Unexpected dynamics (including canard explosion) of fast-slow bitrophic food chains

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Canard: Van der Pol equation (Eckhaus 1983)

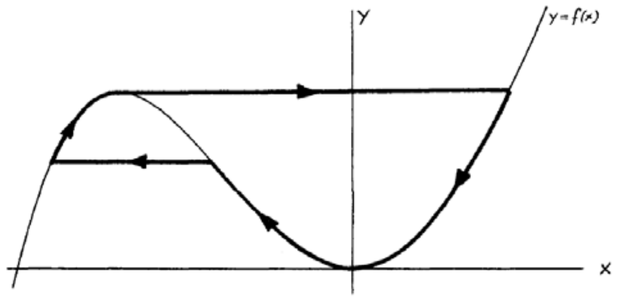

Fig. 1.3a. *A canard limit cycle*

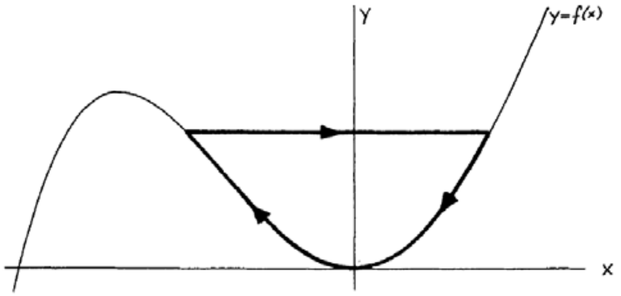

Fig. 1.4. *The duck has lost its head*

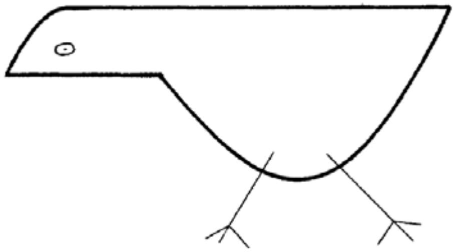

Fig. 1.3b. *The french duck*

Outline

- Introduction
- Rosenzweig-MacArthur predator–prey model
- RM_1 model, variable efficiency
- RM_2-model, constant efficiency
- MB nutrient–prey–predator model
- Conclusions

- In the classical Rosenzweig-MacArthur (RM) model in absence of the predator the prey grows logistically and nutrients are not modelled
  - Fast-slow dynamics,
  - Singular perturbation technique,
  - Canards
- In mass balance (MB) chemostat model this nutrient is explicitly modelled
  - Bifurcation analysis

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Rosenzweig-MacArthur predator–prey model
RM$_1$-model, variable efficiency

$$\frac{dx_1}{dt} = f(x_1, x_2, \varepsilon) = x_1(1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1})$$

$$\frac{dx_2}{dt} = \varepsilon g(x_1, x_2, \varepsilon) = \varepsilon x_2(\frac{a_1 x_1}{1 + b_1 x_1} - 1)$$

parameter	Interpretation
t	Time variable
x_1	Prey density
x_2	Predator biomass density
a_1	Searching rate
b_1	Searching rate × handling time
ε	Efficiency and predator death rate

The hyperbolic relationship

$$F(x_1, x_2) = \frac{a_1 x_1}{1 + b_1 x_1}$$

- Ecology: Holling type II functional response
- Biochemistry: Michaelis-Menten kinetics

Derivation using time-scale separation: searching and feeding is much faster than population physiological processes, such as growth

Here the parameters are:
$a_1 = b$; searching rate
$b_1 = b/k$; searching rate × handling time

The biological interpretation of ε is the yield in Microbiology, or assimilation efficiency in Ecology and here besides a time-scale parameter also predator death rate factor

Bifurcation analysis of RM$_1$ predator–prey model

$$\frac{dx_1}{dt} = x_1(1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1})$$
$$\frac{dx_2}{dt} = \varepsilon x_2(\frac{a_1 x_1}{1 + b_1 x_1} - 1)$$

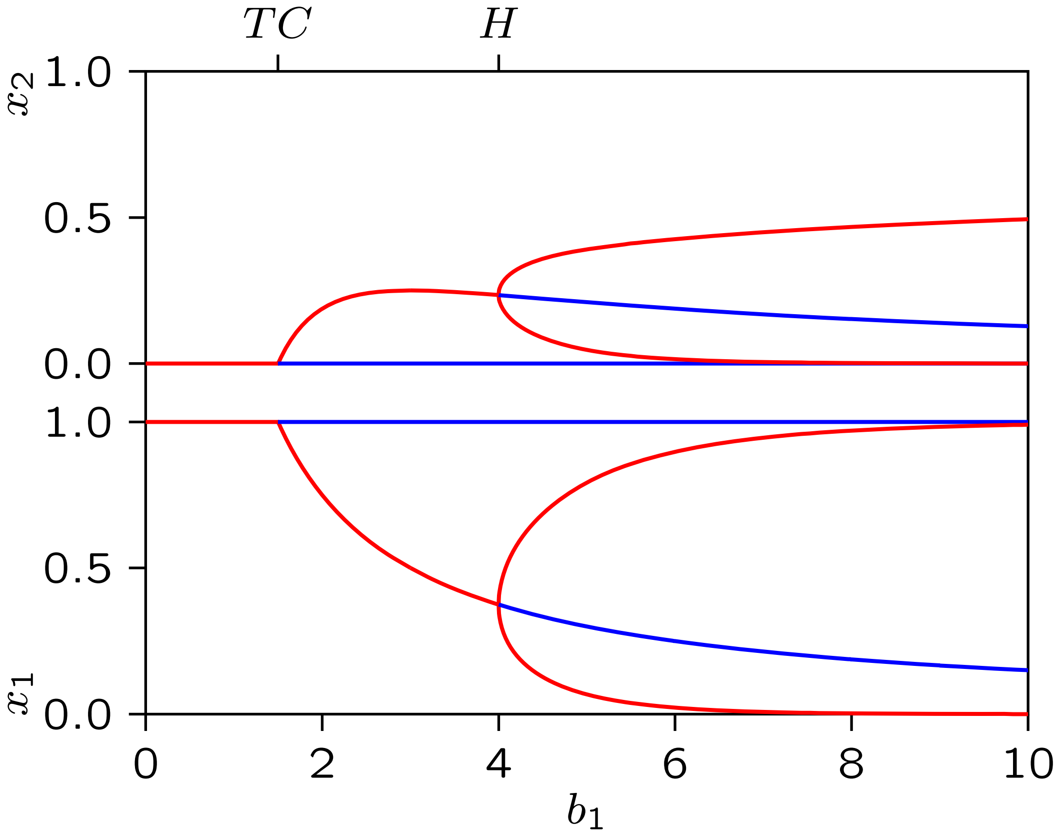
Bifurcation	Description
TC	Transcritical bifurcation: invasion through boundary equilibrium
T	Tangent bifurcation: collapse of the system
H	Hopf bifurcation: origin of (un)stable limit cycle

Literature ($\varepsilon = 1$):

Yu. A Kuznetsov, *Elements of Applied Bifurcation Theory*, Applied Mathematical Sciences 112, Springer-Verlag, 2004

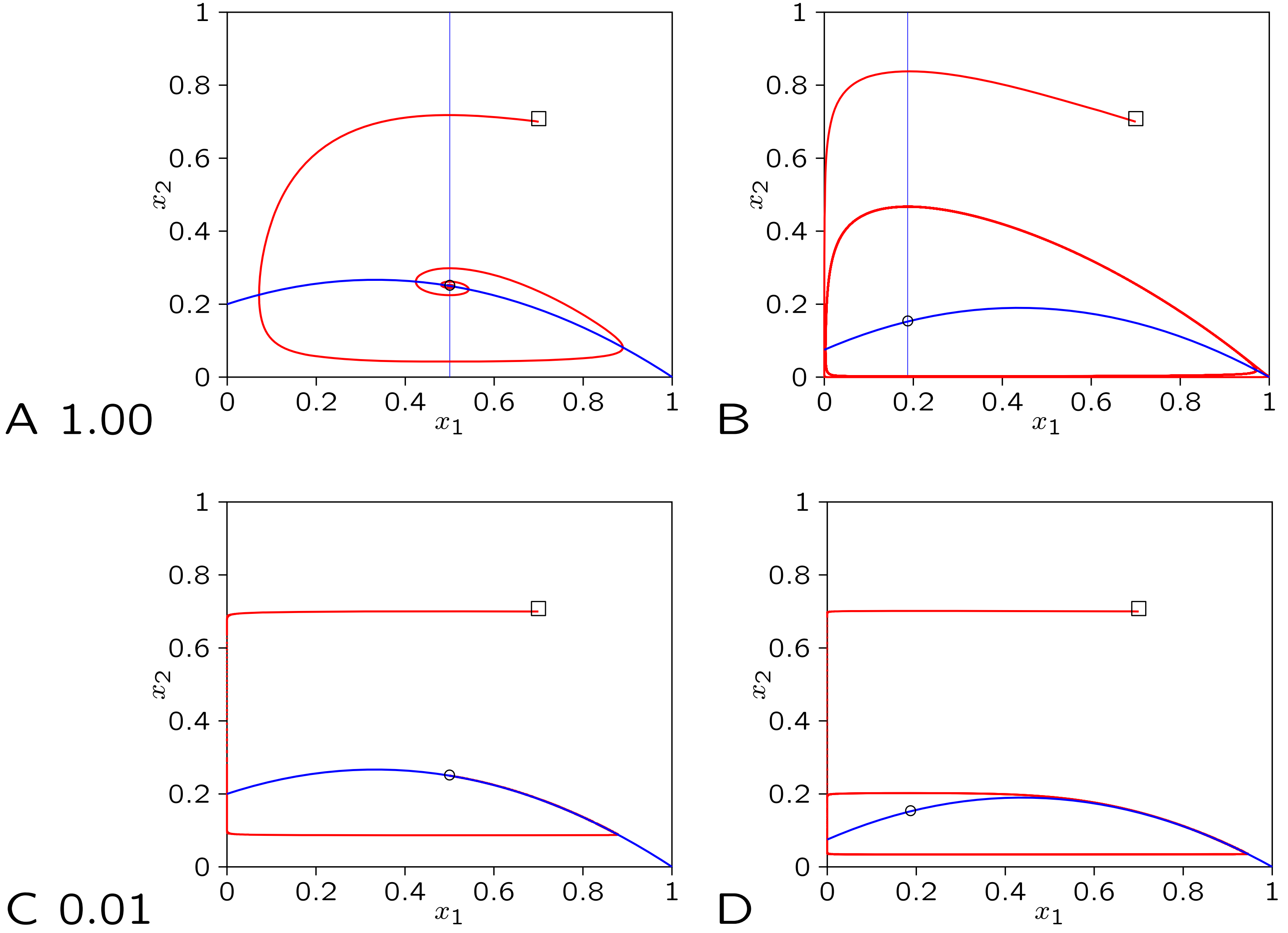
RM$_1$-model

One-parameter diagram x_i vs b_1: $a_1 = 5/3\, b_1$, $\epsilon = 1$

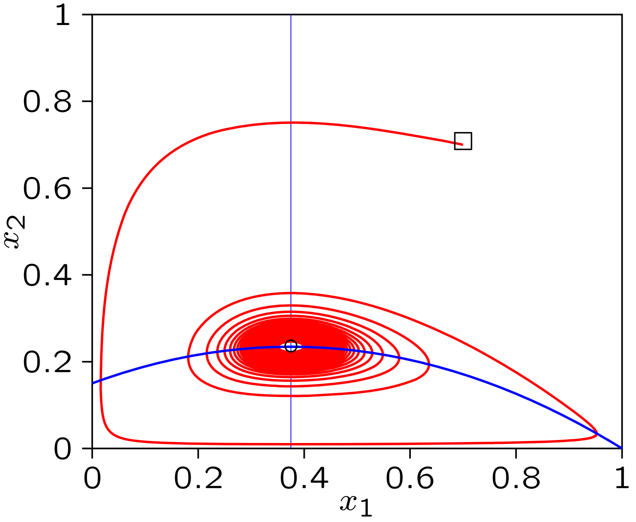


Transcritical TC, Hopf H bifurcations

Transient dynamics $b_1 = 3$ and $b_1 = 8$, $\varepsilon =$



Transient dynamics $b_1 = 4$ Hopf bifurcation point H: $\varepsilon =$



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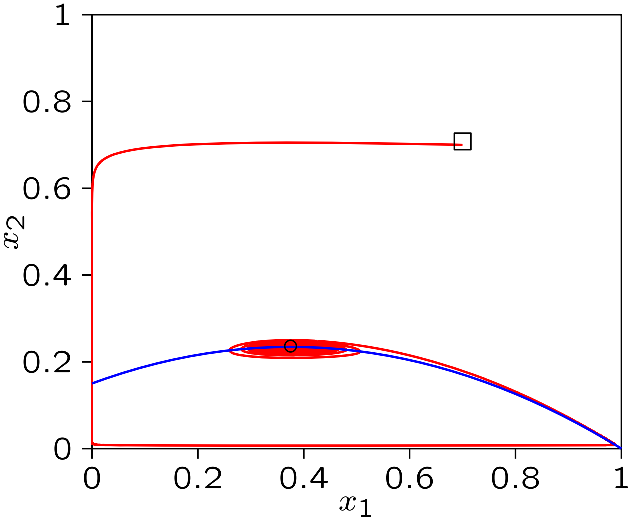
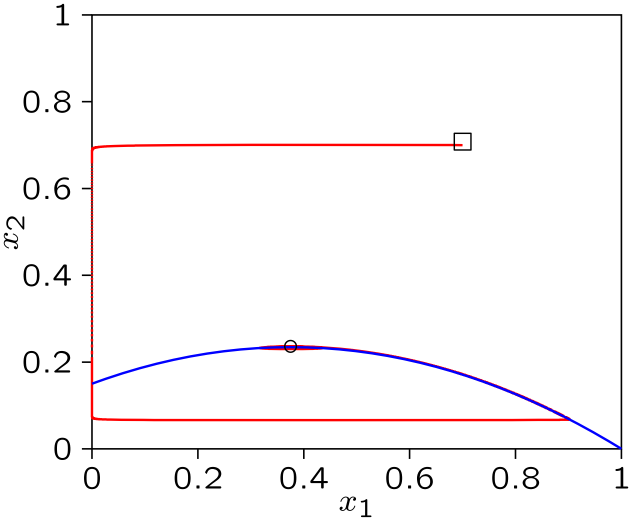


0.1



0.01

fast system

$$\varepsilon \to 0$$

$$\frac{dx_1}{dt} = f(x_1, x_2, \varepsilon) \qquad \frac{dx_1}{dt} = f(x_1, x_2, 0)$$

$$\frac{dx_2}{dt} = \varepsilon g(x_1, x_2, \varepsilon) \qquad \frac{dx_2}{dt} = 0$$

layer system

slow system $\tau = \varepsilon t$

$$\varepsilon \to 0$$

$$\varepsilon \frac{dx_1}{d\tau} = f(x_1, x_2, \varepsilon) \qquad 0 = f(x_1, x_2, 0)$$

$$\frac{dx_2}{d\tau} = g(x_1, x_2, \varepsilon) \qquad \frac{dx_2}{d\tau} = g(x_1, x_2, 0)$$

reduced system

Evolution of the slow variable on critical manifold

Introduce the function

$$x_2 = q(x_1) = \frac{1}{a_1}(1 - x_1)(1 + b_1 x_1)$$

Formally from

$$\frac{dx_2}{d\tau} = g(x_1, q(x_1)) = \frac{dq}{dx_1}\frac{dx_1}{d\tau}$$

we get

$$\frac{dx_1}{d\tau} = \frac{q(x_1)(a_1 x_1 - (1 + b_1 x_1)}{dq/dx_1}$$

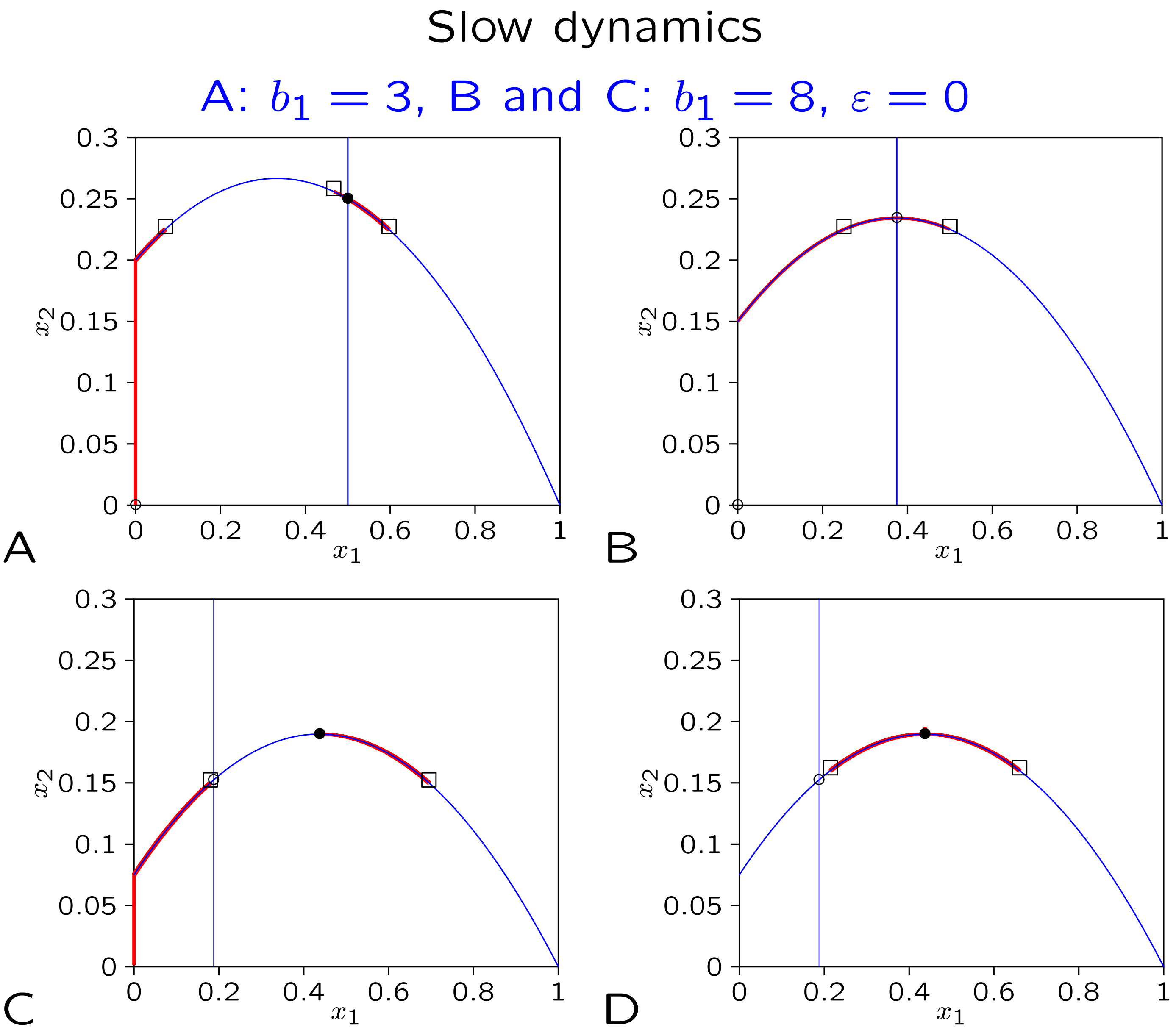
It describes the slow dynamics on the critical manifold: the parabola $f(x_1, x_2, 0) = 0$.

Note that this expression is zero at the top of the parabola point $(\overline{x}_1, \overline{x}_2)$ where $\overline{x}_1 = (b_1 - 1)/(2b_1)$

This point is a fold point, the denominator is at that point zero

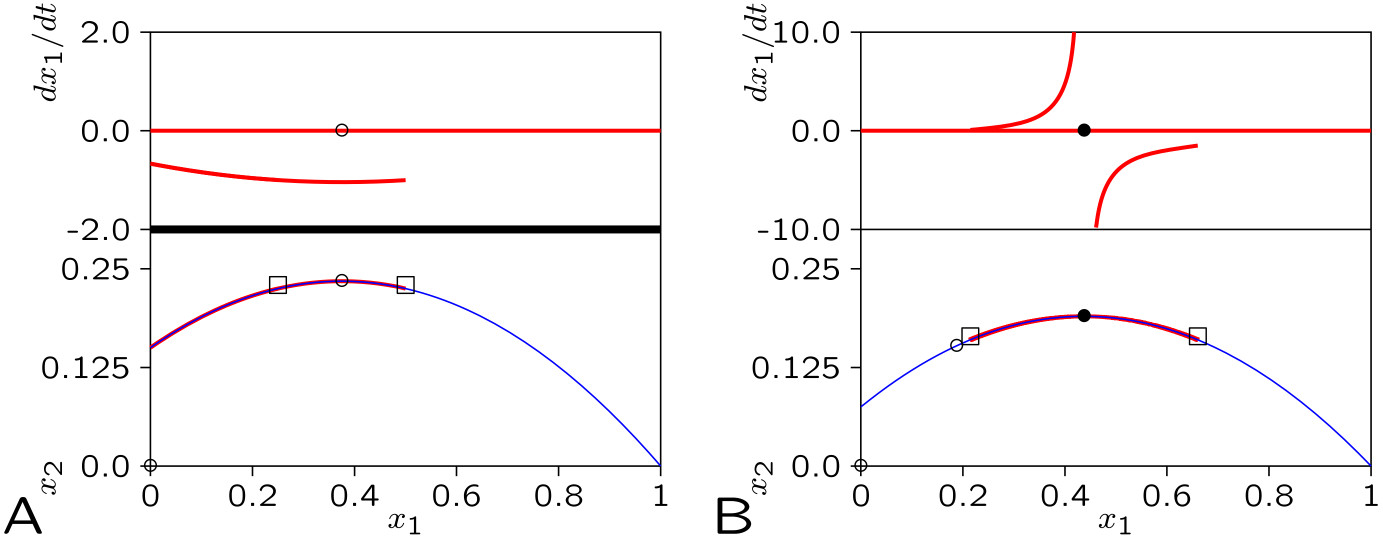
For $b_1 = 4$ (Hopf bifurcation) also the numerator is zero since it is also an equilibrium

Then slow flow is possible in that fold point because the zero's cancel


Slow dynamics
A: $b_1 = 3$, B and C: $b_1 = 8$, $\varepsilon = 0$
x_2
x_1
0
0.05
0.1
0.15
0.2
0.25
0.3
0.2
0.4
0.6
0.8
1
A
B
C
D

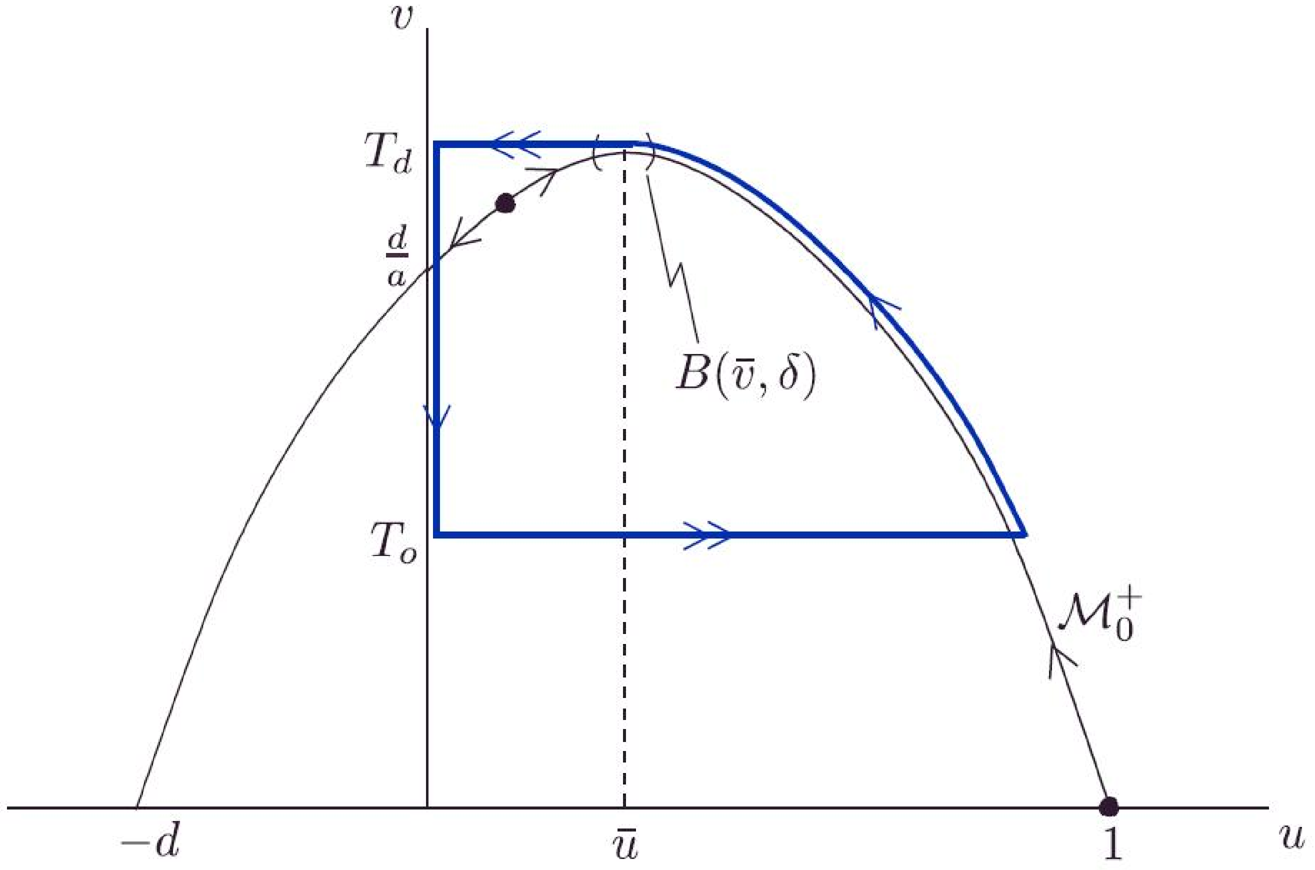
Slow dynamics

A: $b_1 = 4$, (Hopf)   B: $b_1 = 8$, $\varepsilon = 0$



Geometric singular perturbation techniques

(N. Fenichel 1997, G. Hek 2010)



Approximations techniques slow manifolds, $x_2 = q_\varepsilon(x_1)$

Using its invariance the perturbed manifold $\mathcal{M}^1_\varepsilon$ can be described as a graph

$$\{(x_1, x_2) | x_2 = q_\varepsilon(x_1), x_1 \geq 0, x_2 \geq 0\}$$

This manifold is invariant when

$$\frac{dx_2}{dt} = \frac{dx_2}{dx_1}\frac{dx_1}{dt} = \frac{dq_\varepsilon}{dx_1}\frac{dx_1}{dt}$$

The following asymptotic expansion or power series expansion in ε is introduced:

$$\begin{aligned} x_2 = q_\varepsilon(x_1) =& q_0(x_1) + \varepsilon q_1(x_1) + \varepsilon^2 q_2(x_1) + \ldots\ , \\ q_0 =& \frac{(1 - x_1)(1 + b_1 x_1)}{a_1}\ , \quad q_1 = q_0 \frac{(x_1(a_1 - b_1) - 1)}{x_1(2x_1 b_1 + 1 - b_1)} \\ q_2 =& \cdots \end{aligned}$$

In order to simulate the model we solve the uncoupled system

$$\frac{d\tilde{x}_1}{dt} = \tilde{x}_1\Big(1 - \tilde{x}_1 - \frac{a_1 q_\varepsilon(\tilde{x}_1)}{1 + b_1\tilde{x}_1}\Big) \quad \text{master}$$

$$\frac{d\tilde{x}_2}{dt} = \varepsilon q_\varepsilon(\tilde{x}_1)\Big(\frac{a_1\tilde{x}_1}{1 + b_1\tilde{x}_1} - 1\Big) \quad \text{slave}$$

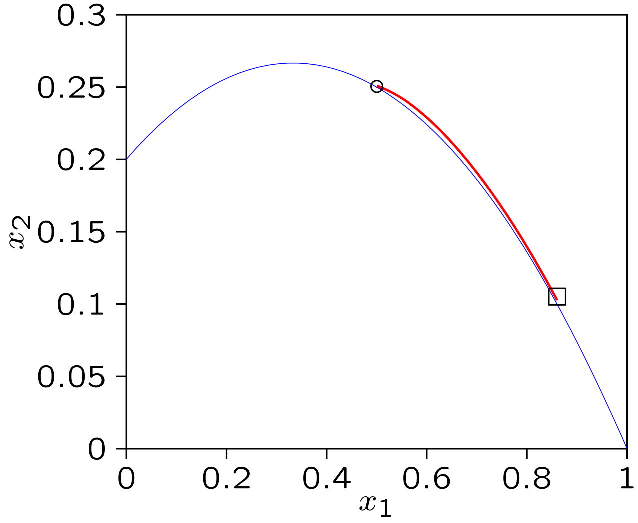
where the initial values are chosen as:

$\tilde{x}_1 = x_1(0)$ and $\tilde{x}_2 = q_\varepsilon(x_1(0))$

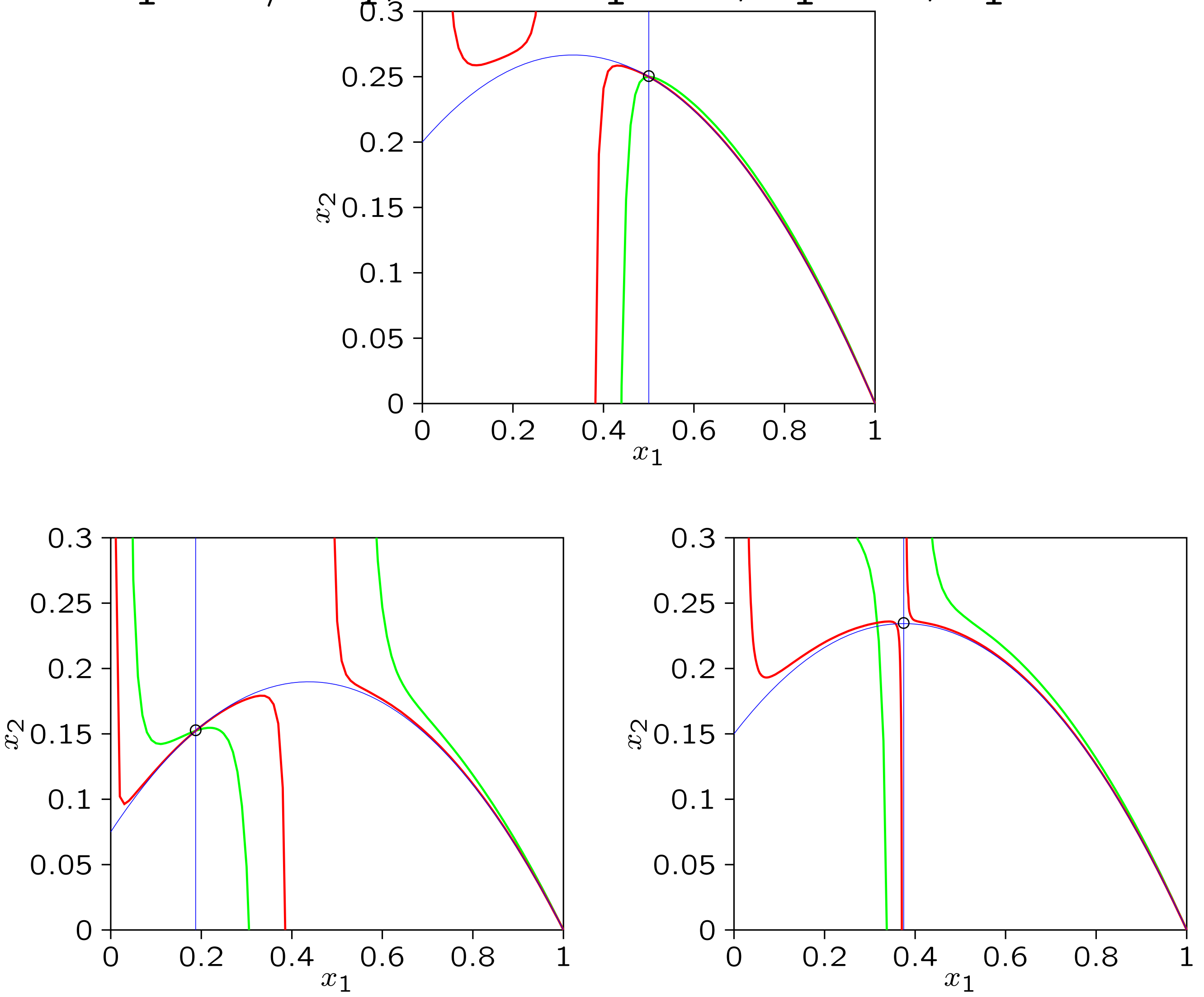
$a_1 = 5/3\ b_1$, where $b_1 = 3$

asymptotic expansion approximation

$x_2 = q_\varepsilon(x_1)$, $\varepsilon = 0.1$

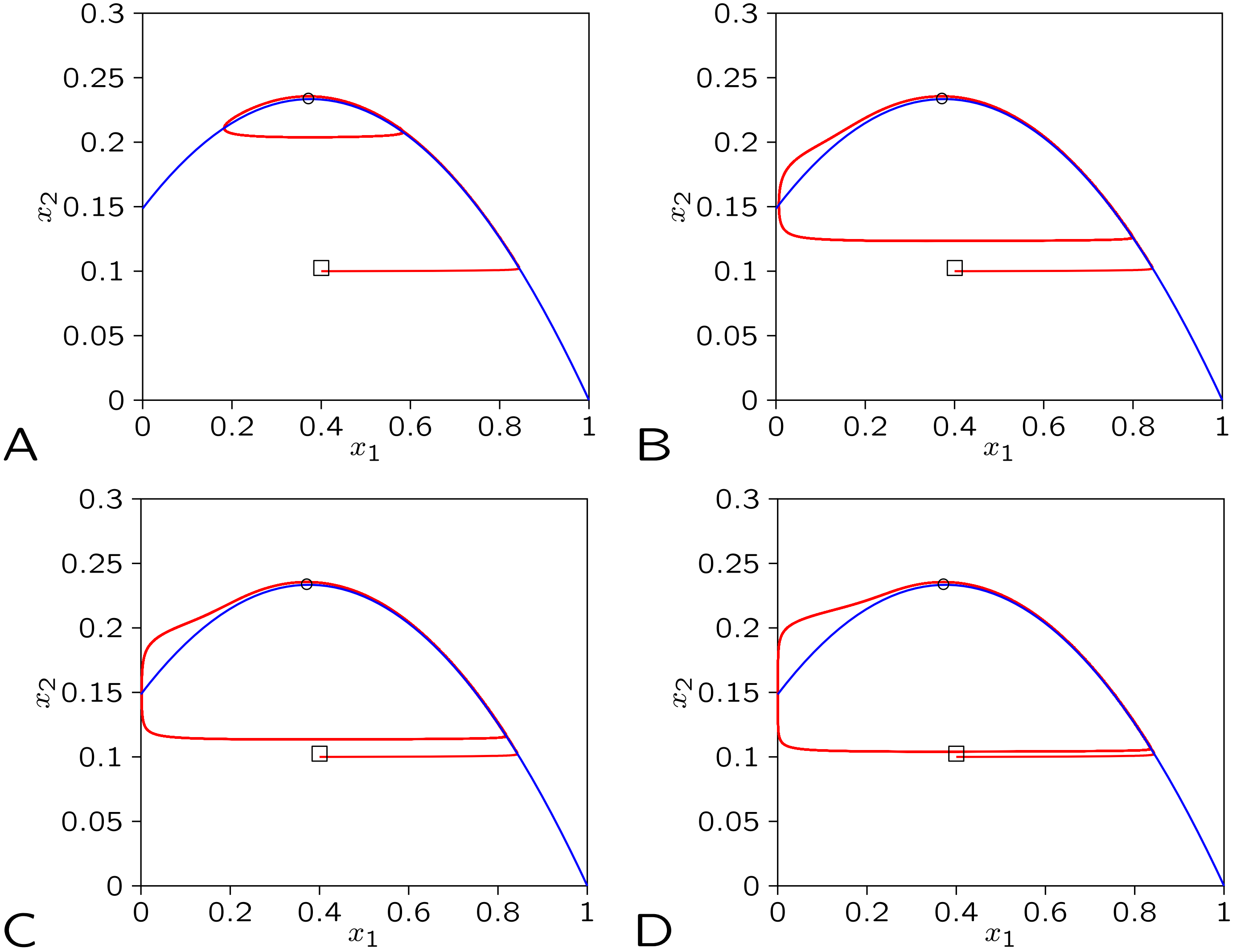


$a_1 = 5/3\ b_1$, where $b_1 = 3$, $b_1 = 8$, $b_1 = 4$

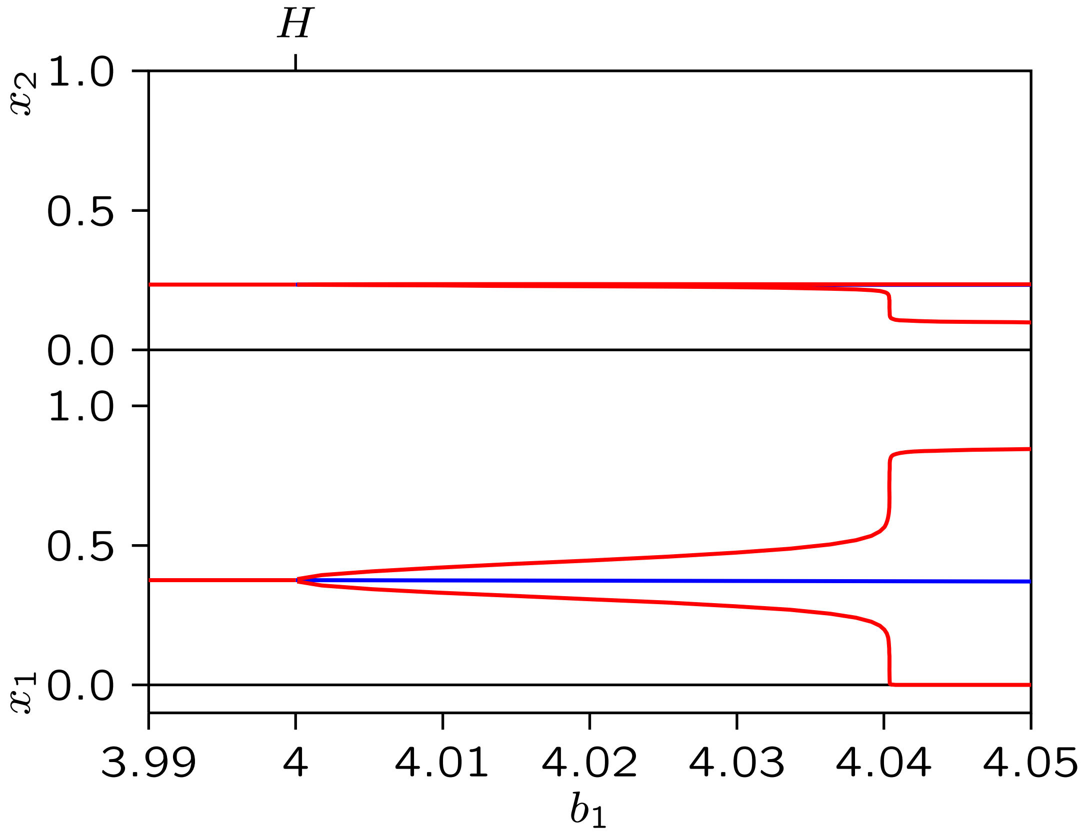


RM$_1$-model: $a_1 = 5/3b_1$, $\varepsilon = 0.01$,

A: $b_1 = 4.0402$, B: $b_1 = 4.0404$, C: 4.0405, D: 4.042

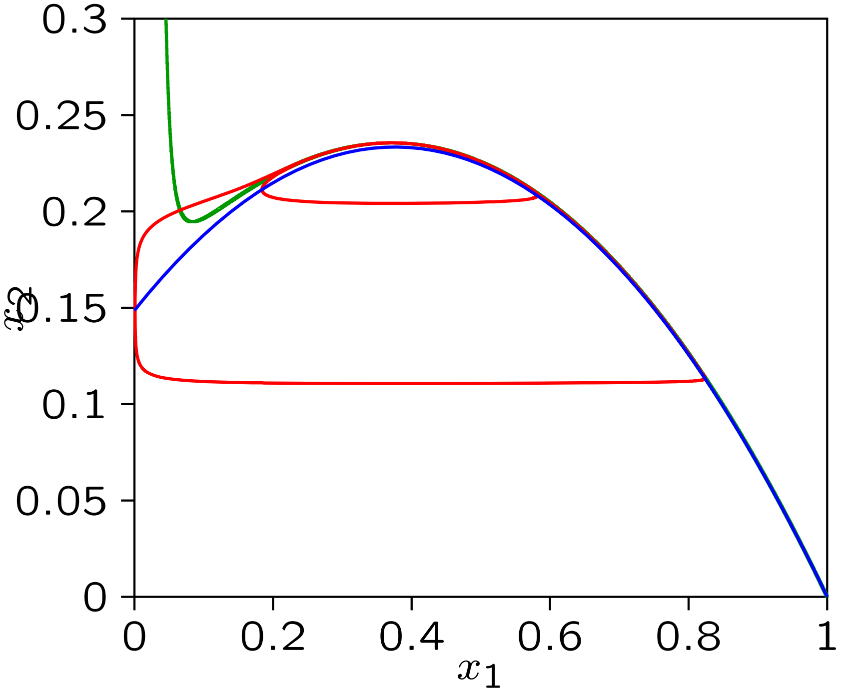


One-parameter diagram x_i vs b_1, $\varepsilon = 0.01$



Hopf H bifurcation

RM_1-model asymptotic expansion approximation $r(x_1, \varepsilon = 0.01)$: $a_1 = 5/3b_1$, $b_1 = 4.0403$



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RM$_2$ predator–prey model, constant efficiency

$$\frac{dx_1}{dt} = x_1\Big(1 - x_1 - \varepsilon\frac{a_1 x_2}{1 + b_1 x_1}\Big)$$

$$\frac{dx_2}{dt} = \varepsilon x_2\Big(\frac{a_1 x_1}{1 + b_1 x_1} - 1\Big)$$

This model has been studied in:

Hek. Geometric singular perturbation theory in biological practice. *Journal of Mathematical Biology*, 60:347–386, 2010.

However, without motivation for the extra ε factor

Simulation results are shown which indicate unrealistic unbounded solutions when $\varepsilon \to 0$

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MB nutrient–prey-predator model

$$\frac{dx_0}{dt} = (x_r - x_0)\varepsilon d - a_0 x_0 x_1$$
$$\frac{dx_1}{dt} = a_0 x_0 x_1 - \varepsilon d x_1 - \varepsilon \frac{a_1 x_1 x_2}{1 + b_1 x_1}$$
$$\frac{dx_2}{dt} = \varepsilon \frac{a_1 x_1 x_2}{1 + b_1 x_1} - \varepsilon d x_2$$

parameter	Interpretation
t	Fast time variable
x_0	Nutrient density
x_i	Population biomass density
x_r	Nutrient concentration in reservoir
d	Dilution rate
a_0	Searching rate
a_1	Searching rate
b_1	Searching rate × handling time

It is possible to decouple the system by introduction of the total biomass

$$H(t) = x_0(t) + x_1(t) + x_2(t) - x_r \quad t \geq 0$$
$$\frac{dH}{dt} = -\varepsilon dH$$

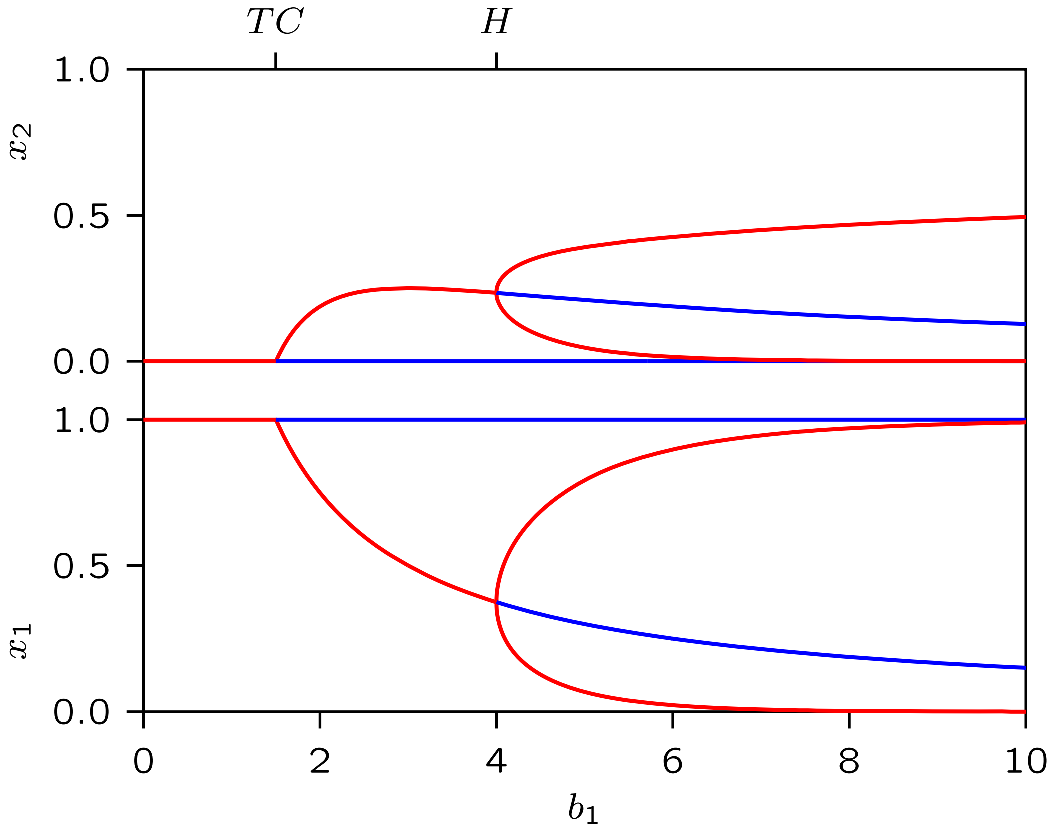
In order to be able to compare the three models RM$_1$, RM$_2$ and MB we make the following assumptions: $H(0) = 0$ and this gives:

$$\frac{dx_1}{dt} = x_1\left(1 - x_1 - x_2 - \varepsilon\frac{a_1x_2}{1 + b_1x_1}\right)$$
$$\frac{dx_2}{dt} = \varepsilon x_2\left(\frac{a_1x_1}{1 + b_1x_1} - 1\right)$$

Extra x_2 shows that prey has less nutrients available that are indirectly consumed by the predator

RM_1-model

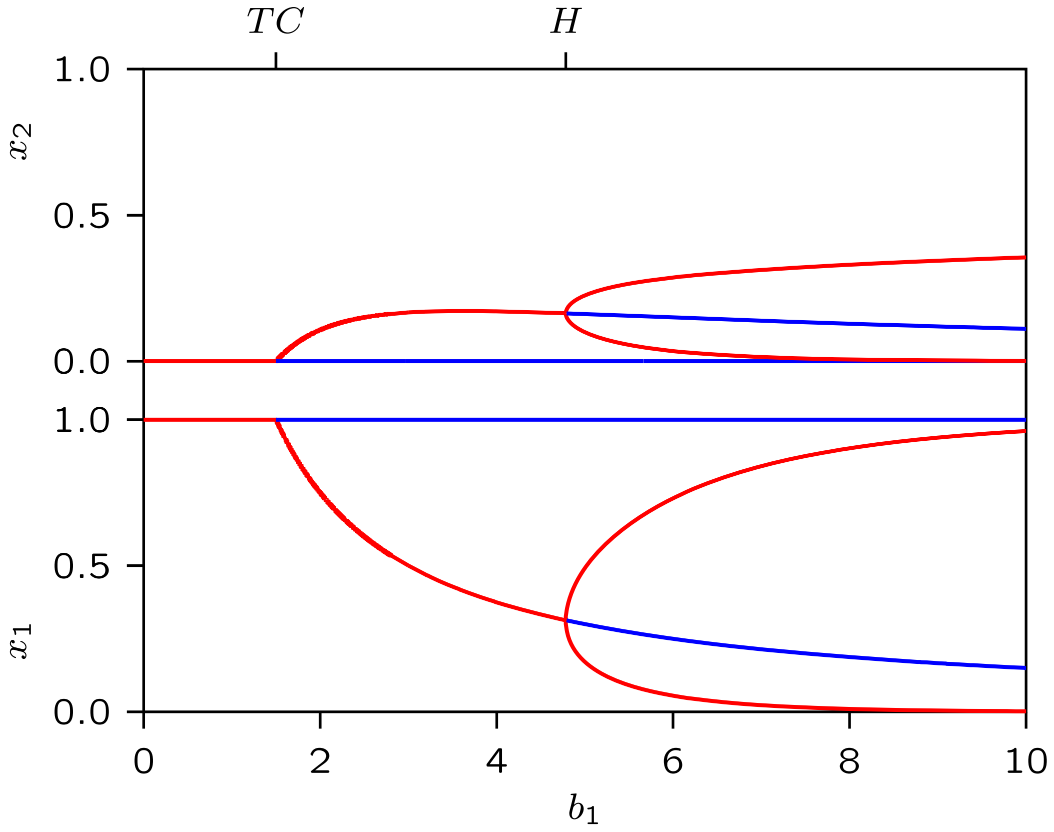
One-parameter diagram x_i vs b_1: $a_1 = 5/3\, b_1$, $\varepsilon = 1$



Transcritical TC, Hopf H bifurcations

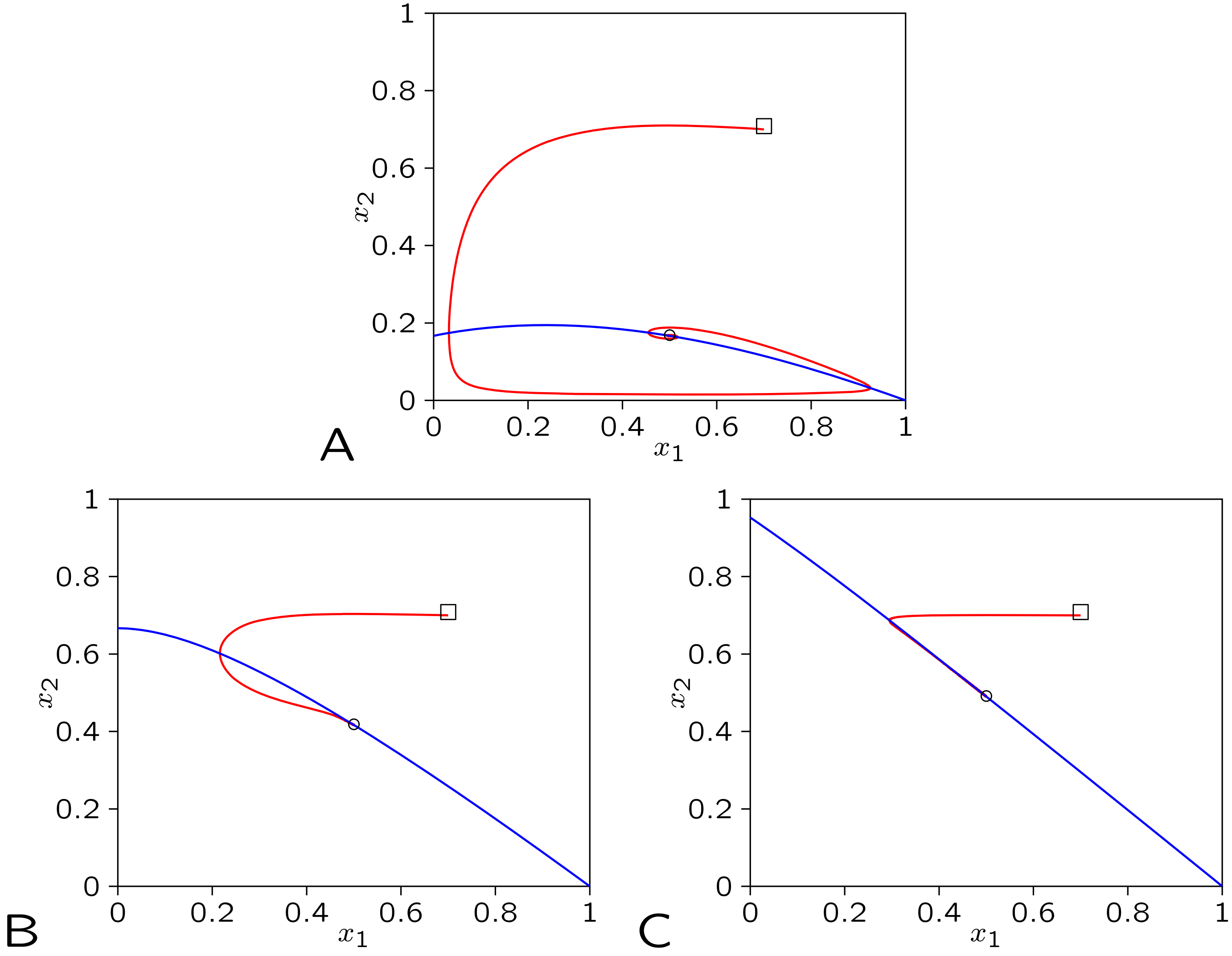
MB-model

One-parameter diagram x_i vs b_1: $a_1 = 5/3\,b_1$, $\varepsilon = 1$

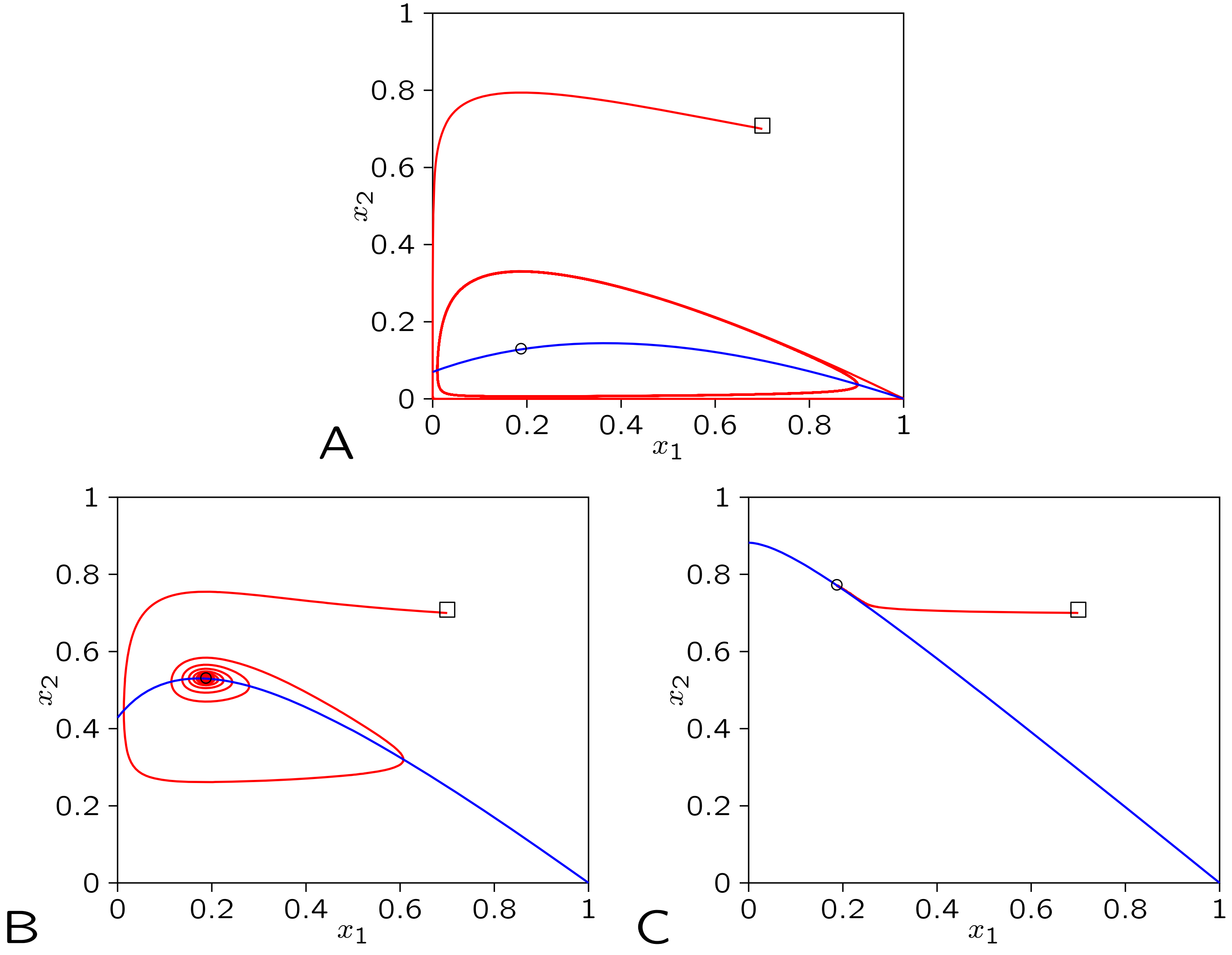


Transcritical TC, Hopf H bifurcations

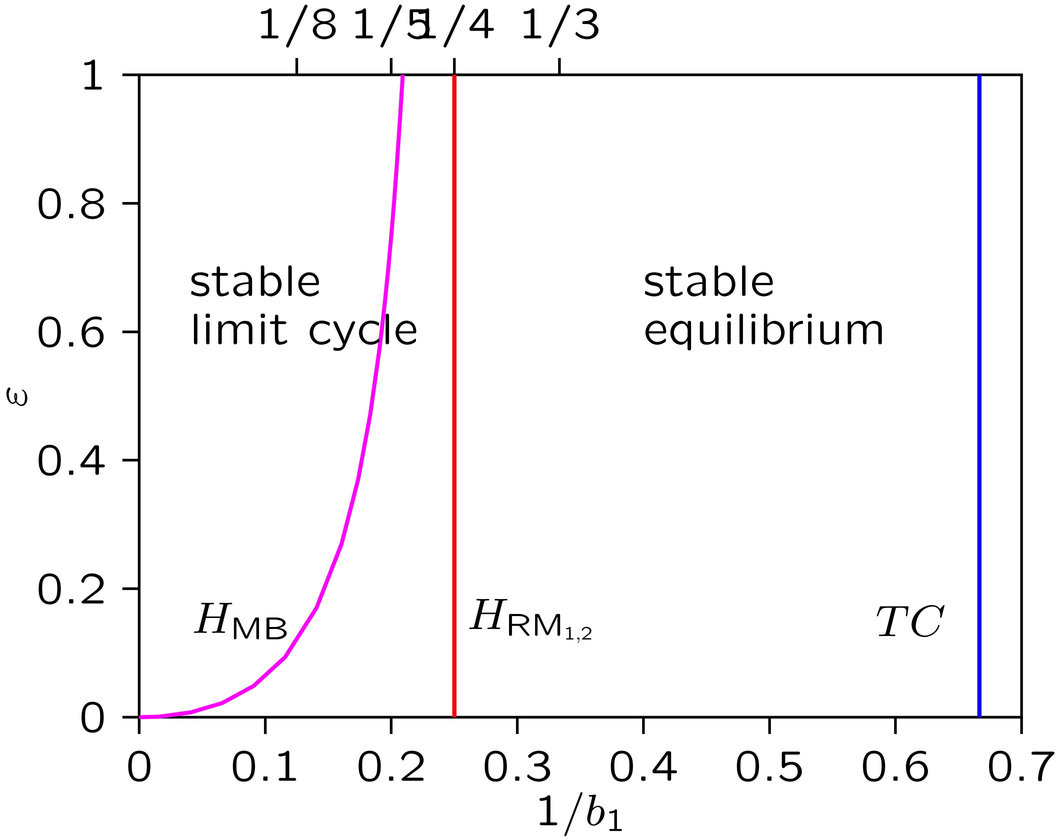
$b_1 = 3$ and A:$\varepsilon = 1$, B: $\varepsilon = 0.1$, C: $\varepsilon = 0.01$



$b_1 = 8$ and A:$\varepsilon = 1$, B: $\varepsilon = 0.1$, C: $\varepsilon = 0.01$



Two-parameter bifurcation diagram ε vs b_1



Hopf H_{MB} MB model; Hopf $H_{RM_{1,2}}$ $\mathrm{RM}_{1,2}$ model; Transcritical TC all models

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Conclusions (1)

- ($\mathrm{RM}_1 \Rightarrow \mathrm{RM}_2$) Making the RM_1 model more realistic leads in RM_2 model to unrealistic unbounded solutions when $\varepsilon \to 0$

- ($\mathrm{RM}_2 \Rightarrow \mathrm{MB}$) Introduction of dynamics of nutrients in the model leads to realistic solution and less complex dynamics when $\varepsilon \to 0$

Conclusions (2)

- Integrated approach is important: Modelling, bifurcation analysis and perturbation theory

- Proper modelling gives perturbation parameter ε a biological interpretation not just a mathematical perturbation parameter

- In RM_1 model a canard occurs just above the Hopf bifurcation and not in the MB model