Analysis of a predator-prey model with two different time scales

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Outline

- Introduction

- Rosenzweig-MacArthur predator–prey RM model
  - □ Fast-slow analysis, Relaxation oscillations
  - □ Asymptotic expansion
  - □ Canard location
  - □ Geometric singular perturbation theory (GSPT)
  - □ Blow-up technique, Existence of Canards

- Conclusions

Canard: Van der Pol equation (Eckhaus 1983)

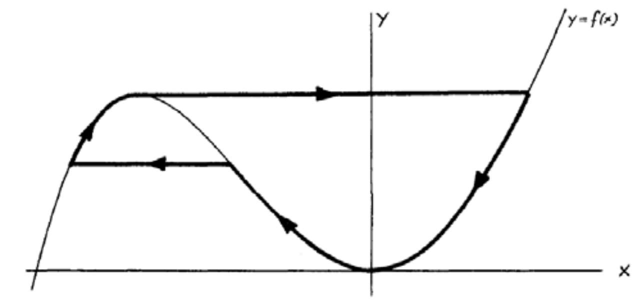

Fig. 1.3a. *A canard limit cycle*

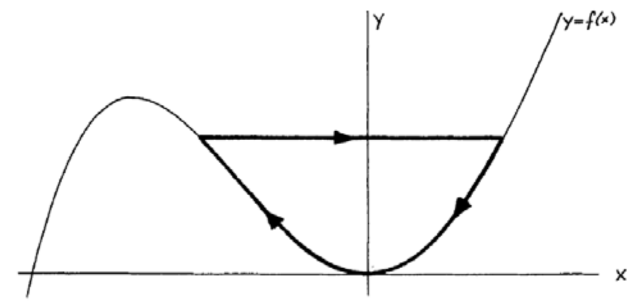

Fig. 1.4. *The duck has lost its head*

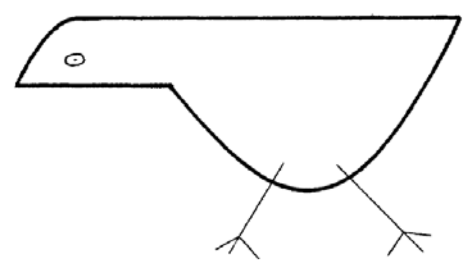

Fig. 1.3b. *The french duck*

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Rosenzweig-MacArthur predator–prey model
RM-model, 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 $\times$ 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 and death

Here the parameters are:
$a_1 = b$; searching rate
$b_1 = b/k$; searching rate $\times$ 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 predator–prey model

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

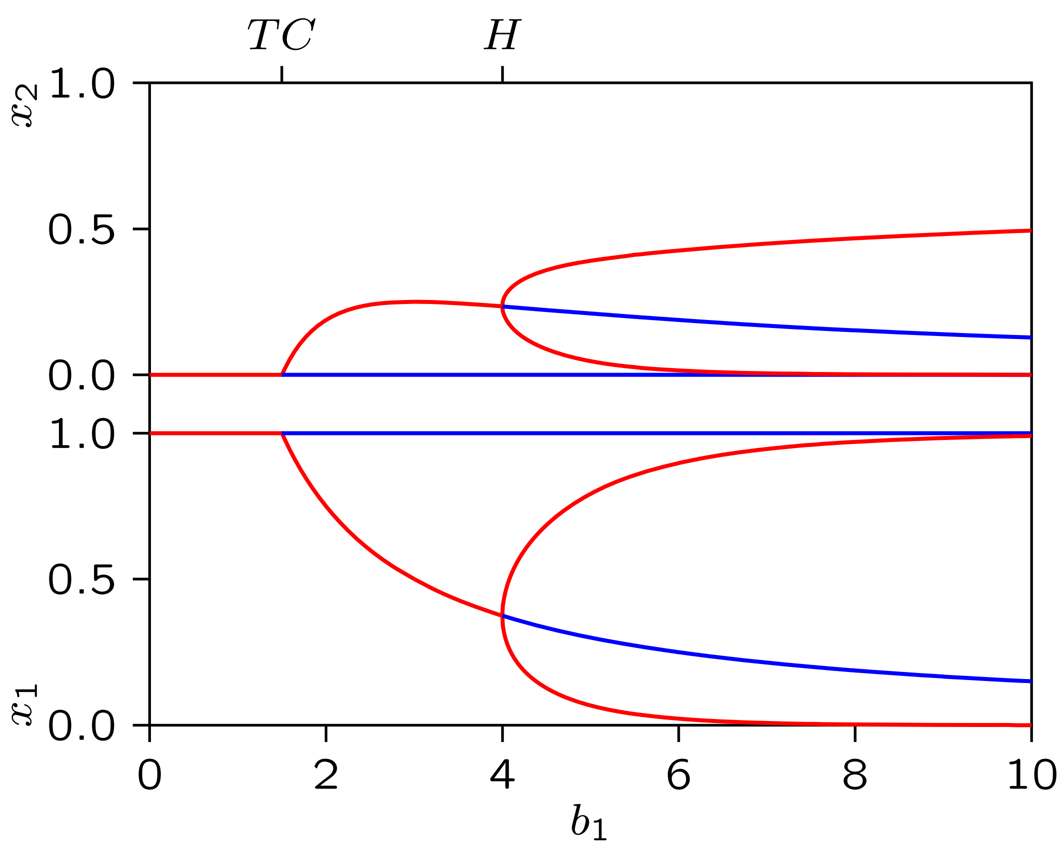
Bifurcation	Description
TC	Transcritical bifurcation: invasion through boundary equilibrium
T	Tangent bifurcation: collapse of the system
H	Hopf bifurcation: origin of (un)stable limit cycle

Literature ($\varepsilon = 1$):

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

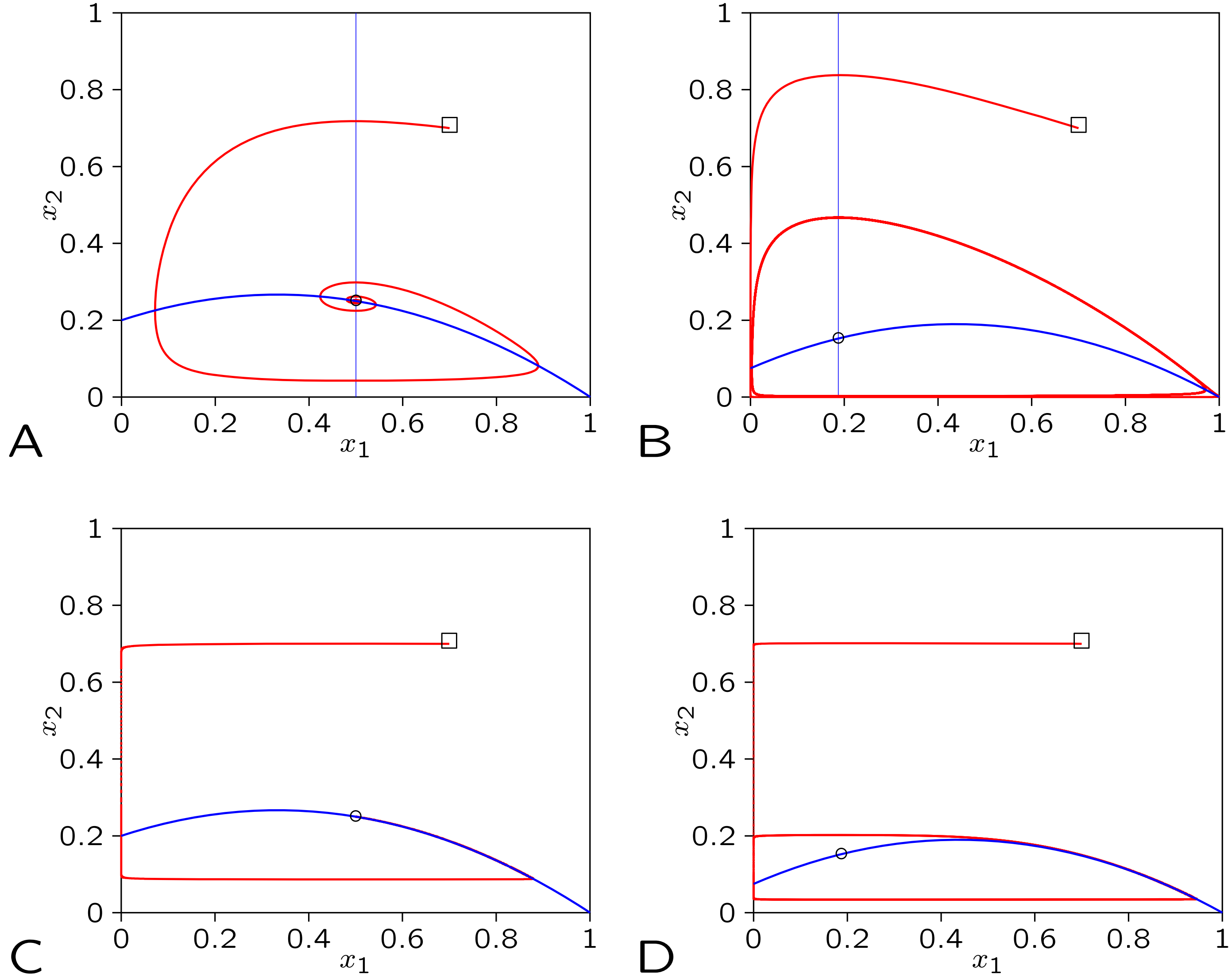
RM-model

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

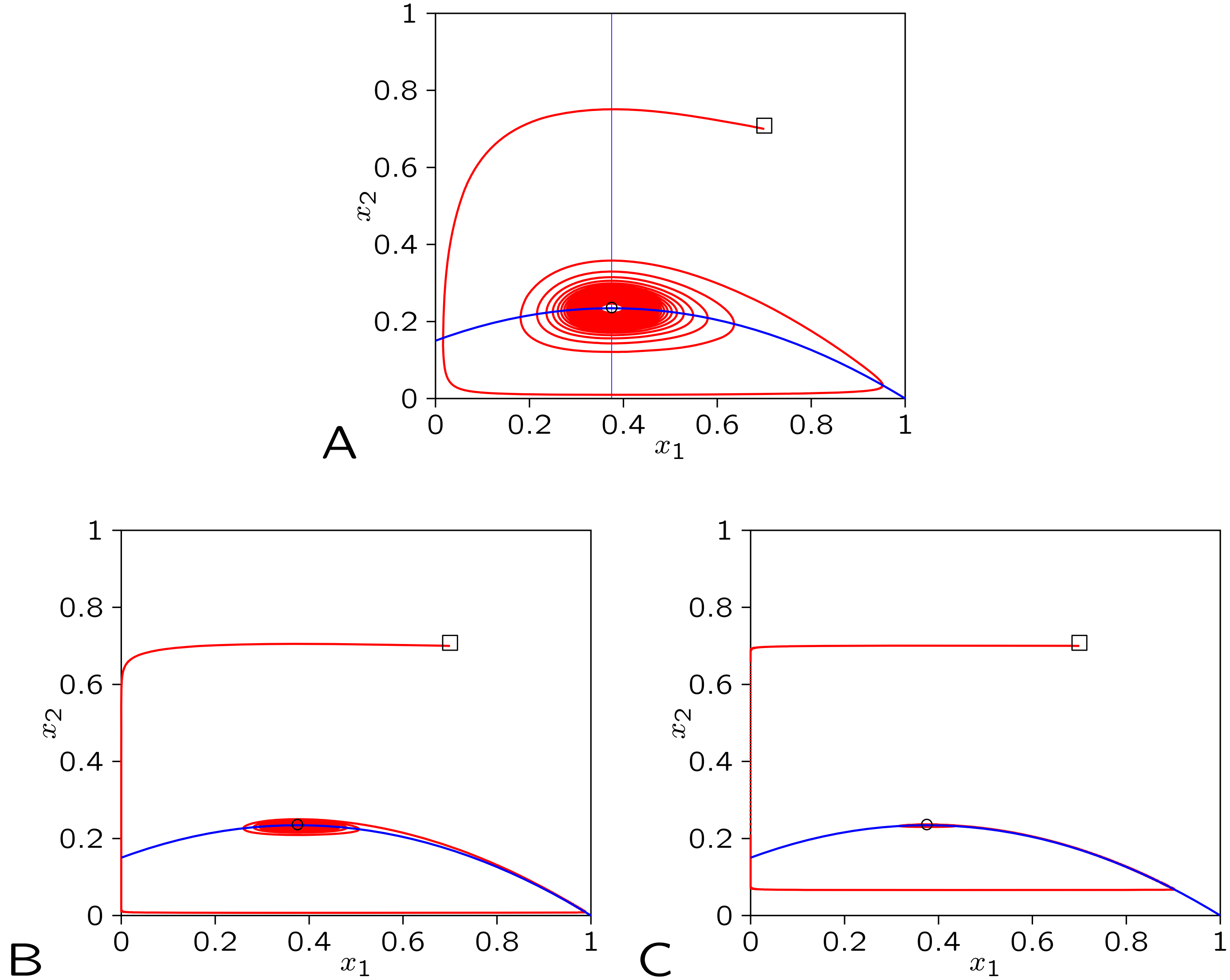


Transcritical TC, Hopf H bifurcations

Transient dynamics A,C $b_1 = 3$; A,B $\varepsilon = 1$; B,D $b_1 = 8$; C,D $\varepsilon = 0.01$



Transient dynamics $b_1 = 4$ H A $\varepsilon = 1$; B $\varepsilon = 0.11$; C $\varepsilon = 0.01$



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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 $\tau = \varepsilon t$

$$\varepsilon \to 0$$

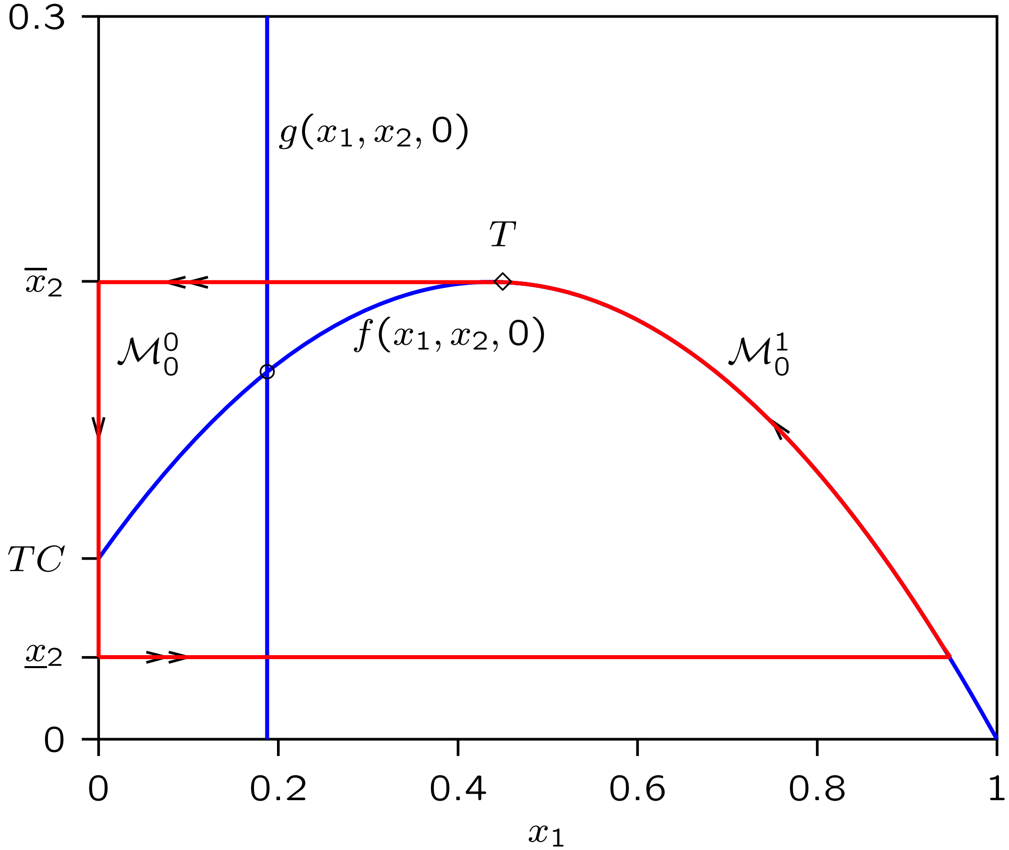
$$\varepsilon \frac{dx_1}{d\tau} = f(x_1, x_2, \varepsilon) \qquad 0 = f(x_1, x_2, 0)$$

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

reduced system

Relaxation oscillations

(G. Hek 2010)



Single arrow slow; double arrow fast

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

Perturbed manifold $\mathcal{M}_\varepsilon^1$ 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 or power series expansion in ε is introduced:

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

In order to simulate the model we solve the uncoupled system

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

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

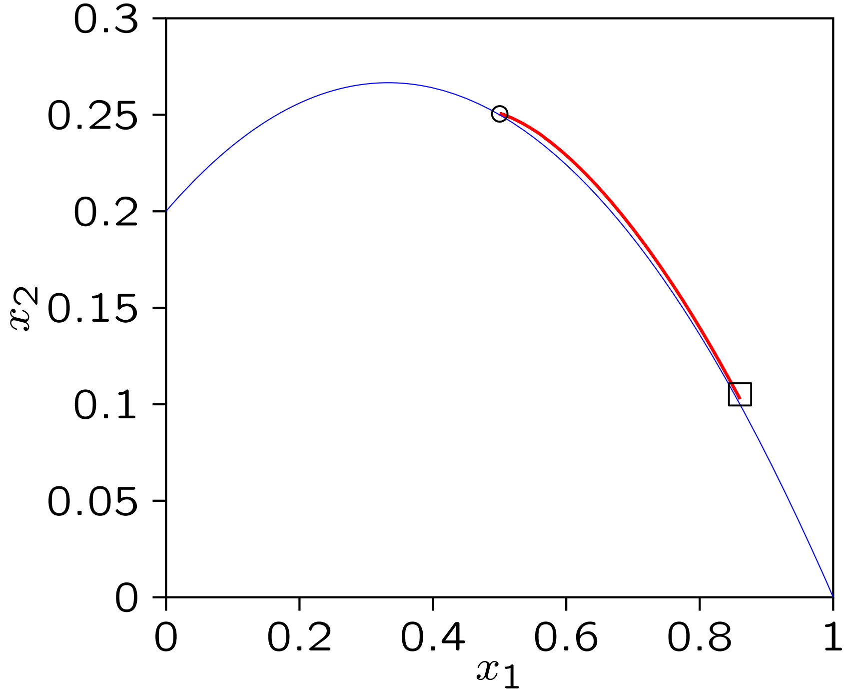
where the initial values are chosen as:

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

Second order asymptotic expansion approximation

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

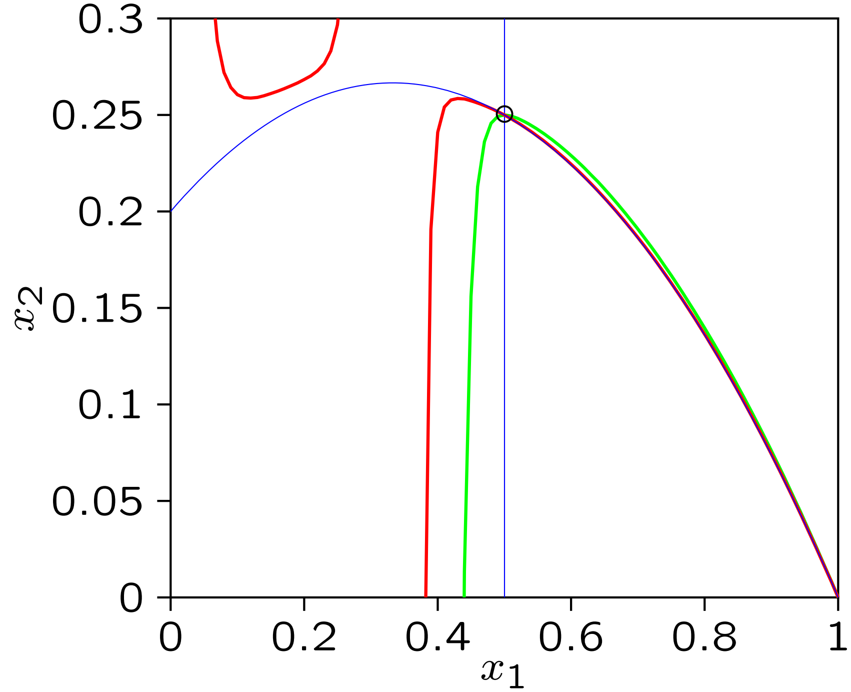
$x_2 = q_\varepsilon(x_1)$, $\varepsilon = 0.1$



Stable equilibrium $b_1 = 3$

Second order approximation

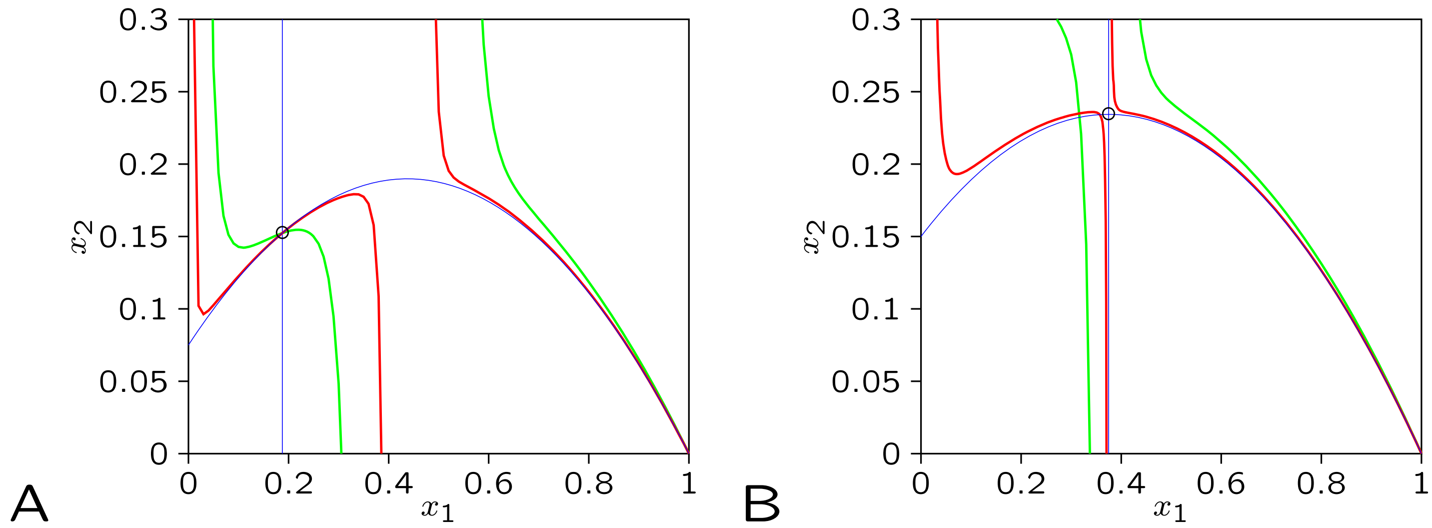
$a_1 = 5/3\ b_1,\ b_1 = 3,\ \varepsilon = 0.01,\ \varepsilon = 0.1$



Stable equilibrium $b_1 = 3$

Second order approximation

$a_1 = 5/3\ b_1$, A:$b_1 = 8$, B:$b_1 = 4$, $\varepsilon = 0.01$, $\varepsilon = 0.1$



Unstable equilibrium $b_1 = 8$; Hopf $b_1 = 4$

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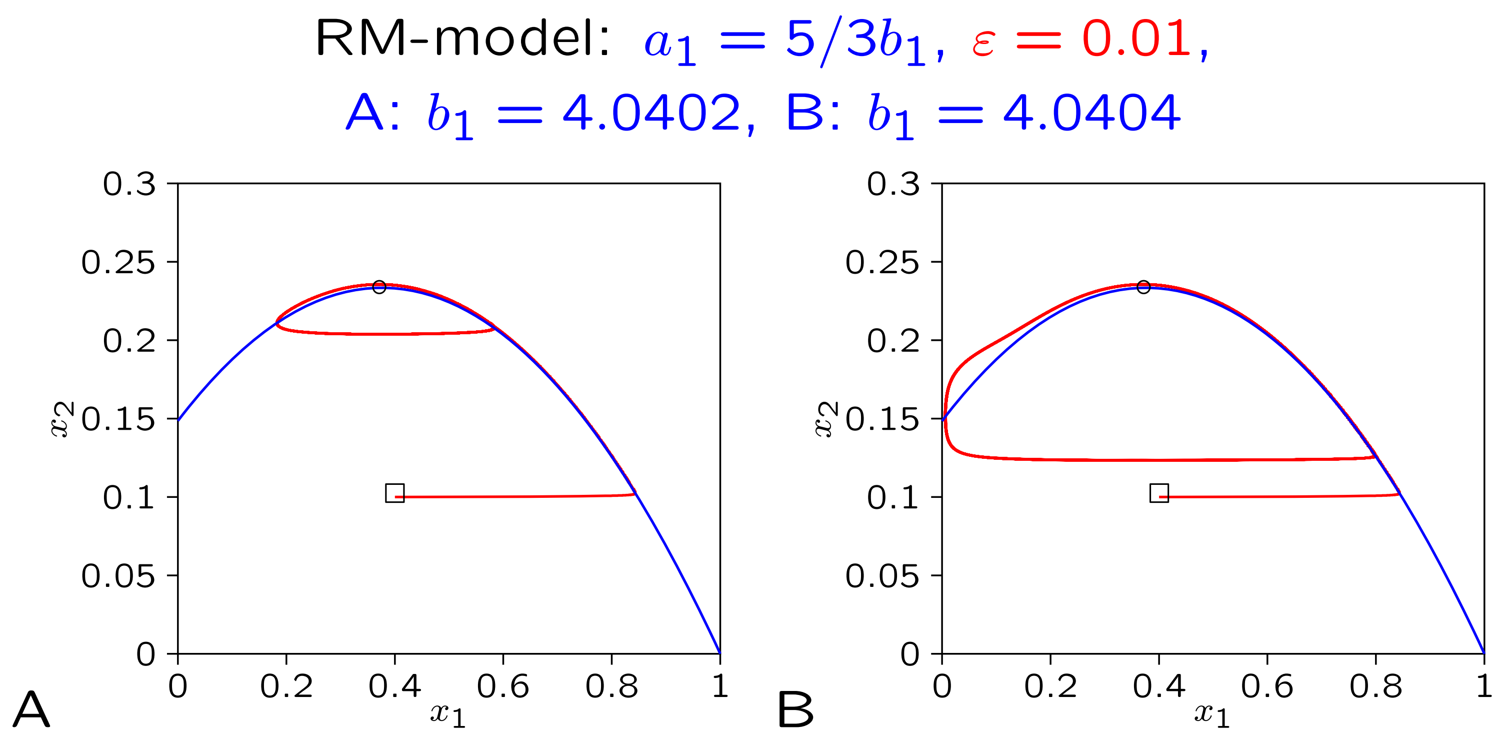
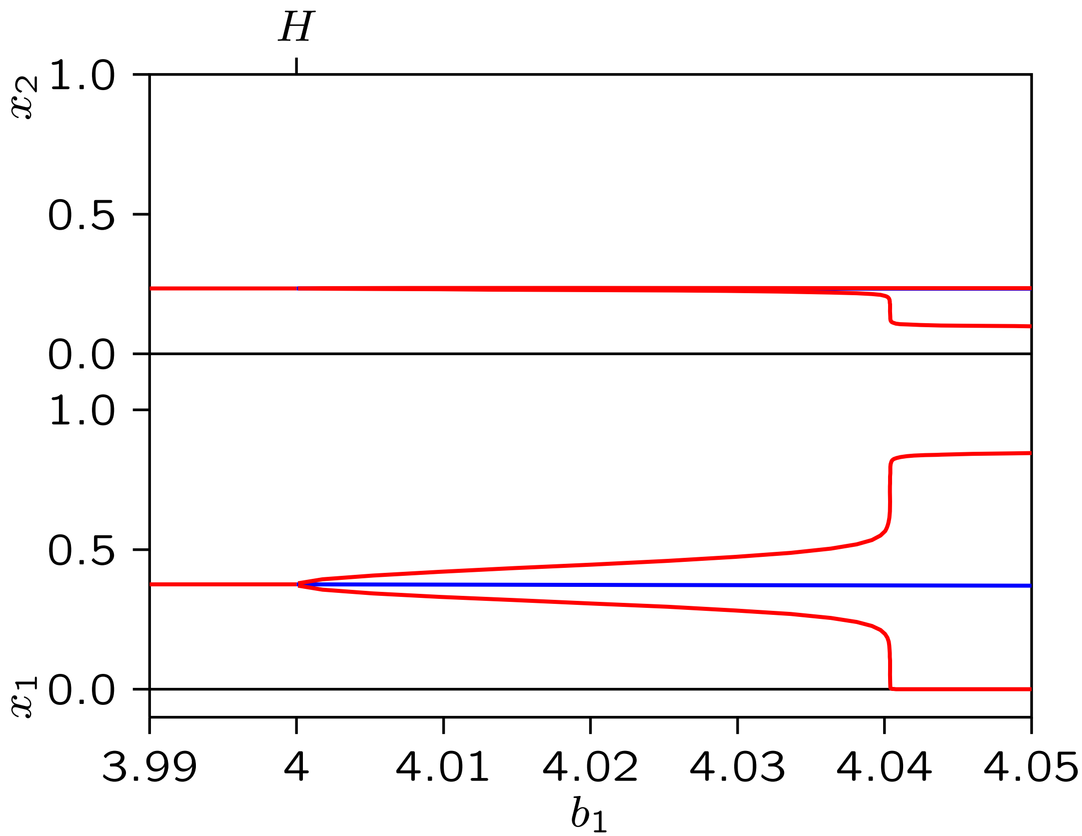


RM-model: $a_1 = 5/3b_1$, $\varepsilon = 0.01$,
A: $b_1 = 4.0402$, B: $b_1 = 4.0404$
0.3
0.25
0.2
0.15
0.1
0.05
0
x_2
0
0.2
0.4
0.6
0.8
1
x_1
A
B

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



Hopf H bifurcation

Where is the canard location?

To avoid unboundedness at Hopf bifurcation point we also take expansion of parameter b_1

Asymptotic expansion expansion in ε now near the Hopf bifurcation point of $r(x_1, \varepsilon)$

$$x_2 = r(x_1, \varepsilon) = r_0(x_1) + \varepsilon r_1(x_1) + \varepsilon^2 r_2(x_1) + \dots$$

and of bifurcation parameter b_1

$$b_1(\varepsilon) = b_{10} + \varepsilon b_{11} + \varepsilon^2 b_{12} + \dots$$

where r_j and b_{ji}, $j = 1 \cdots$ are fixed by an invariance condition at Hopf bifurcation point by equality order by order of powers of ε

Equating $\mathcal{O}(1)$ terms yields:

$$r_0 = \frac{(1-x_1)(1+b_{10}x_1)}{5/3\, b_{10}}$$

Equating $\mathcal{O}(\varepsilon)$ terms yields:

$$r_1 = \frac{(1-x_1)(-3b_{10}+3b_{11}x_1(b_{10}-1)-6b_{11}x_1^2b_{10}-x_1b_{10}^2+2x_1^2b_{10}^3)}{b_{10}^2(1+2x_1b_{10}-b_{10})x_1}$$

$$b_{10} = 4$$

However $1+2x_1b_{10}-b_{10} = 0$ evaluated at $b_{10} = 4$ and equilibrium $x_1 = x_1^* = \overline{x}_1$ at Hopf bifurcation point

Determine b_{11} so that besides denominator numerator is zero

This gives $b_{11} = 100/27$

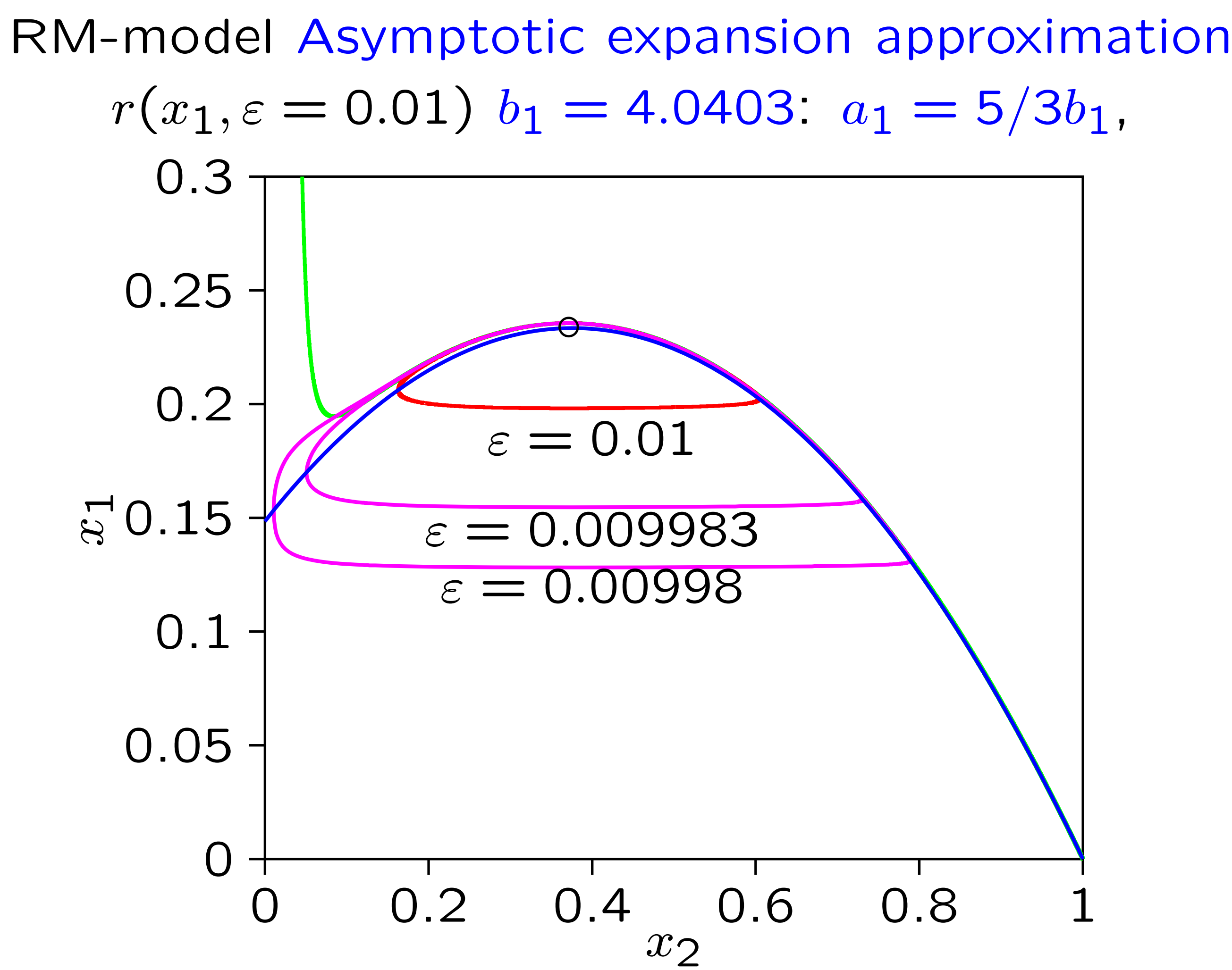
In a similar way we can get higher order approximations

For $\varepsilon = 0.01$ we calculated for the second order term

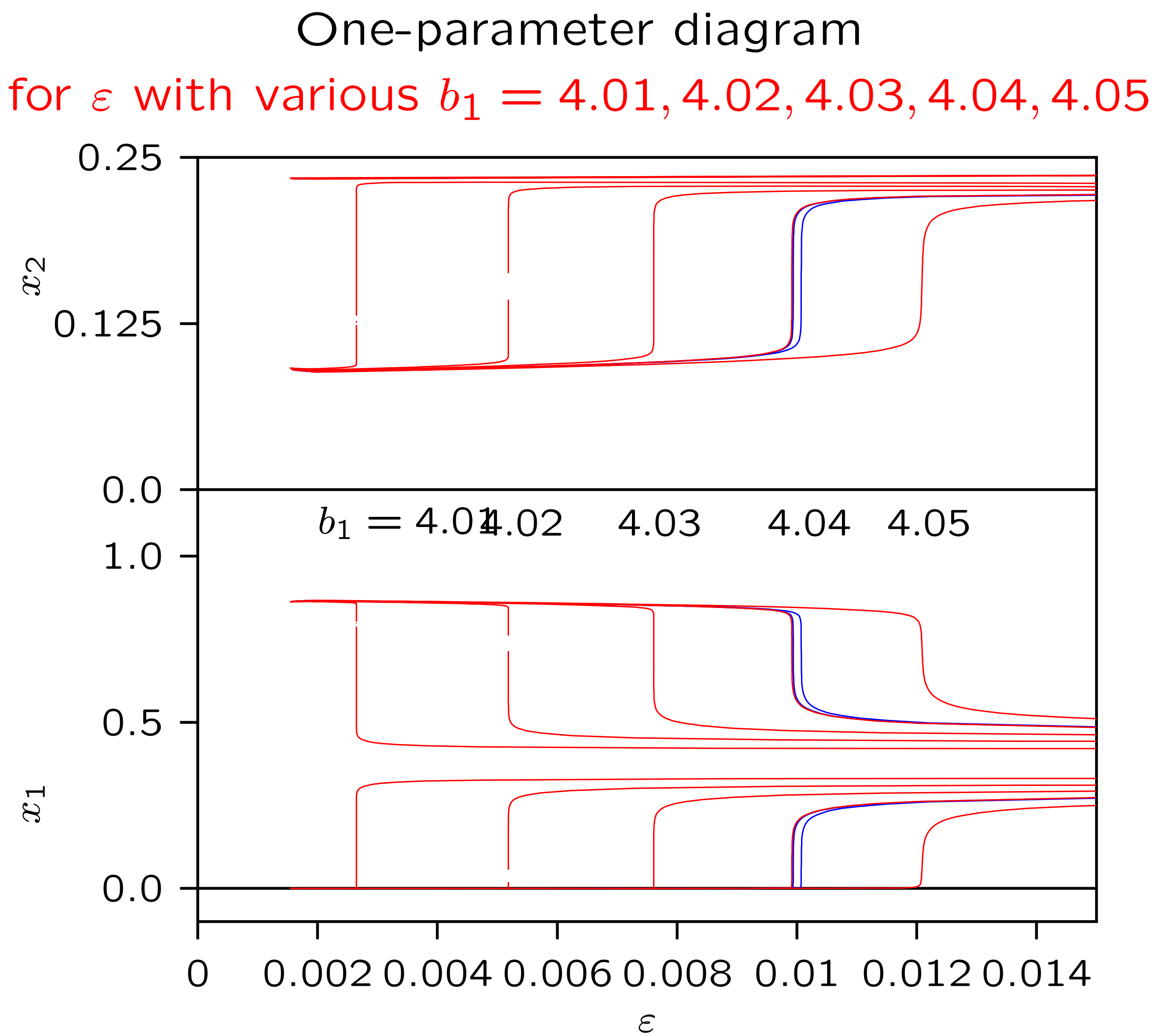
$$b_1(\varepsilon) = b_{10} + b_{11}\varepsilon + b_{12}\varepsilon^2 + \dots$$

$$b_1(\varepsilon) = 4 + 100/27\,\varepsilon + 58700/2187\,\varepsilon^2 = 4.04018$$

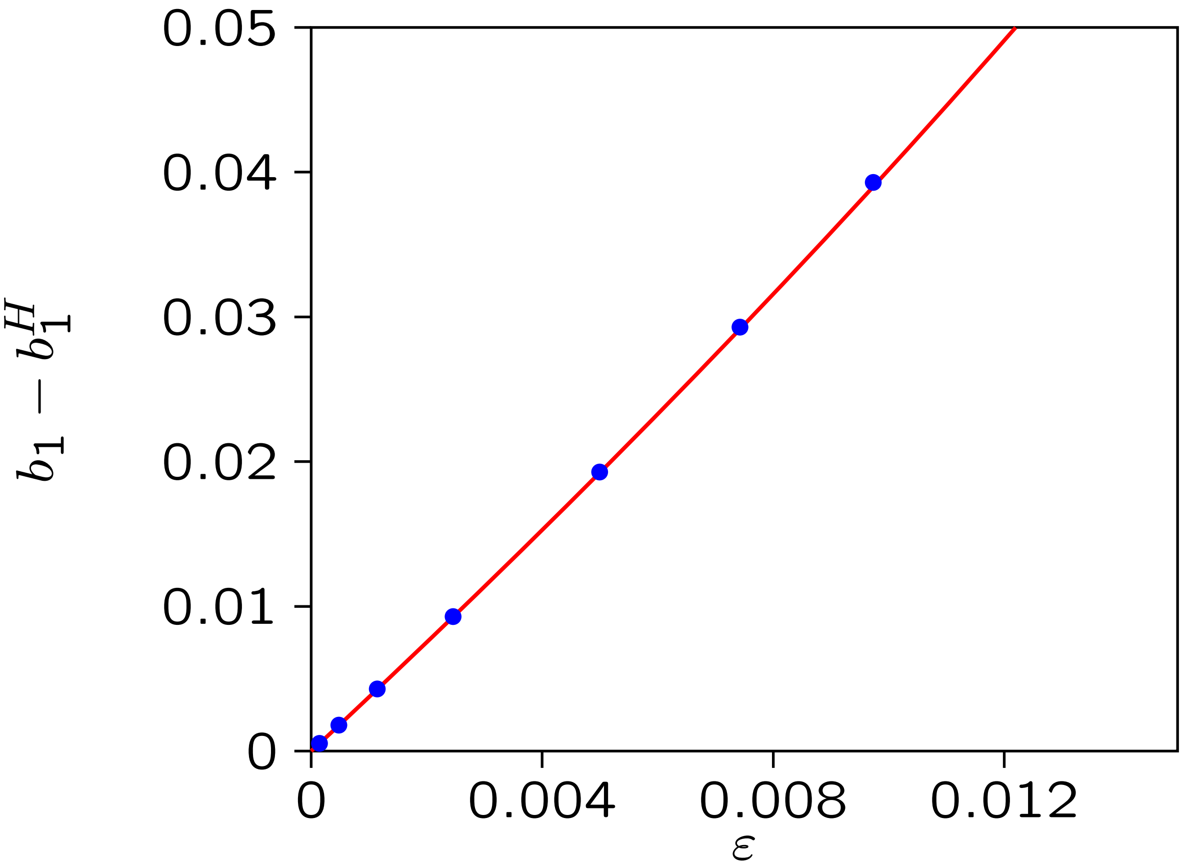
Higher order terms can be calculated with
symbolic algebra packages using the iterative scheme



RM-model Asymptotic expansion approximation
$r(x_1, \varepsilon = 0.01)$ $b_1 = 4.0403$: $a_1 = 5/3b_1$,
0.3
0.25
0.2
0.15
0.1
0.05
0
x_1
0
0.2
0.4
0.6
0.8
1
x_2
$\varepsilon = 0.01$
$\varepsilon = 0.009983$
$\varepsilon = 0.00998$



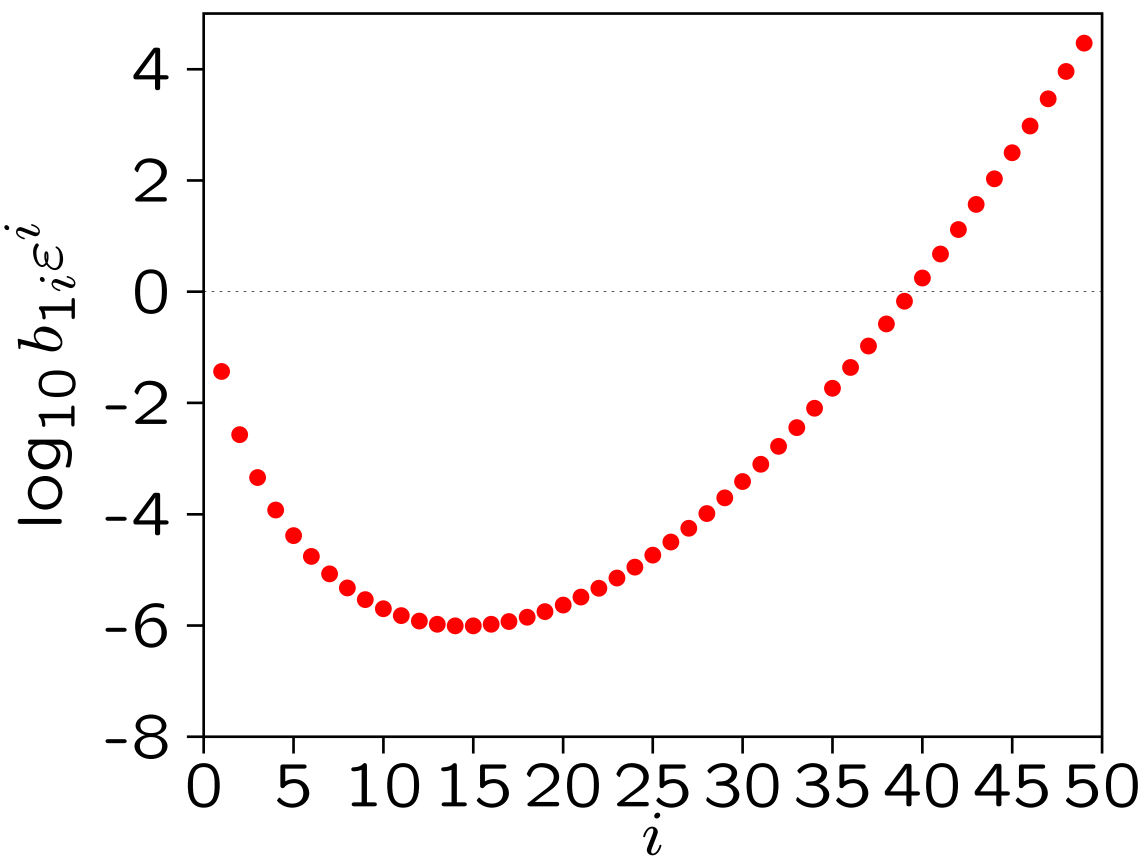
One-parameter diagram
for ε with various $b_1 = 4.01, 4.02, 4.03, 4.04, 4.05$
0.25
0.125
0.0
x_2
$b_1 = 4.01$
4.02
4.03
4.04
4.05
1.0
0.5
0.0
x_1
0
0.002
0.004
0.006
0.008
0.01
0.012
0.014
ε



Distance parameter value b_1 where canard explosion occurs and b_1^H Hopf bifurcation point as function of ε
Line graph of truncated expression and dots from AUTO continuation results

Asymptotic expansion approximation $r(x_1, \varepsilon)$ is divergent

Terms $b_{1i}\varepsilon^i$ as function of i with $\varepsilon = 0.01$.



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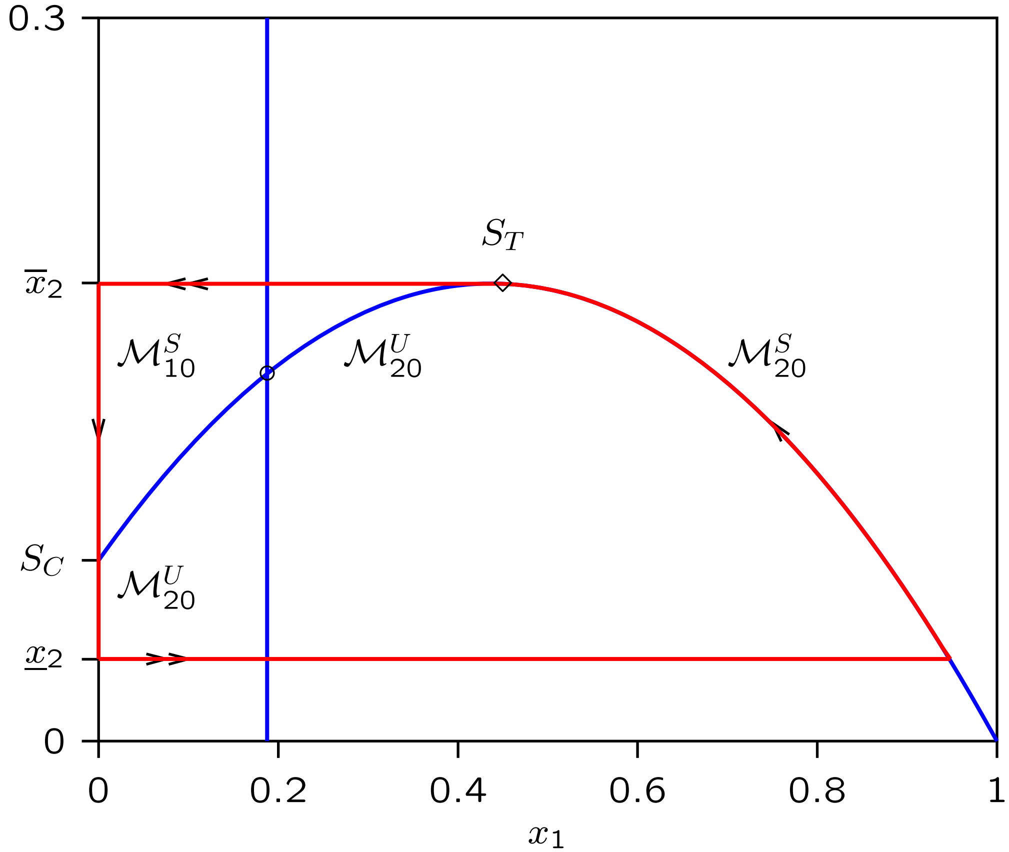
Relaxation oscillations

(Pogiale 2019)



Polynomial vector field

The studied polynomial version is orbitally equivalent with the original system

$$\frac{dx}{dt} = x\left(b + (1-b)x - ay - x^2\right)$$
$$\frac{dy}{dt} = \varepsilon\left((a-1)x - b\right)y$$

where we use the transformations $a = a_1/b_1$, $b = 1/b_1$ $m = 1$, $x = x_1/b$, $y = x_2/b$ defined for positive invariant domain $K^+ = \{(x,y)/x \geq 0, y \geq 0\}$

Geometrical Singular Perturbation Theory (GSPT), initiated by Fenichel's work, provides mathematical results for analyzing the dynamics around invariant manifolds when they are normally hyperbolic

Extrapopation of properties from $\varepsilon = 0$ to $0 < \varepsilon \ll 1$

Positive equilibrium point $E = (x_E, y_E)$ with

$$x_E = \frac{mb}{a-1}\,, \quad y_E = \frac{(1-x_E)(b+x_E)}{a}$$

Top of parabola and intersection with vertical axis

$$S_T = (x_T, y_T) = (\frac{1-b}{2}, \frac{(1+b)^2}{4a})$$
$$S_C = (x_C, y_C) = \left(0, \frac{b}{a}\right)$$

At these points the invariant sets are **not** normally hyperbolic : $\mathcal{M}_{10}$ loses the normal hyperbolicity at S_C and $\mathcal{M}_{20}$ loses the normal hyperbolicity at S_C and S_T. S_T is called a fold point because when $\varepsilon = 0$ and y increases and crosses the y-value of S_T, a fold bifurcation takes place

Singular points on the invariant manifolds

Extension methods have been provided for singular points on the invariant manifolds where the normal hyperbolicity is lost

The blow-up technique allows to build a new geometrical object and a new vector field on this object, by change of variables, such that for the new system, the invariant manifolds are normally hyperbolic

This is a so-called desingularization method. We apply this approach to study the dynamics of the RM model with two time scales around the singular points S_T and S_C

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Brief description of the blow-up technique

Analyzing fold points like S_T, a translation is made such that the fold point is moved to the origin

Here, it does not matter because as we will analyse the Hopf bifurcation at this point, S_T and E coincide at the bifurcation

Then our change of coordinates is efficient to understand the bifurcation and the occurrence of a canard phenomenon

Moreover we take a second bifurcation parameter λ and replace the parameter a

$$\lambda = 1 - b - 2x_E \ , \quad a = m\frac{1+b-\lambda}{1-b-\lambda}$$

Bifurcation occurs at $\lambda = 0$

Let $X = x - x_E$ and $Y = y - y_E$ and λ defined as above

$$\frac{dX}{dt} = (X + x_E)\left(\lambda X - m\frac{1+b-\lambda}{1-b-\lambda}Y - X^2\right)$$
$$\frac{dY}{dt} = \varepsilon\frac{2bm}{1-b-\lambda}X(Y + y_E)$$

To analyze this singular fold point, we complete this system by

$$\frac{d\varepsilon}{dt} = 0$$
$$\frac{d\lambda}{dt} = 0$$

Family of vector fields

System on $\tilde{K}^+ = \{(X,Y), X \geq -x_E, Y \geq -y_E\}$ will be considered as a differential system defining a family of vector fields $\mathcal{X}_\mu$ on $\tilde{K}^+$ where $\mu = (\varepsilon, \lambda) \in \Lambda$ with $\Lambda = [0; \varepsilon_0) \times I$ where I is a small interval containing 0 and $\varepsilon_0 > 0$

In this family, the point $(0,0,0,0) \in K^+ \times \Lambda$ is a so called non-degenerate singular fold point

Fenichel's theorem does not apply at these points because of the loss of normal hyperbolicity at S_T (fold T) and S_C (transcritical TC)

Dumortier and Roussarie (2000,1996) developed the general approach for analyzing singular fold points in dynamical systems with two time scales using the blow-up technique.

In Krupa and Szmolyan (2001) the authors address the study of non-degenerate singular fold points and extend the previous results

Our case is a particular case of this general study

For all $\lambda \in I$, the parabola defined by

$$Y = \frac{(1 - b - \lambda)}{m(1 + b - \lambda)}(\lambda X - X^2)$$

is invariant when $\varepsilon = 0$

Union of all these parabolas constitutes an invariant 3-dimensional manifold for $\varepsilon = 0$ that we denote by $\tilde{\mathcal{M}}_{20}$.

$\tilde{\mathcal{M}}_{20}^{S}$ is the stable branch and $\tilde{\mathcal{M}}_{20}^{U}$ unstable branch

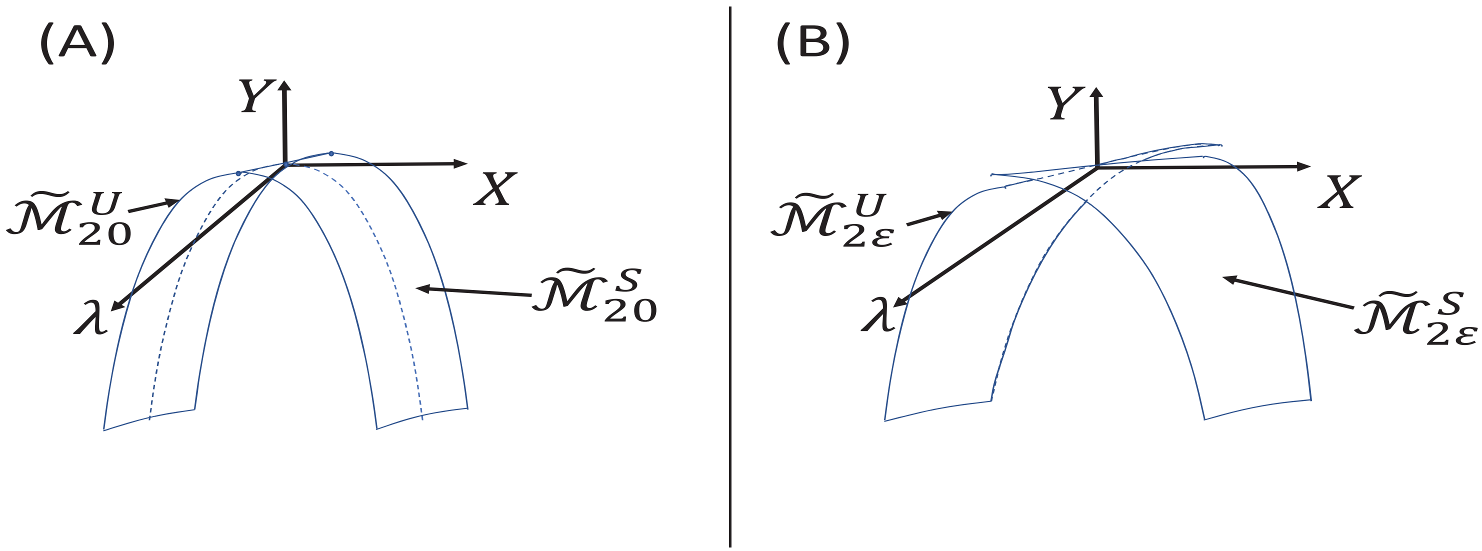
For $\varepsilon = 0$, the stable branch and the unstable branch of the manifold are connected

Attracting slow branch $\tilde{\mathcal{M}}_{2\varepsilon}^{S}$ may connect to repelling slow branch $\tilde{\mathcal{M}}_{2\varepsilon}^{U}$ at isolated values $\lambda = \lambda(\varepsilon)$

Transition between small and large oscillations is via a maximal canard

Scheme of invariant manifolds $\mathcal{M}_{2\varepsilon}$

A: $\varepsilon = 0$ and B for $0 < \varepsilon \ll 1$



We desingularize the point $(0,0,0,0) \in \tilde{K}^{+} \times \Lambda$ by considering the blow-up :

$$\begin{array}{rcl} \Psi : S^3 \times [0; +\infty[& \longrightarrow & \mathbb{R}^4 \\ (X_1, Y_1, \lambda_1, \varepsilon_1, r) & \mapsto & (X, Y, \varepsilon, \lambda) = \left(rX_1, r^2 Y_1, r^2 \varepsilon_1, r\lambda_1\right) \end{array}$$

where

$$X_1^2 + Y_1^2 + \lambda_1^2 + \varepsilon_1^2 = 1$$

To understand the dynamics on this hemisphere, we use charts
$\{X_1 = \pm 1\}$, $\{Y_1 = \pm 1\}$, $\{\varepsilon_1 = 1\}$

For instance, the chart $\{X_1 = 1\}$ describes the dynamics of the new vector field around the hemisphere S^{3+} for positive X_1

To get the chart $\{X_1 = 1\}$, we consider the change of coordinates $(X, Y, \varepsilon, \lambda) = (r, r^2 Y_1, r^2 \varepsilon_1, r\lambda_1)$ which leads to:

$$\frac{dr}{dt} = \frac{dX}{dt}$$
$$\frac{dY_1}{dt} = \frac{1}{r^2}\Big[\frac{dY}{dt} - 2rY_1\frac{dr}{dt}\Big]$$
$$\frac{d\varepsilon_1}{dt} = -\frac{2\varepsilon_1}{r}\frac{dr}{dt}$$
$$\frac{d\lambda_1}{dt} = -\frac{\lambda_1}{r}\frac{dr}{dt}$$

Special case of system with $\dfrac{dX_1}{dt} = 0$ because $X_1 = 1$ hence $X = r$. After some straightforward calculations, assuming that r is small and expanding the equations with respect to r, one gets:

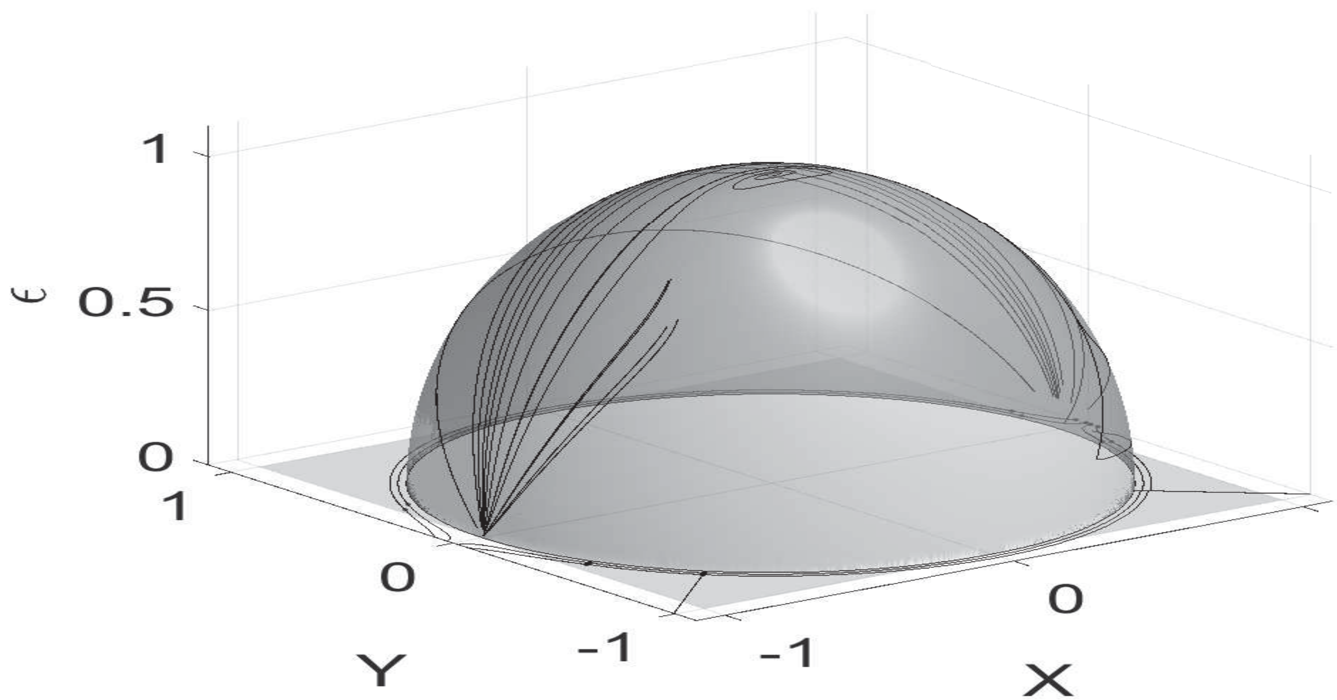
$$\frac{dr}{dt} = r^2 \frac{1-b}{2}\Big(-1 + \lambda_1 - \frac{1+b}{1-b} Y_1 \Big) + O(r^3)$$
$$\frac{dY_1}{dt} = r\Big(b\frac{1+b}{2}\varepsilon_1 - Y_1(1-b)(\lambda_1 - 1 - \frac{1+b}{1-b}Y_1) \Big) + O(r^2)$$

Next figure illustrates the blow-up result

The singular fold point has been replaced by a hemisphere

The vector field on the horizontal set $\{\varepsilon = 0\}$ has been determined from analysis in charts $\{X_1 = \pm 1\}$ and $\{Y_1 = \pm 1\}$ and then projected on the hemisphere equator (circle)

Scheme of blow-up around the singularity
$(0, 0, 0, 0)$ for a fixed positive λ.



We consider the case $\varepsilon_1 = 0$ and $\lambda_1 = 0$ in the previous system, and after division by r, one gets:

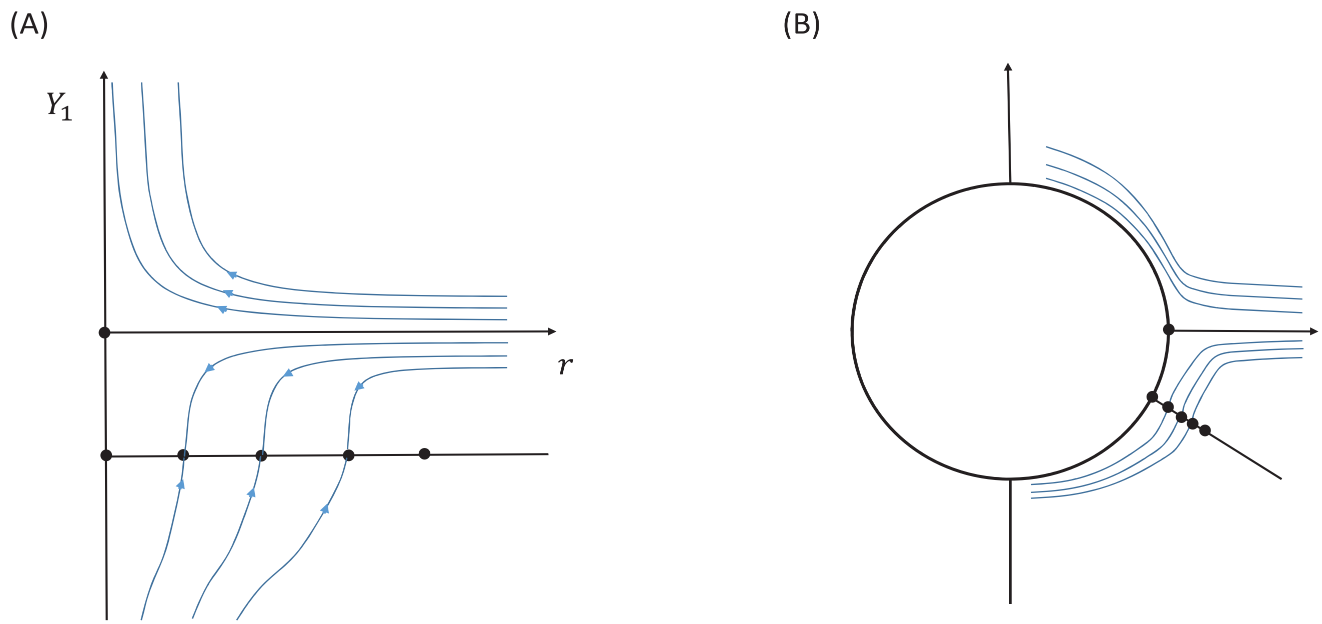
$$\frac{dr}{dt} = r\frac{1-b}{2}\Big(- 1 - \frac{1+b}{1-b}Y_1)\Big) + O(r^2)$$
$$\frac{dY_1}{dt} = -Y_1(1-b)\Big(- 1 - \frac{1+b}{1-b}Y_1\Big) + O(r)$$

Dividing by r for $r > 0$ does not change the trajectories and allows to determine the dynamics around the hemisphere and this is why we can desingularize the origin.

The study of the dynamics is simple and the main results are that the vertical axis $r_1 = 0$ is invariant as well as the straight line defined by $Y_1 = -\dfrac{1-b}{(1+b)}$

These invariant sets in the chart $\{X_1 = 1\}$ correspond to invariant sets on the blown-up geometrical object, namely respectively to the hemisphere equator (circle) and to the stable branch of the parabola (straight lines perpendicular to the circle), in the plane $\{\varepsilon_1 = 0\} \bigcap \{\lambda_1 = 0\}$

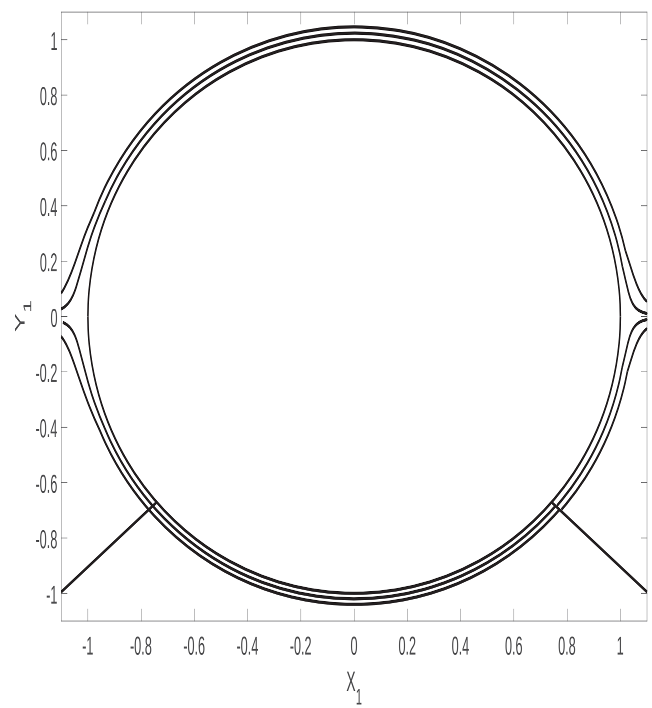
Scheme of dynamics in a chart $\{X_1 = 1\}$



A: for $\varepsilon_1 = 0$, $\lambda_1 = 0$ and and B: dynamics around hemisphere in the plane $\varepsilon_1 = 0$ and $\lambda_1 = 0$

Putting all the charts together and mapping the results onto the blown up object allows to understand the dynamics around the hemisphere

This is actually equivalent to the dynamics of the initial system around the origin.



We now need to analyze the dynamics for positive $0 < \varepsilon \ll 1$. This is done by using the charts $\{\varepsilon_1 = 1\}$ with $\lambda_1 = -0.1$ in (A), $\lambda_1 = 0$ in (B) and $\lambda_1 = 0.1$ in (C)

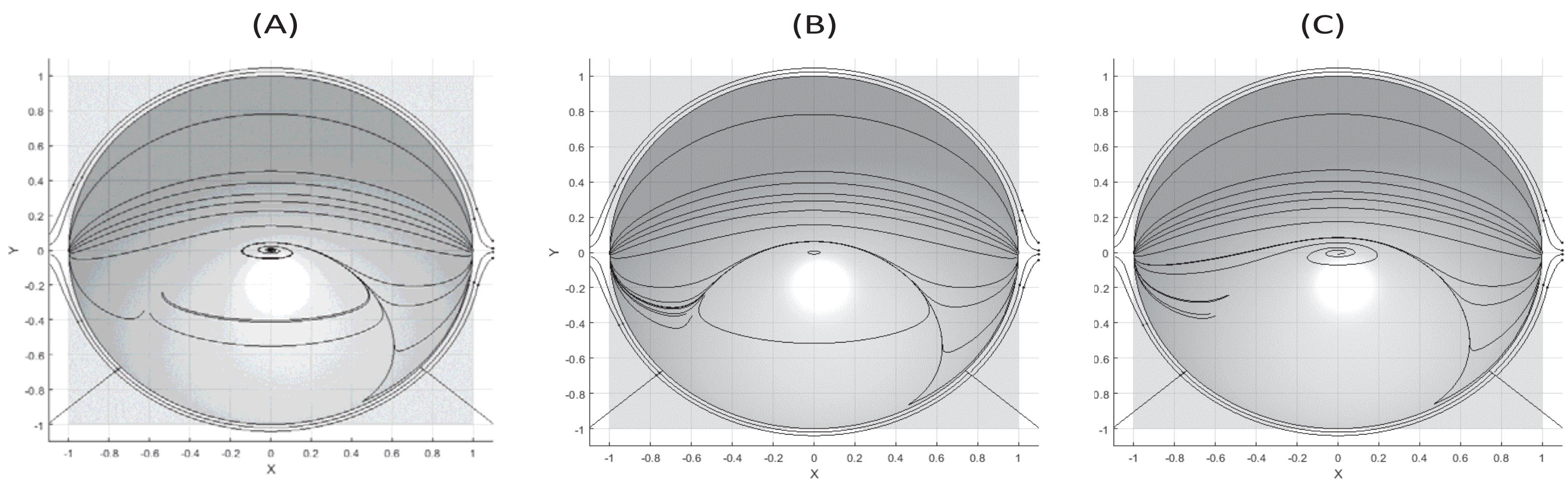


Illustration of the dynamics induced by the vector field on the blown up object for three values of λ_1 in the chart $\{\varepsilon_1 = 1\}$

A: $\lambda_1 < 0$, origin is a stable equilibrium attracting trajectories initiated under the parabola, while trajectories initiated above this parabola leave the hemisphere by the West point

B: $\lambda_1 = 0$, the origin is a center. All trajectories initiated below the parabola are closed curves surrounding the origin. The trajectories initiated above the parabola leave the hemisphere by the West point. The parabola is invariant under the flow

C: $\lambda_1 > 0$ origin is an unstable focus. All trajectories leave the hemisphere by the West point

Main result Theorem Poggiale et al. (2019)

For $\varepsilon > 0$ small enough, the polynomial system admits maximal canard solutions when λ becomes positive and close to zero. More precisely, there exists a function defined in the vicinity of $0 \in \mathbb{R}$ with $\varepsilon \mapsto \lambda_c(\varepsilon)$ such that for all $\varepsilon > 0$ close to 0, there exists $\lambda = \lambda_c(\varepsilon) > 0$ for which the system exhibits a maximal canard

An approximation of this function is given by:

$$\lambda_c(\varepsilon) = \frac{b(1+b)^2}{(1-b)^3}\varepsilon + O(\varepsilon^{3/2})$$

Define the Hamiltonian function H as follows :

$$H(X_1, Y_1) = \exp\left(\frac{2(1-b)}{b(1+b)}Y_1\right)\Big(X_1^2 + \frac{(1+b)}{1-b}Y_1 - \frac{b(1+b)^2}{2(1-b)^2}\Big)$$

This function vanishes on the parabola $\mathcal{P}$ and is positive below the parabola Level curves of H correspond to trajectories of system when $\lambda_1 = 0$

Let denote by γ the trajectory on the hemisphere, it connects the stable branch $\mathcal{M}_{20}^S$ to the unstable branch $\mathcal{M}_{20}^U$ on the equator of the hemisphere. Along this trajectory, H remains equal to 0

The curve γ can be parameterized as follows:

$$\gamma(t) = \begin{pmatrix} t \\ -\frac{1-b}{m(1+b)}t^2 + \frac{b(1+b)}{2(1-b)} \end{pmatrix}$$

The theorem claims that for all small $\varepsilon > 0$, there exists a value of λ such that the unstable manifold and stable manifold are connected

Actually, the connection will be established from γ

We will then prove that for all sufficiently small ε, there exists a value of λ for which the distance between these manifolds vanishes

To calculate the distance between the stable and unstable branch of the invariant manifold in the chart $\{\varepsilon_1 = 1\}$, we calculate the deviation of the value taken by $H(t)$ along the whole curve γ for every $(r, \lambda_1) \simeq (0, 0)$.

The distance between $\bar{\mathcal{M}}^S_{2\varepsilon}$ and $\bar{\mathcal{M}}^U_{2\varepsilon}$ is:

$$\delta(r, \lambda_1) = \int_{H(\gamma(-\infty))}^{H(\gamma(+\infty))} dH(\gamma(t)) = \int_{-\infty}^{+\infty} \frac{dH(\gamma(t))}{dt} dt$$

Lemma

There exists a function λ_{1c} depending on r in a neighborhood of 0 such that $\delta(r, \lambda_{1c}(r)) = 0$

This lemma proves the existence of canard solutions.

We get finally

$$\lambda_{1c}(r) = \frac{b(1+b)^2}{(1-b)^3} r + O(r^2)$$

We work in the chart $\{\varepsilon_1 = 1\}$ and we use the following blow-up:

$$\begin{array}{rcl} \Psi : S^3 \times [0;+\infty[& \longrightarrow & \mathbb{R}^4 \\ (X_1, Y_1, \lambda_1, \varepsilon_1, r) & \mapsto & (X, Y, \varepsilon, \lambda) = \left(rX_1, r^2 Y_1, r^2 \varepsilon_1, r\lambda_1\right) \end{array}$$

Hence $r = \sqrt{\varepsilon}$ and $\lambda = \sqrt{\varepsilon}\lambda_1$, we conclude:

$$\lambda_c(\sqrt{\varepsilon}) = \frac{mb(1+b)^2}{(1-b)^3}\varepsilon + O(\varepsilon^{3/2})$$

This is the same first order approximation as found previously with the asymptotic approximation approach

Outline

- Introduction

- Rosenzweig-MacArthur predator–prey RM model
  - □ Fast-slow analysis, Relaxation oscillations
  - □ Asymptotic expansion
  - □ Canard location
  - □ Geometric singular perturbation theory (GSPT)
  - □ Blow-up technique, Existence of Canards

- Conclusions

Conclusions

- Existence of canards in the RM-model with two time scales

- Use of biomasses not numbers of individuals

- Numerical approach: asymptiotic expansion in both perturbation parameter and model parameter

- Analytical approach: Proof of existence: Also perturbation parameter and model parameter are used

Literature

B.W. Kooi and J-C. Poggiale, Modelling, singular perturbation and bifurcation analyses of bitrophic food chains, *Mathematical Bioscience*, 301:93-110 2018.

J-C. Poggiale, C. Aldebert, B. Girardot and B.W. Kooi, Analysis of a predator-prey model with specific time scales : a geometrical approach proving the occurrence of canard solutions *Journal of Mathematical Biology*, 2019.