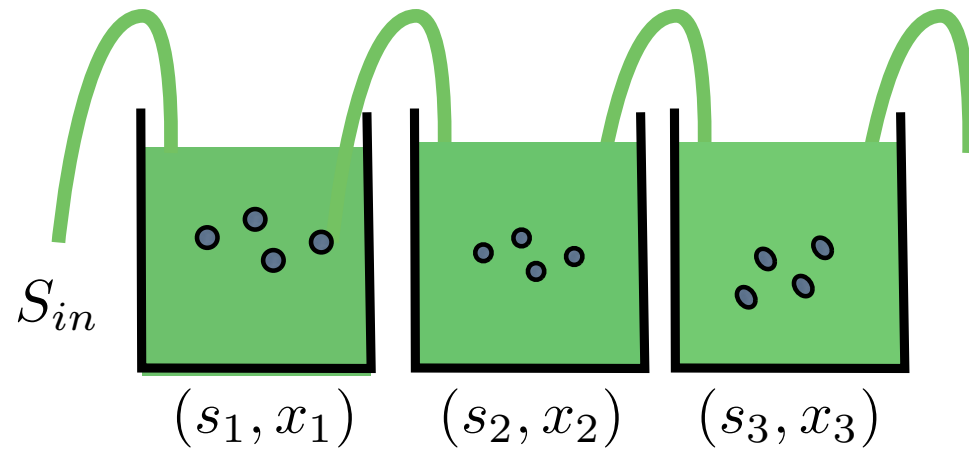
$$(1 + 2 + 3 + 4) \implies U - m \cdot y_3 = 0 \implies y_3 = U/m$$

$$(4) \implies \mu_3(y_2/y_3) = m \implies y_2 = y_3 \mu_3^{-1}(m) = U \mu_3^{-1}(m)/m$$

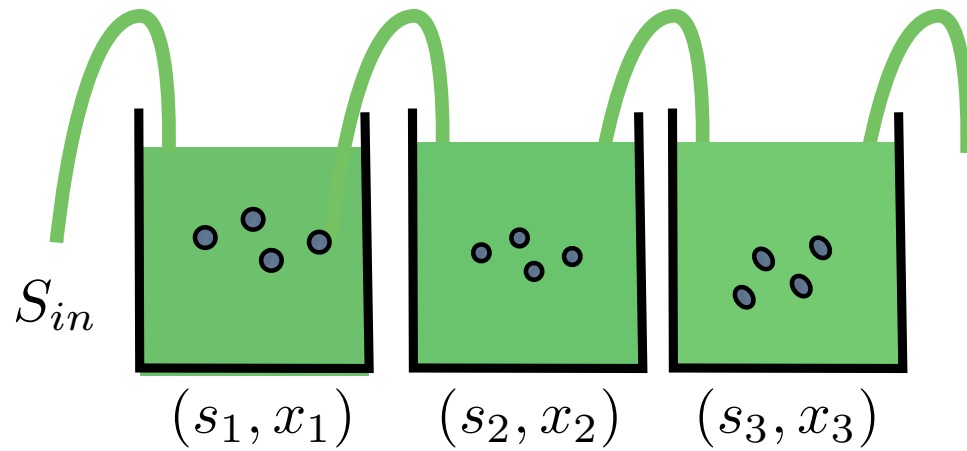
$$(3) \implies \mu_2(y_1/y_2) \mu_3^{-1}(m) = m \implies y_1 = y_2 \mu_2^{-1} \left(\frac{m}{\mu_3^{-1}(m)} \right) = U \cdot c$$

**etc.... Toutes les populations répondent
en croissant linéairement**

Cascades de chemostats

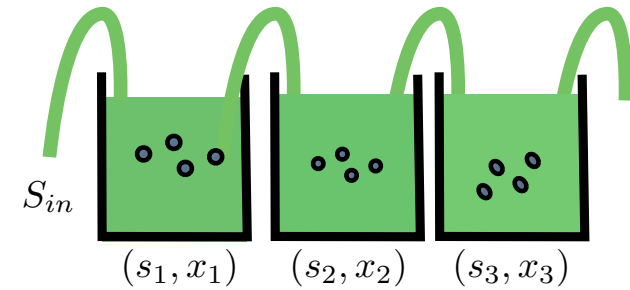


Cascades de chemostats



$$\begin{aligned} \dot{s} &= d \cdot (S_{in} - s) - \mu(s)x & \dot{s} &= d \cdot (S_{in} - s) - \nu(s/x)x \\ \dot{x} &= (\mu(s) - d) \cdot x & \dot{x} &= (\nu(s/x) - d) \cdot x \end{aligned}$$

Cascades de chemostats

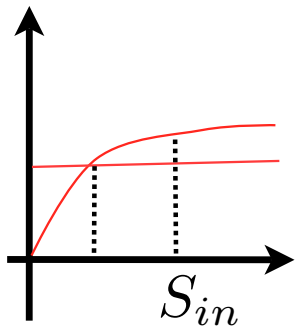


$$\dot{s} = d \cdot (S_{in} - s) - \mu(s)x$$

$$\dot{x} = (\mu(s) - d) \cdot x$$

$$\text{Si } S_{in} > \mu^{-1}(d) \quad \begin{cases} x_e = S_{in} - s_e \\ s_e = \mu^{-1}(d) \end{cases}$$

$$\text{Si } S_{in} \leq \mu^{-1}(d) \quad \begin{cases} x_e = 0 \\ s_e = S_{in} \end{cases}$$



$$\dot{s}_1 = d \cdot (S_{in} - s_1) - \mu(s_1)x_1$$

$$\dot{x}_1 = (\mu(s_1) - d) \cdot x_1$$

$$\dot{s}_2 = d \cdot (s_1 - s_2) - \mu(s_2)x_2$$

$$\dot{x}_2 = (\mu(s_2) - d) \cdot x_2$$

$$\dot{s}_3 = d \cdot (s_2 - s_3) - \mu(s_3)x_3$$

$$\dot{x}_3 = (\mu(s_3) - d) \cdot x_3$$

$$\begin{pmatrix} s_{1,e} = \mu^{-1}(d) \\ x_{1,e} = S_{in} - s_{1,e} \end{pmatrix} \begin{pmatrix} s_{2,e} = s_{1,e} \\ x_{2,e} = 0 \end{pmatrix} \begin{pmatrix} s_{3,e} = s_{1,e} \\ x_{3,e} = 0 \end{pmatrix}$$

Cascades de chemostats

$$\dot{s} = d \cdot (S_{in} - s) - \nu(s/x)x$$

$$\dot{x} = (\nu(s/x) - d) \cdot x$$

Si $d > \max \nu(\cdot)$ alors $x_e = 0$ et $s_e = S_{in}$

sinon

$$s_e + x_e = S_{in}$$

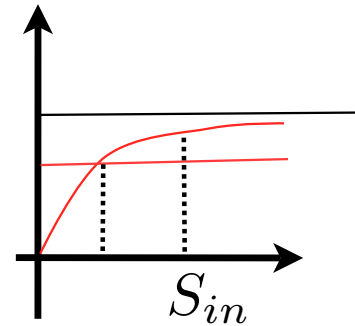
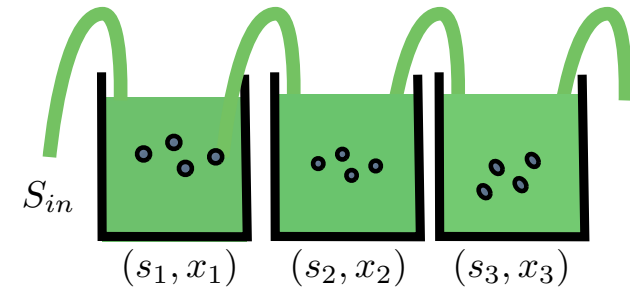
$$\nu(s_e/x_e) = d$$

$$s_e = \frac{S_{in}}{1 + \nu^{-1}(d)}$$

$$s_e/x_e = \nu^{-1}(d)$$

$$s_e = S_{in} \frac{\nu^{-1}(d)}{1 + \nu^{-1}(d)}$$

$$x_e = S_{in} \frac{1}{1 + \nu^{-1}(d)}$$



Lessivage indépendant de S_{in}

Cascades de chemostats

$$\dot{s} = d \cdot (S_{in} - s) - \nu(s/x)x$$

$$\dot{x} = (\nu(s/x) - d) \cdot x$$

$$s_e + x_e = S_{in}$$

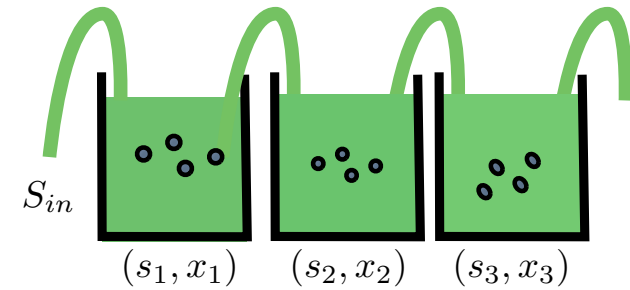
$$\nu(s_e/x_e) = d$$

$$s_e = \frac{S_{in}}{1 + \nu^{-1}(d)}$$

$$s_e/x_e = \nu^{-1}(d)$$

$$s_e = S_{in} \frac{\mu^{-1}(d)}{1 + \mu^{-1}(d)}$$

$$x_e = S_{in} \frac{1}{1 + \mu^{-1}(d)}$$



$$x_{1e} = S_{in} \frac{1}{1 + \nu^{-1}(d)}$$

Cascades de chemostats

$$\dot{s} = d \cdot (S_{in} - s) - \nu(s/x)x$$

$$\dot{x} = (\nu(s/x) - d) \cdot x$$

$$s_e + x_e = S_{in}$$

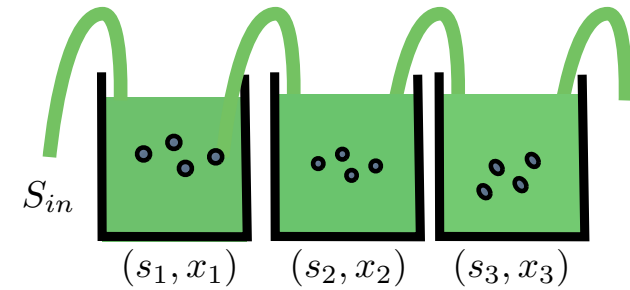
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$$x_e = S_{in} \frac{1}{1 + \mu^{-1}(d)}$$



Progression géométrique
décroissante

$$x_{1e} = S_{in} \frac{1}{1 + \mu^{-1}(d)}$$

$$x_{2e} = S_{in} \frac{\mu^{-1}(d)}{(1 + \mu^{-1}(d))^2}$$

$$x_{3e} = S_{in} \frac{(\mu^{-1}(d))^2}{(1 + \mu^{-1}(d))^3}$$

Cascades de chemostats

$$\dot{s} = d \cdot (S_{in} - s) - \nu(s/x)x$$

$$\dot{x} = (\nu(s/x) - d) \cdot x$$

$$s_e + x_e = S_{in}$$

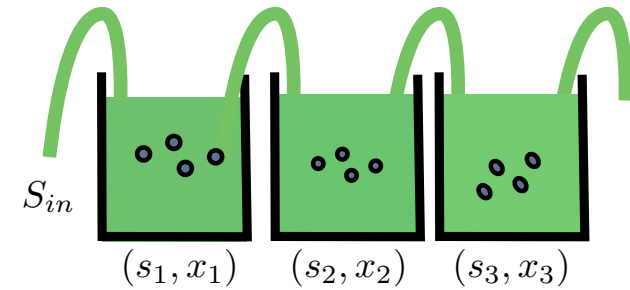
$$\nu(s_e/x_e) = d$$

$$s_e = \frac{S_{in}}{1 + \nu^{-1}(d)}$$

$$s_e/x_e = \nu^{-1}(d)$$

$$s_e = S_{in} \frac{\mu^{-1}(d)}{1 + \mu^{-1}(d)}$$

$$x_e = S_{in} \frac{1}{1 + \mu^{-1}(d)}$$



$$x_{1e} = S_{in} \frac{1}{1 + \nu^{-1}(d)}$$

$$x_{1e} = S_{in} \frac{1}{1 + \nu^{-1}(d)}$$

$$x_{2e} = S_{in} \frac{\nu^{-1}(d)}{(1 + \nu^{-1}(d))^2}$$

$$x_{1e} = S_{in} \frac{1}{1 + \mu^{-1}(d)}$$

$$x_{2e} = S_{in} \frac{\mu^{-1}(d)}{(1 + \mu^{-1}(d))^2}$$

$$x_{3e} = S_{in} \frac{(\mu^{-1}(d))^2}{(1 + \mu^{-1}(d))^3}$$

Cascades de chemostats

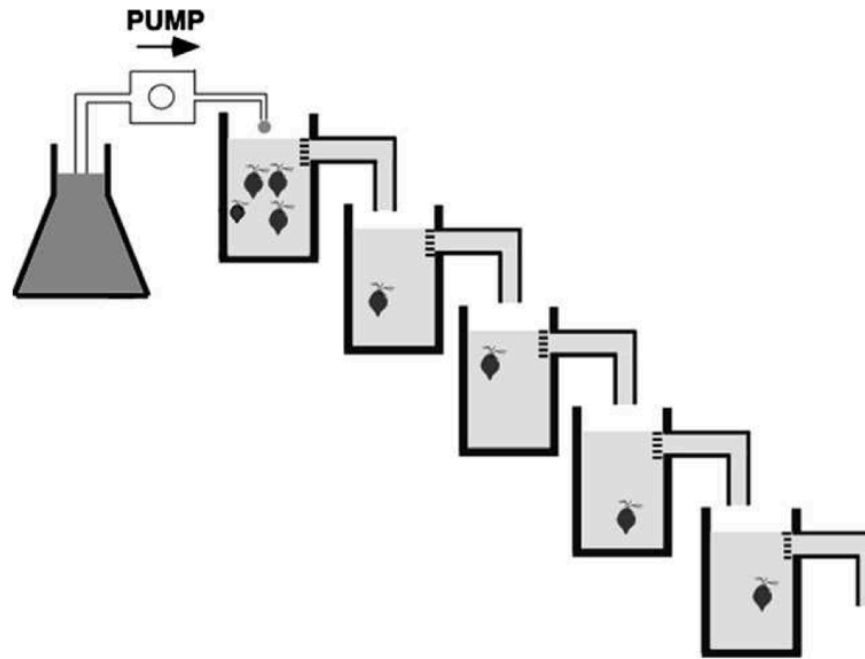
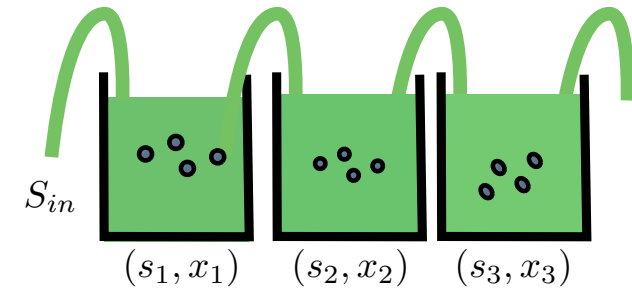


Figure 4.1. General experimental setup of the cascade of five chambers. Algae are pumped at constant flow from a stirred tank into the cascade. Starting with an inoculum of cladocerans in each chamber, populations increase or decline until an equilibrium is reached after a few weeks. Filters prevent the passage of newborn cladocerans through the cascade. After Arditi and Saïah (1992), with permission of the Ecological Society of America.

Cascades de chemostats

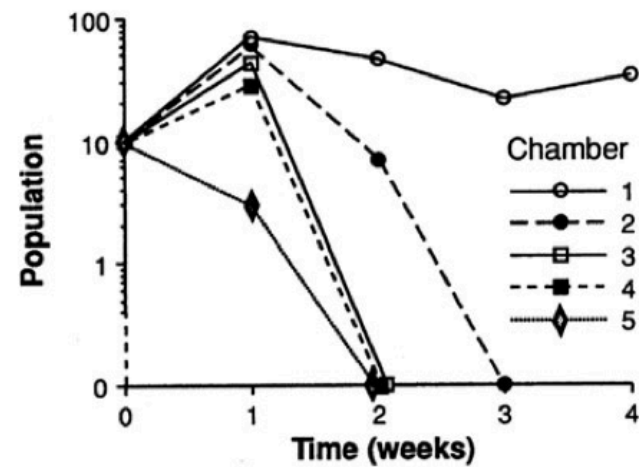
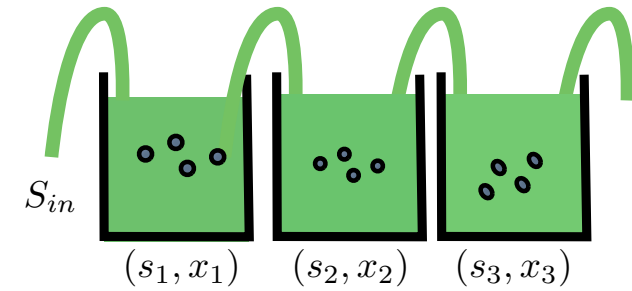


Figure 4.2. Population dynamics (log scale) of *Daphnia magna* in the five chambers of the cascade. With the exception of the first chamber, all populations declined to extinction, as predicted by the prey-dependent hypothesis. After Arditi and Saïah (1992), with permission of the Ecological Society of America.

Cascades de chemostats

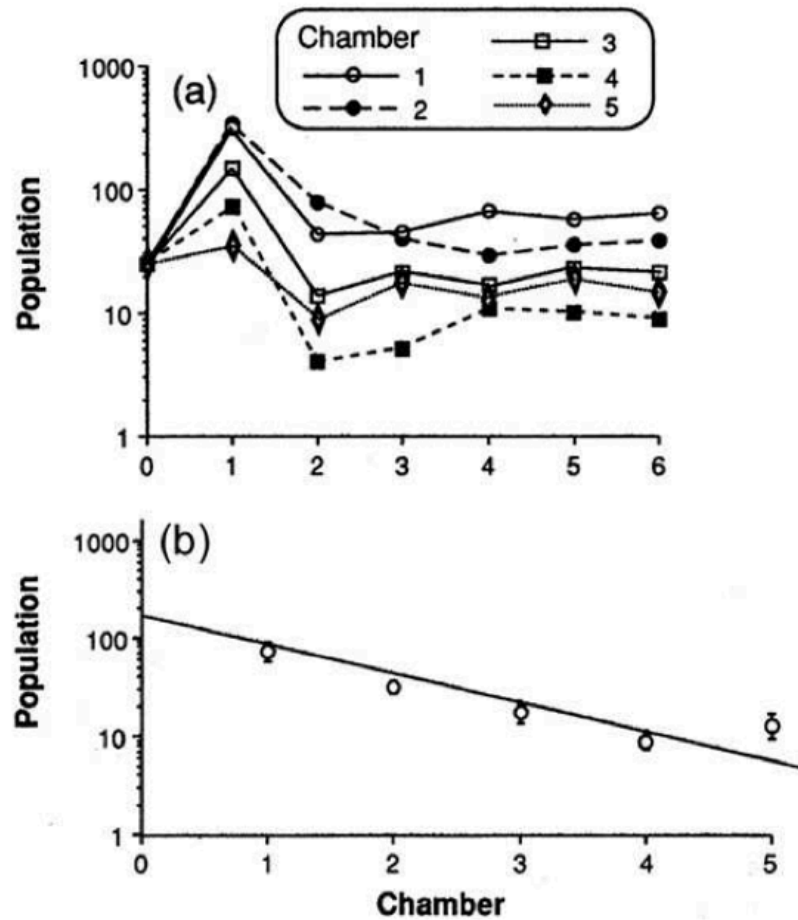
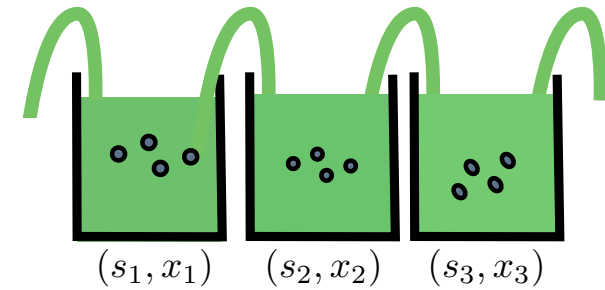


Figure 4.3. (a) Population dynamics (log scale) of *Simocephalus vetulus* in the five chambers of the cascade. All populations stabilized. (b) Population equilibria (log scale) in each chamber. Each point is the average of six values (last three weeks of two replicates). The equilibria follow approximately a geometric sequence, as predicted by the ratio-dependent hypothesis. After Arditi and Saïah (1992), with permission of the Ecological Society of America.