Review of the analysis of Rosenzweig-MacArthur predator-prey model

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Outline

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- Rosenzweig-MacArthur predator–prey RM model
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  - □ (Non-generic) Fold Singularity, Tangent bifurcation
  - □ (Singular) Hopf bifurcation
  - □ Asymptotic expansion, Canard location
  - □ Simulation, Numerical bifurcation analysis
  - □ Geometric singular perturbation theory (GSPT)
  - □ Blow-up technique, Existence of Canards
- Conclusions

Bifurcation analysis of RM predator–prey model

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

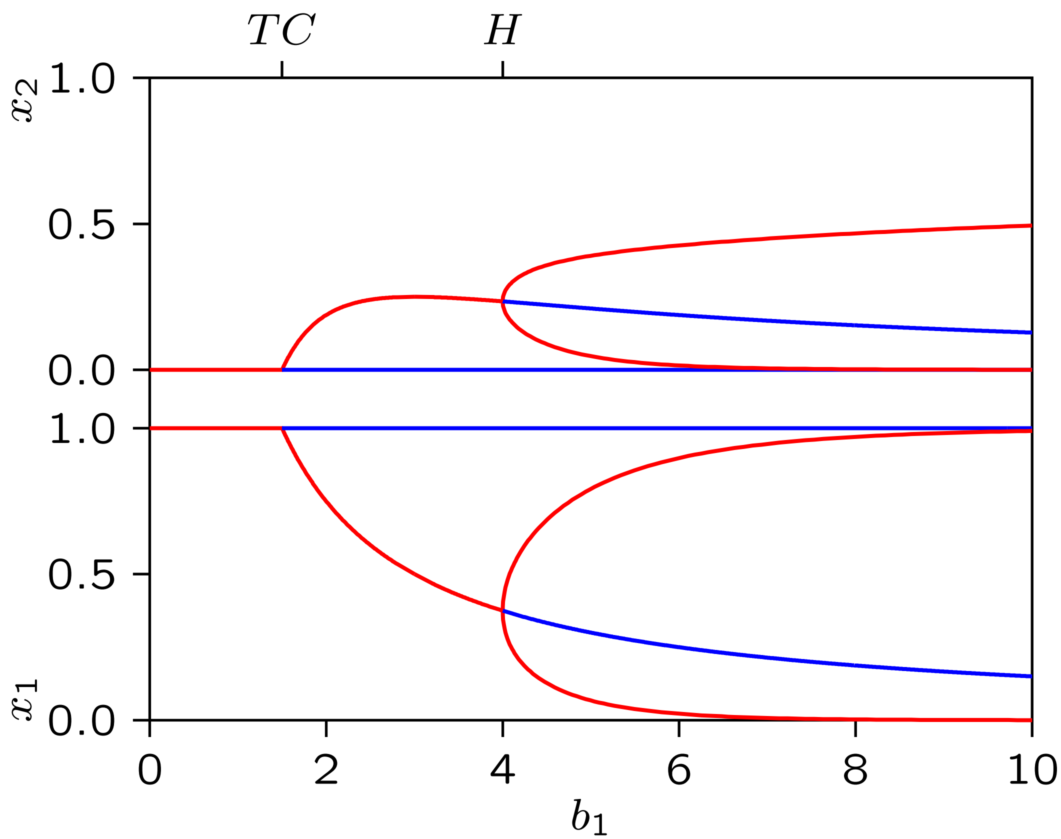
Bifurcation	Description
TC	Transcritical bifurcation: invasion through boundary equilibrium
T	Tangent bifurcation: catastrophic change of the system dynamics
H	Hopf bifurcation: origin of (in)stable limit cycle

Literature ($\varepsilon = 1$):

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

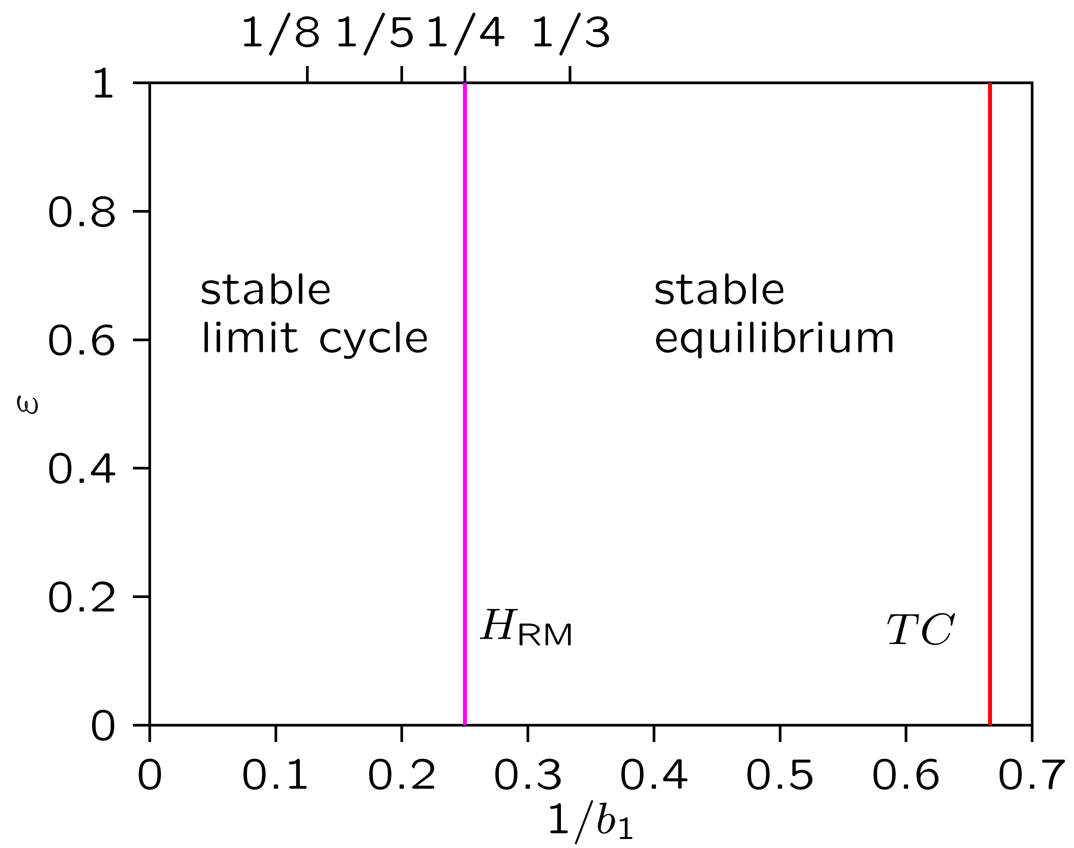
RM-model

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



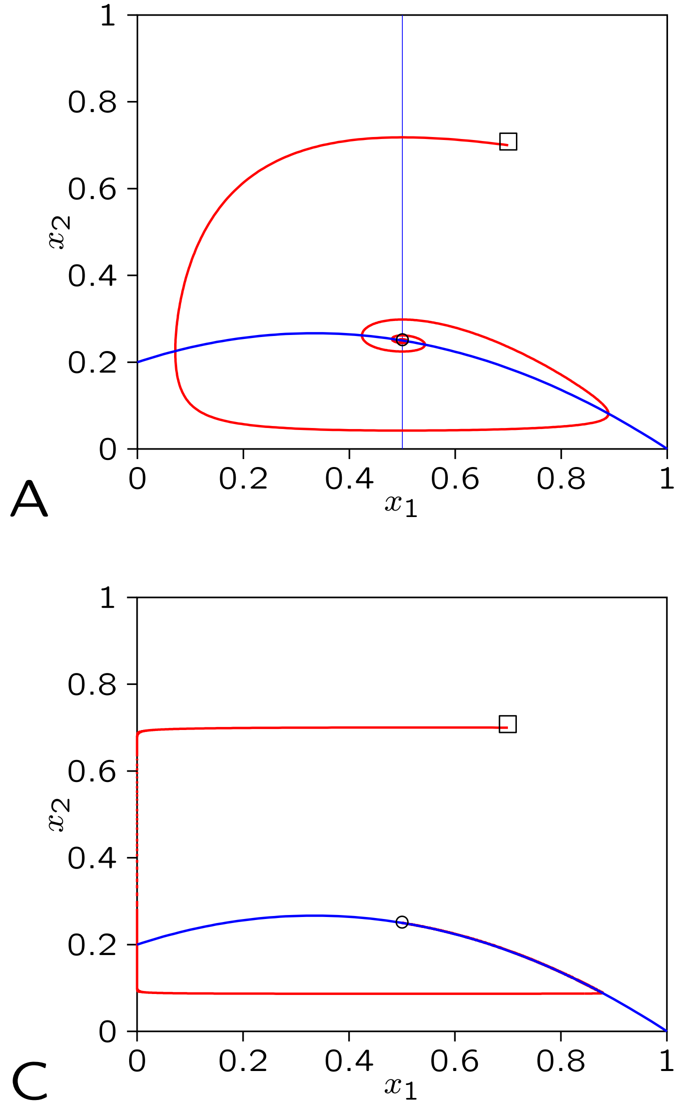
Transcritical TC, Hopf H bifurcations

Two-parameter bifurcation diagram ε vs b_1

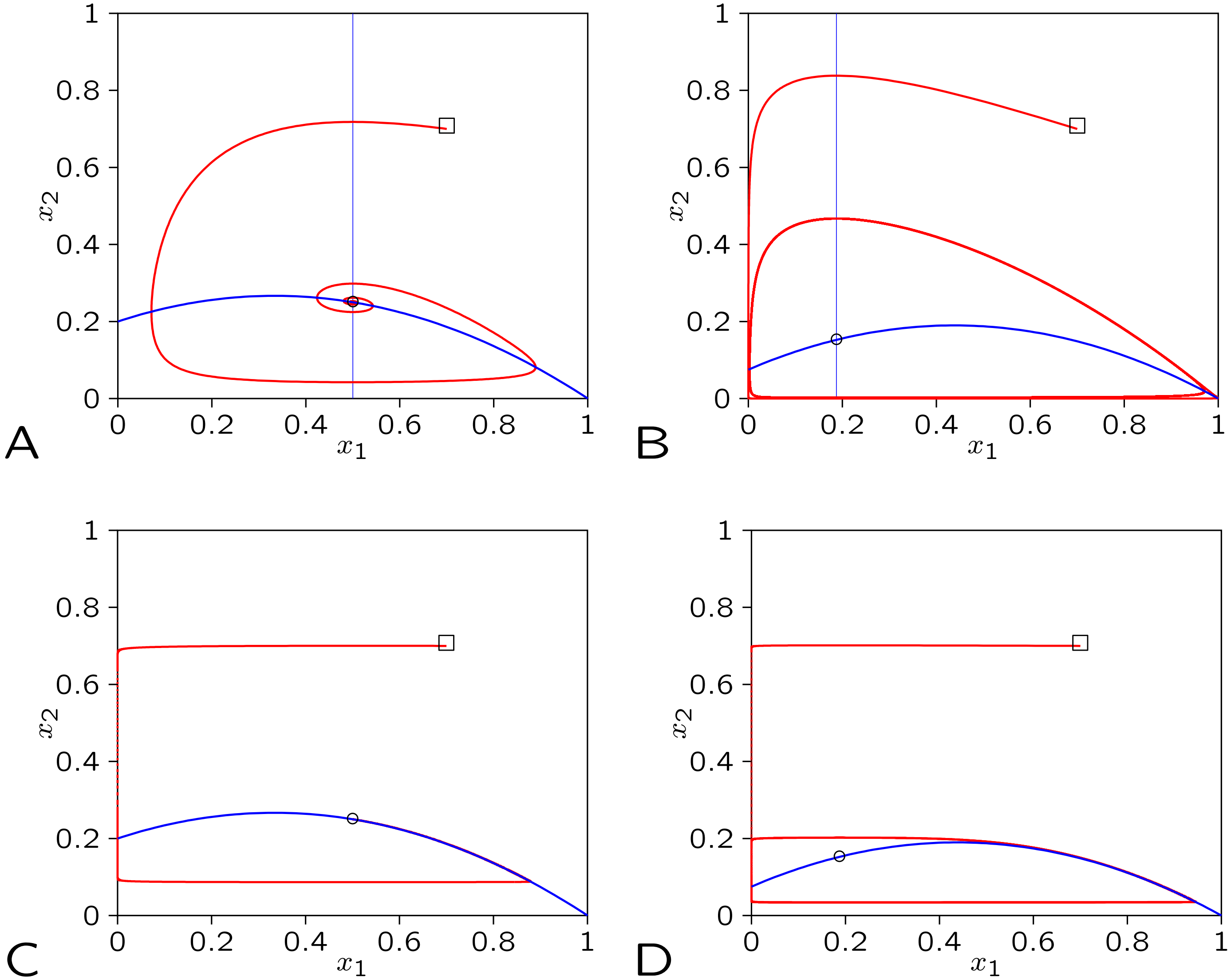


Hopf H_{RM}; Transcritical TC

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



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



Fast-slow system

fast system time t

$\varepsilon \to 0$

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

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

layer system

slow system time $\tau = \varepsilon t$

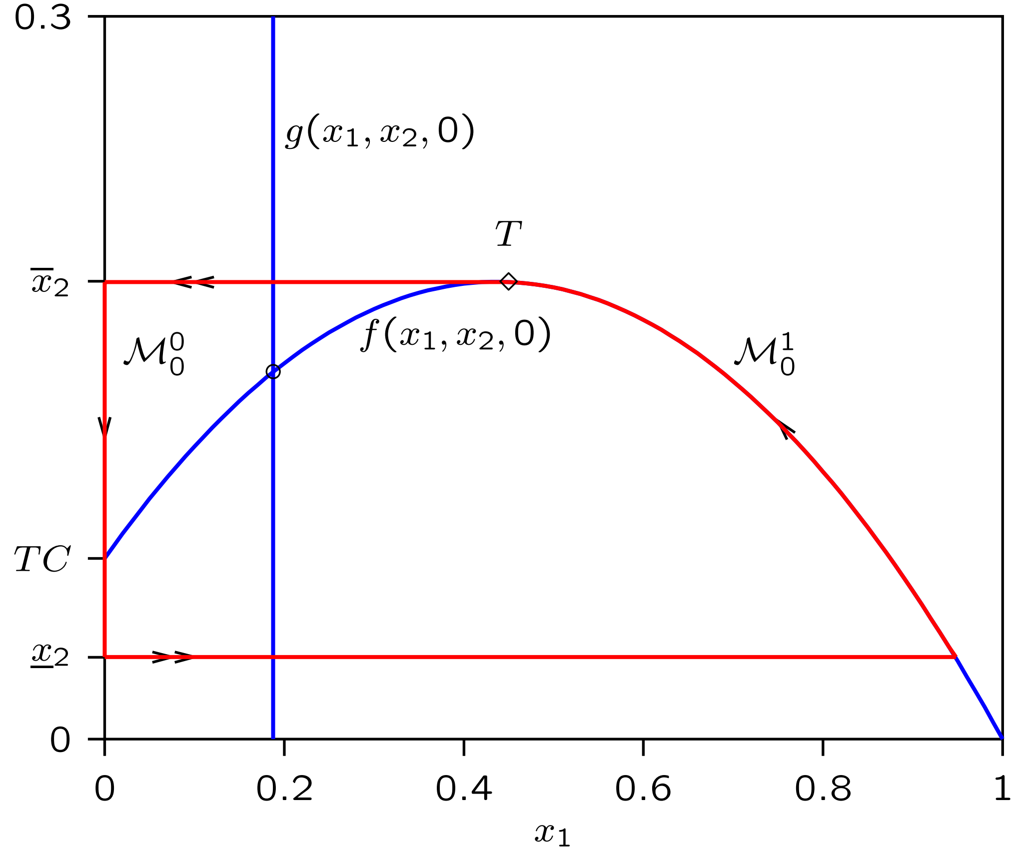
$\varepsilon \to 0$

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

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

reduced system

Relaxation oscillations



Critical manifolds $\mathcal{M}_0^0$, $\mathcal{M}_0^1$

Layer system Tangent bifurcation T with x_2 as parameter

Non-generic Folded point

Topologically equivalent model

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

Equilibria are

$$x_1^* = \frac{1}{a_1 - b_1}\,, \qquad x_2^* = \frac{a_1 - b_1 - 1}{(a_1 - b_1)^2}$$

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

where $a_1 = 5/3b_1$ and substitute $\lambda = 4 - b_1$

Then we have a folded point T where
$x_1^* = 0, x_2^* = 0, \lambda = 0, \varepsilon = 0$

$$f(0,0,0,0) = 0\ , \qquad \frac{\partial f}{\partial x_1} = 0$$

$$\frac{\partial^2 f}{\partial x_1^2}(0,0,0,0) \neq 0\ , \qquad \frac{\partial f}{\partial x_2} \neq 0$$

$$g(0,0,0,0) = 0\ , \qquad \frac{\partial g}{\partial x_1} \neq 0\ , \qquad \frac{\partial g}{\partial \lambda} \neq 0$$

Last condition is not satisfied: $\frac{\partial g}{\partial \lambda} = 0$

Folded point T bifurcation in the RM-model is not generic

(Singular) Hopf bifurcation

The Jacobian matrix evaluated at the Hopf bifurcation point with $\lambda = 0$ reads:

$$\mathbf{J} = \begin{bmatrix} 0 & -5/2 \\ \varepsilon\, 5/8 & 0 \end{bmatrix}$$

Eigenvalues $\mu \pm i\omega$ are pure imaginary pair

$$\mu = 0\,, \qquad \omega = 5/4\sqrt{\varepsilon}$$

Regular Hopf bifurcation for $\varepsilon > 0$ becomes singular when $\lim_{\varepsilon\to 0}\omega = 0$

This is on the fast time scale t on the slow time scale $\tau = \varepsilon t$: $\lim_{\varepsilon\to 0}\omega = \infty$

Both eigenvalues are zero at $\varepsilon = 0$ and the point is a double-zero or a kind of Bogdanov-Takens bifurcation

The first Lyapunov coefficient ℓ^1 is evaluated as

$$\ell^1 = -\frac{16}{5\sqrt{\varepsilon}}$$

Since it is always negative the Hopf bifurcation is super-critical (stable limit cycle)

For $\lim \varepsilon \to 0$ we have $\ell^1 \to -\infty$
That is, the first Lyapunov coefficient ℓ^1 becomes unbounded

At slow timescale τ with $\varepsilon = 0$ gives $\ell^1 = 0$

In this time-frame the Hopf bifurcation is a Bautin bifurcation

Remark

The singular Hopf point at the top of the prey-nullcline is non-generic folded point

Theory in

M Krupa and P Szmolyan. Relaxation oscillation and canard explosion. *Journal of Differential Equations*, 174:312–368, 2001.

C Kuehn. *Multiple Time Scale Dynamics*, volume 191 of *Applied Mathematical Sciences*. Springer-Verlag, New York, 2015.

is not directly applicable

Remark

The singular Hopf point at the top of the prey-nullcline is a singular Hopf bifurcation point

Theory in

SM Baer and T Erneux. Singular Hopf bifurcation to relaxation oscillations. *SIAM Journal on Applied Mathematics*, 46:721–739, 1986.

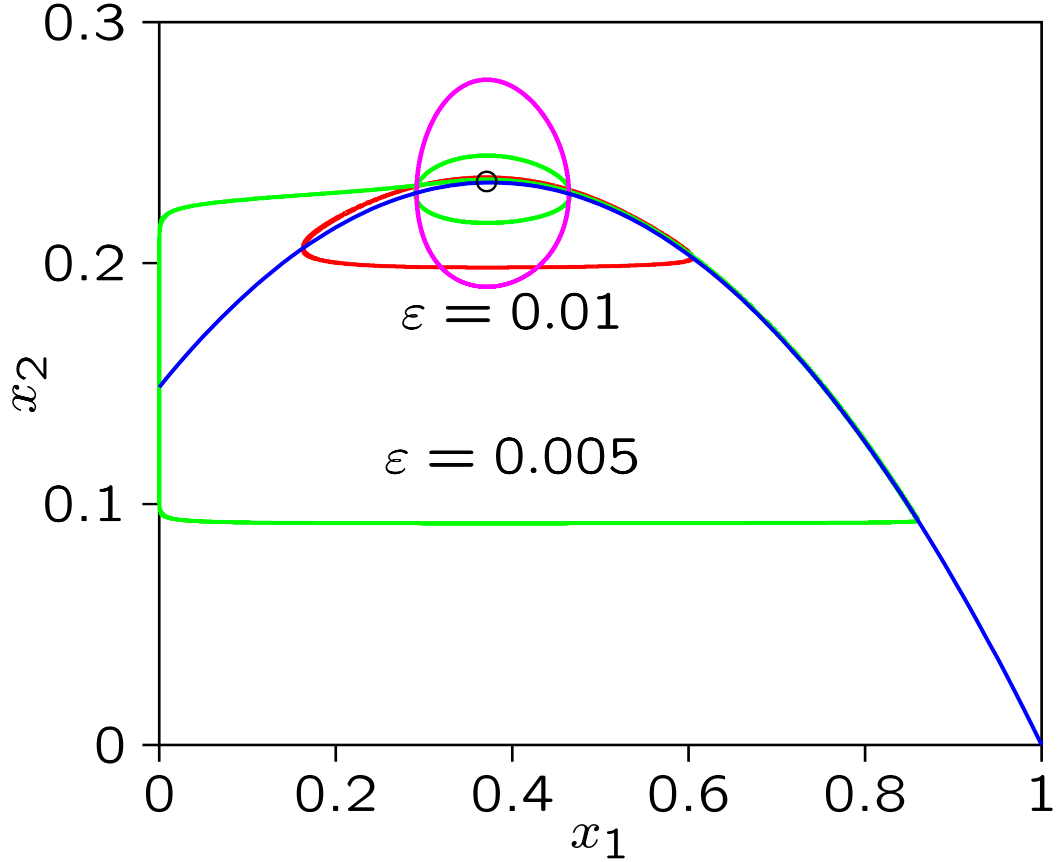
SM Baer and T Erneux. Singular Hopf bifurcation to relaxation oscillations ii. *SIAM Journal on Applied Mathematics*, 52:1651–1664, 1992.

B Braaksma. Singular Hopf bifurcation in systems with fast and slow variables. *J. Nonlinear Sci.*, 8(5):457–490, 1998.

is applicable but elaboration depends on model

Simulation study $b_1 = 4.0403$

$\varepsilon = 1$, $\varepsilon = 0.1$, $\varepsilon = 0.01$ and $\varepsilon = 0.005$



from relaxation oscillation $\varepsilon = 0.005$ to limit cycle $\varepsilon = 0.1$

Canard: Van der Pol equation (Eckhaus 1983)

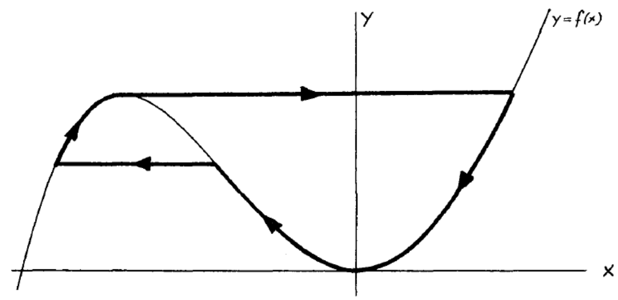


Fig. 1.3a. *A canard limit cycle*

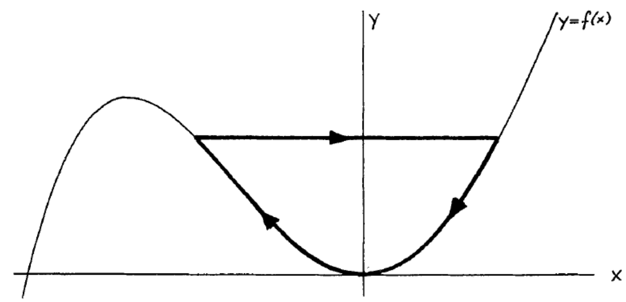


Fig. 1.4. *The duck has lost its head*

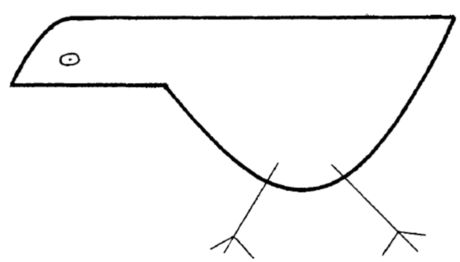


Fig. 1.3b. *The french duck*

Where is the canard location: phase-plane analysis

Using its invariance the perturbed manifold $\mathcal{M}_\varepsilon^1$ can be approximated by asymptotic expansions or power series expansion in ε, that it can be described as a graph

$$\left\{(x_1, x_2)\Big| x_2 = r(x_1, b_1, \varepsilon),\ x_1 \geq 0,\ x_2 \geq 0\right\}$$

This manifold is invariant if the following equality holds

$$\frac{dx_2}{dt} = \frac{dx_2}{dx_1}\,\frac{dx_1}{dt} = \frac{dr(x_1, b_1, \varepsilon)}{dx_1}\,\frac{dx_1}{dt}$$

$$\frac{dr(x_1, b_1, \varepsilon)}{dx_1} x_1\big(1 - x_1 - \frac{a_1 r(x_1, b_1, \varepsilon)}{1 + b_1 x_1}\big) = \varepsilon r(x_1, b_1, \varepsilon)\big(\frac{a_1 x_1}{1 + b_1 x_1} - 1\big)$$

Asymptotic expansion expansion in ε now near the Hopf-tangent bifurcation point of $r(x_1, b_1, \varepsilon)$

Two parameters ε and b_1 function of x_1: $x_2 = r(x_1, b_1, \varepsilon)$:

$$r(x_1, b_1, \varepsilon) = r_0(x_1, b_{10}) + \sum_{i=1} \varepsilon^i r_i(x_1, b_{1i-1}, b_{1i}) + \ldots$$

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

where r_i and b_i, $i = 1 \cdots$ are independent of ε and are fixed by the invariance criterion and by equality order by order of powers of ε together with a continuity condition at Hopf bifurcation point H and calculated recursively

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

$$r_0 = \frac{(1 - x_1)(1 + b_{10}x_1)}{5/3\, b_{10}} = \frac{1 - x_1 + b_{10}x_1 - b_{10}x_1^2}{5/3\, b_{10}}$$

where $x_1 = 3/(2b_1)$ and $b_{10} = b_1 = 4$ evaluated at Hopf bifurcation point H and tangent for layer system T where x_2 is treated as a parameter, situated at the top of the parabola in the phase-plane

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

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

However, evaluated at $b_{10}=4$ and equilibrium $x_1=x_1^*$ we have $1+2x_1b_{10}-b_{10}=0$.

Then b_{11} is chosen such that also the nominator is zero

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

In a similar way we can get higher order approximations

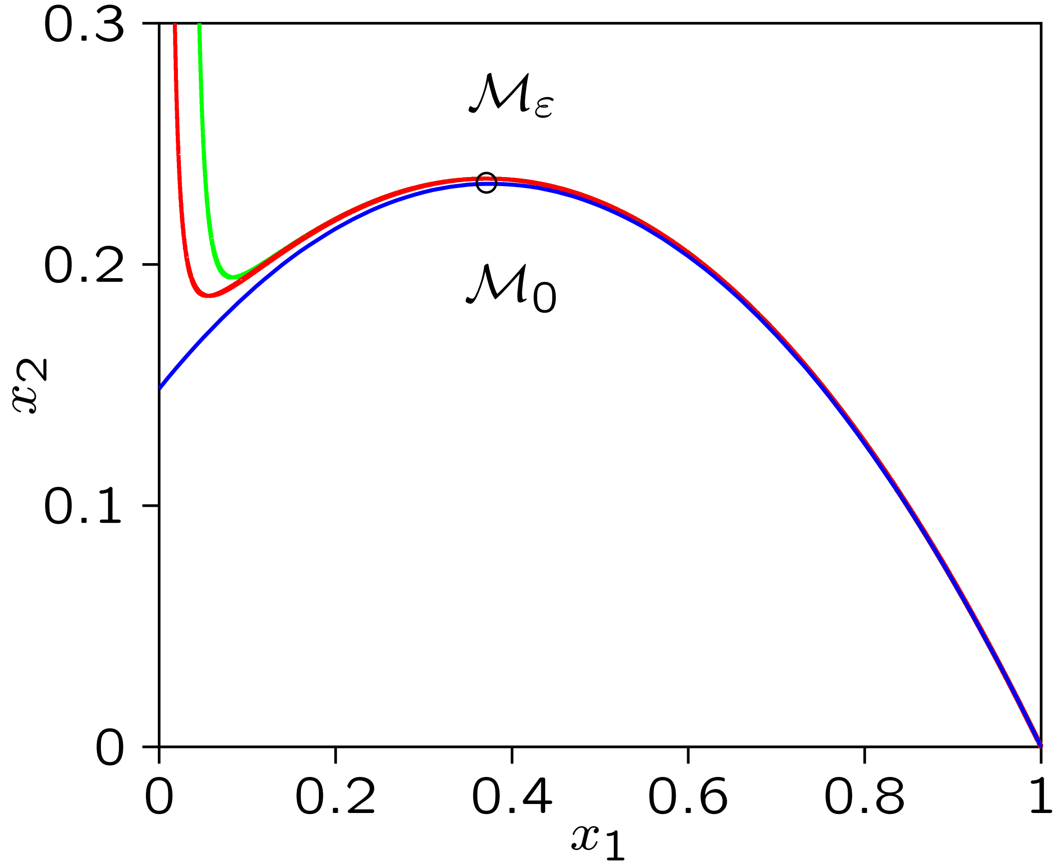
For $\varepsilon = 0.01$ we calculated for the second order term

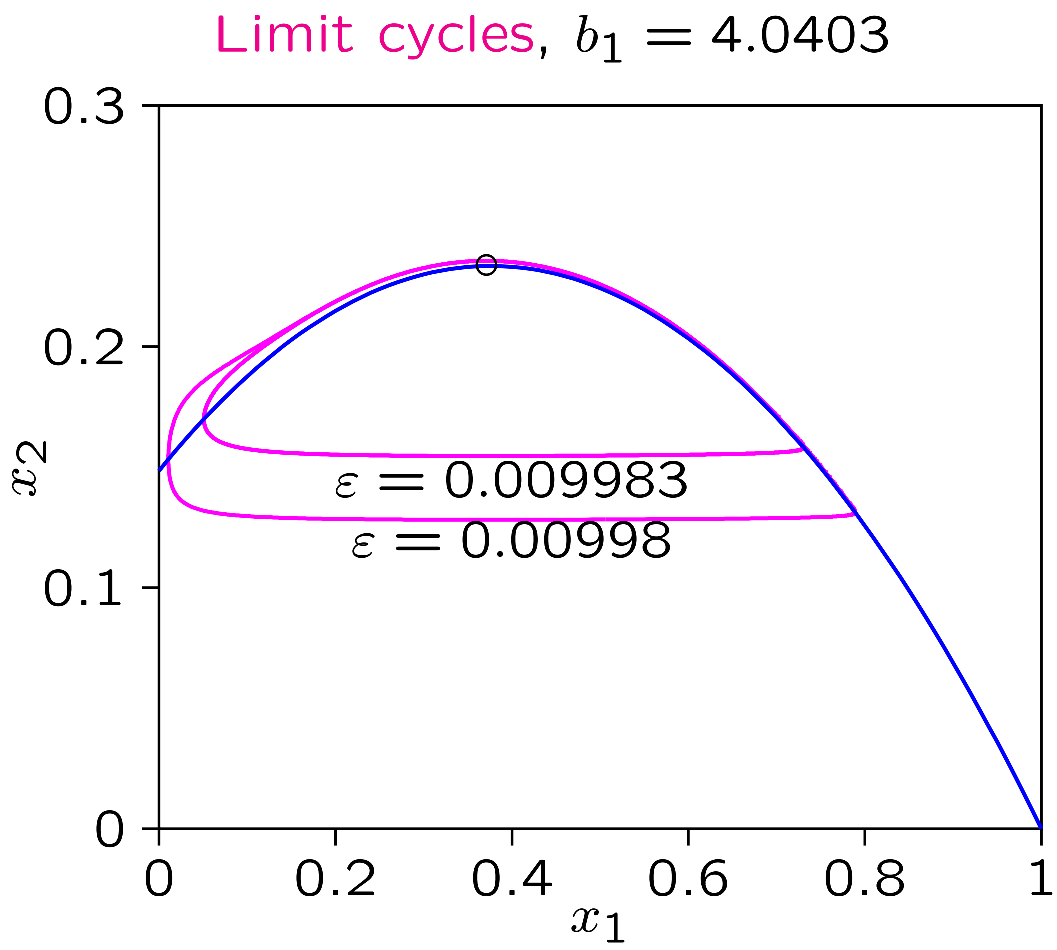
$$b_1(\varepsilon) = b_{10} + b_{11}\varepsilon + b_{12}\varepsilon^2 + b_{13}\varepsilon^3 + \dots$$

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

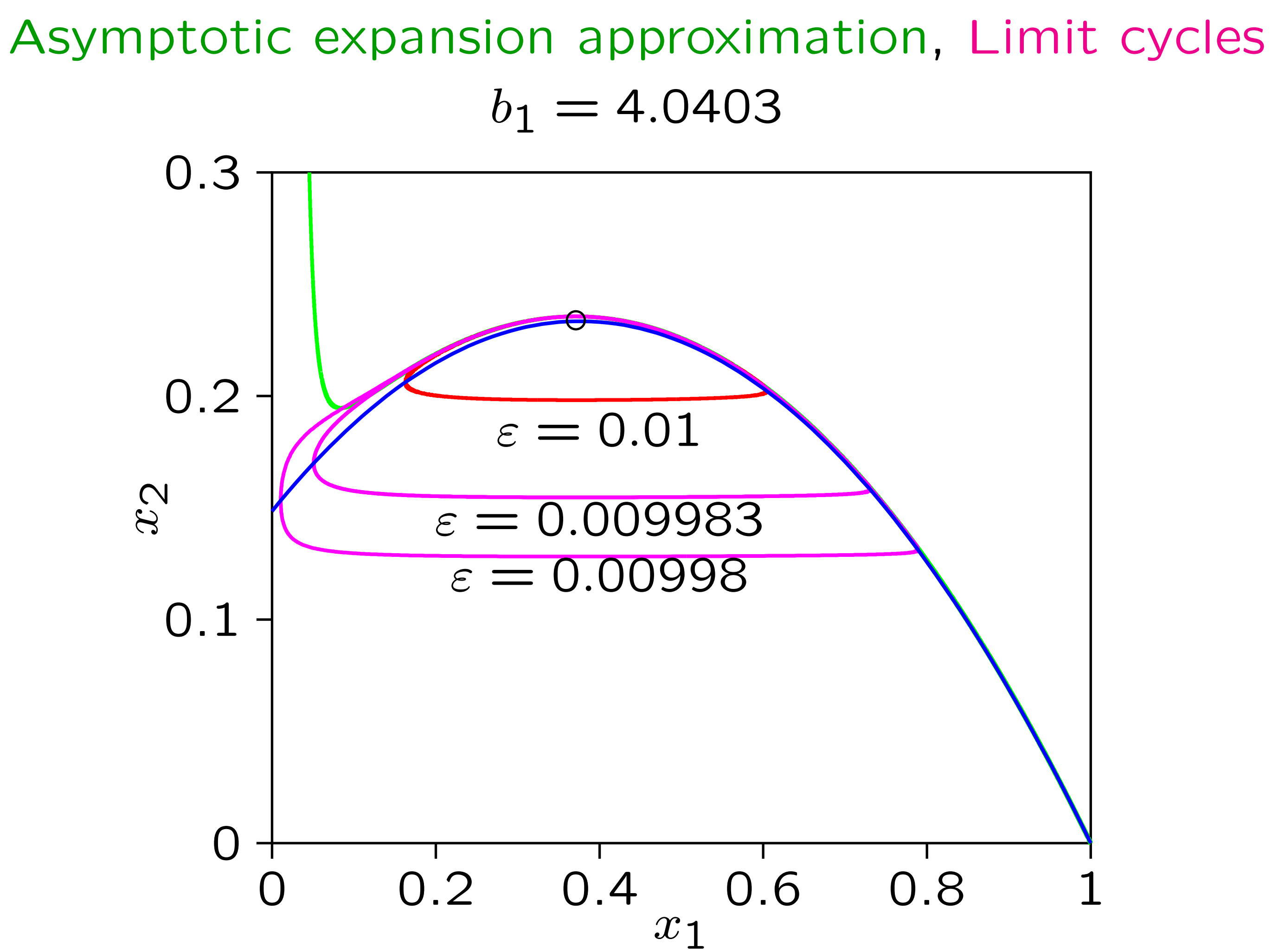
Higher order terms can be calculated with symbolic algebra packages using the iterative scheme

Asymptotic expansion approximation $r(x_1, \varepsilon = 0.01)$:
$\mathcal{O}(2)$ and $\mathcal{O}(4)$



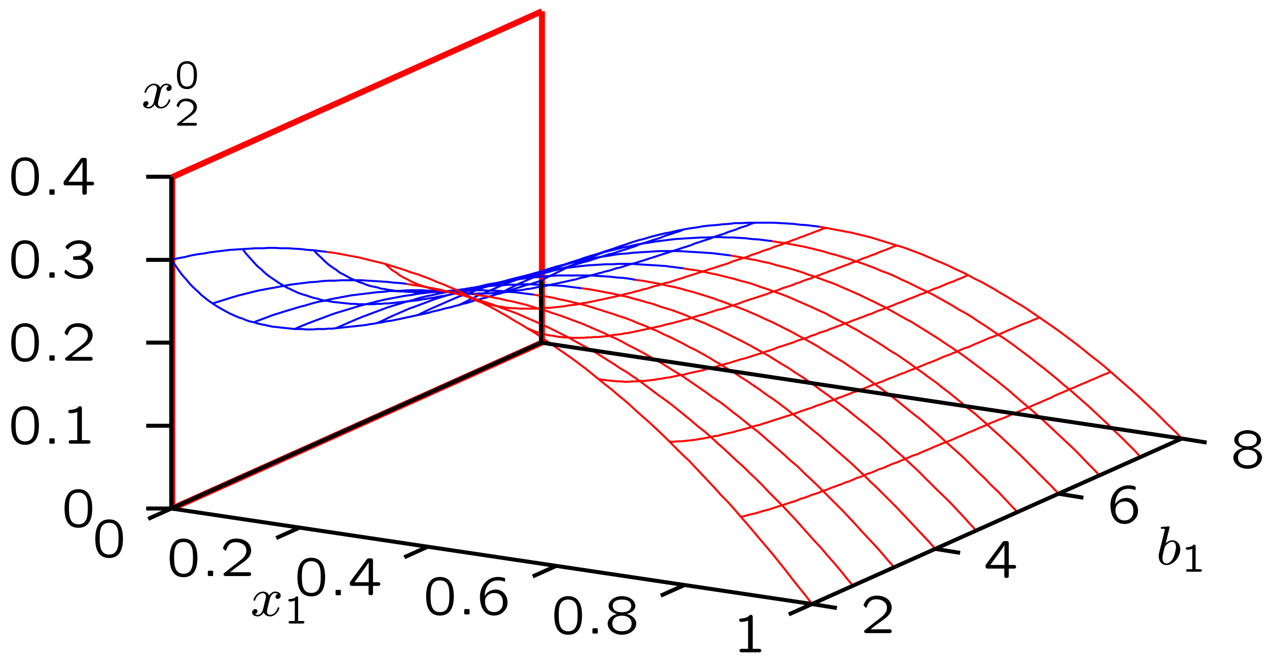


Limit cycles, $b_1 = 4.0403$
0.3
0.2
0.1
0
0
0.2
0.4
0.6
0.8
1
x_1
x_2
$\varepsilon = 0.009983$
$\varepsilon = 0.00998$



Asymptotic expansion approximation, Limit cycles
$b_1 = 4.0403$
0.3
0.2
0.1
0
x_2
$\varepsilon = 0.01$
$\varepsilon = 0.009983$
$\varepsilon = 0.00998$
0
0.2
0.4
0.6
0.8
1
x_1

Logistic growth and constant predation x_2^0, $\varepsilon = 0$



stable equilibrium unstable equilibrium

plane $x_1 = 0$ is also stable

Rosenzweig-MacArthur predator–prey model

Homotopy method RM-model, prey input

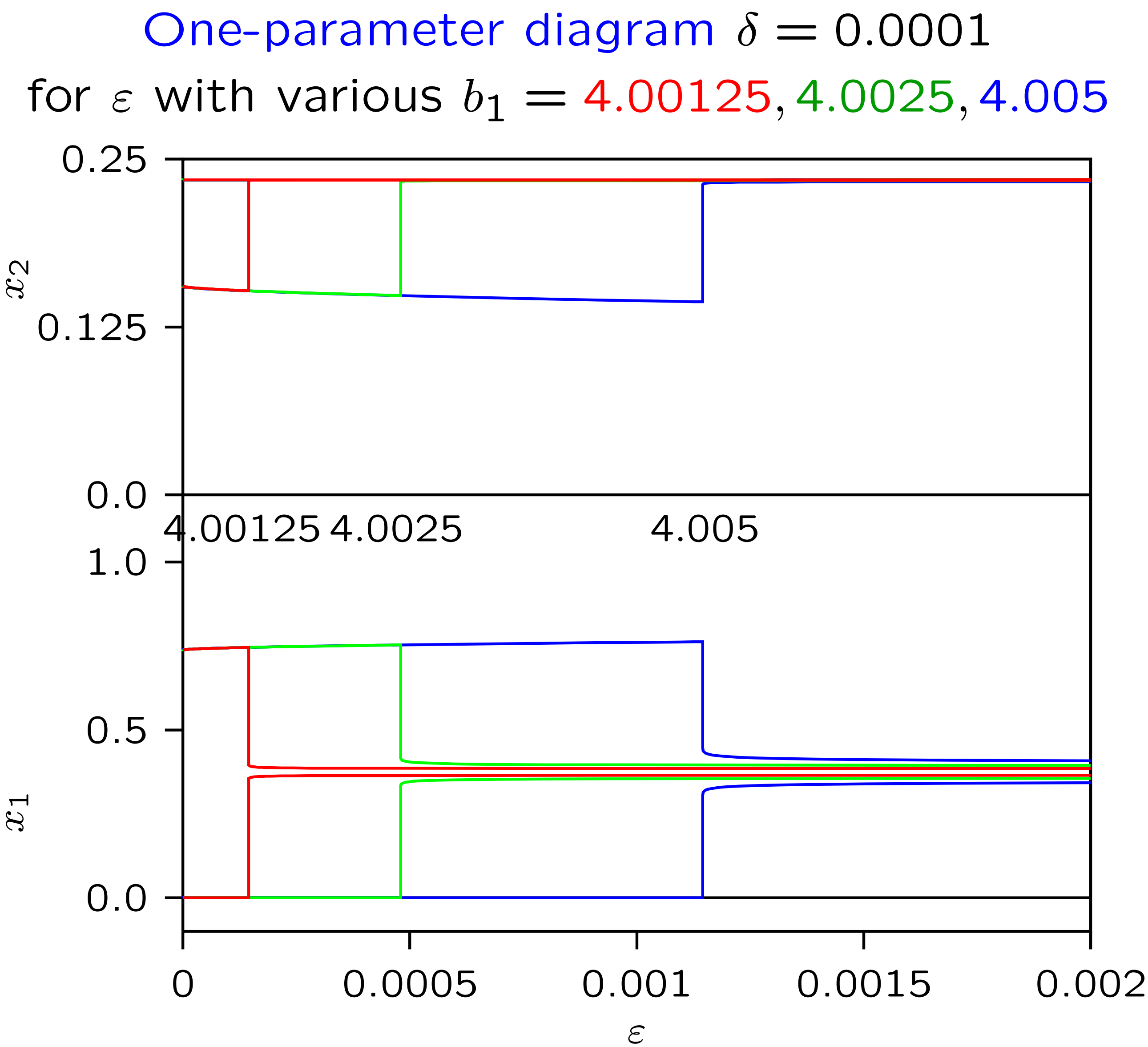
$$\frac{dx_1}{dt} = \delta + f(x_1, x_2, \varepsilon) = \delta + x_1(1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1}) \ ,$$
$$\frac{dx_2}{dt} = \varepsilon g(x_1, x_2, \varepsilon) = \varepsilon x_2(\frac{a_1 x_1}{1 + b_1 x_1} - 1) \ ,$$

where δ is a small input rate of the prey population

Addition of this extra term removes the transcritical bifurcation at $x_2 = 1/a_1$

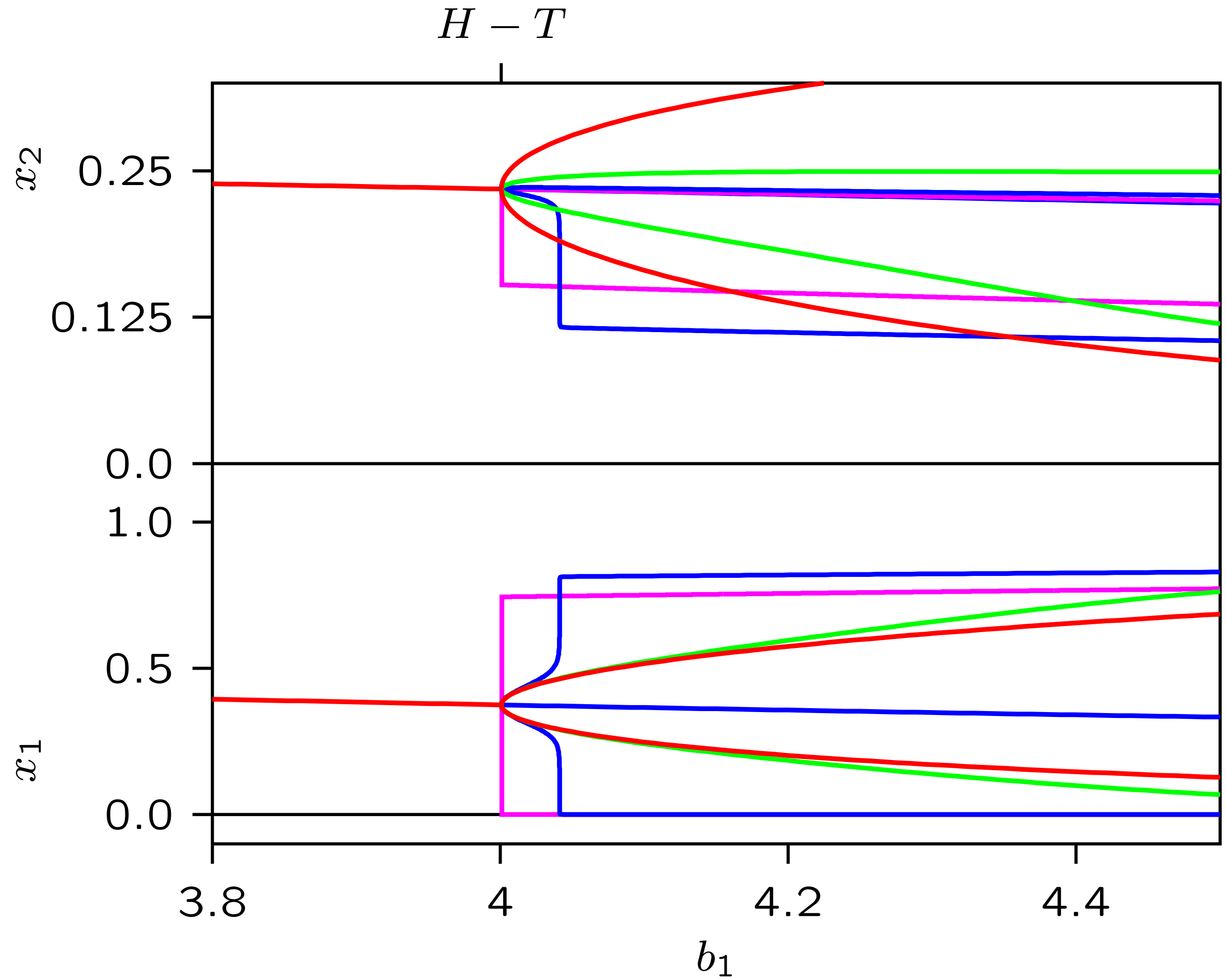
It is structurally unstable with respect to such a perturbation

Focus is only on Hopf bifurcation

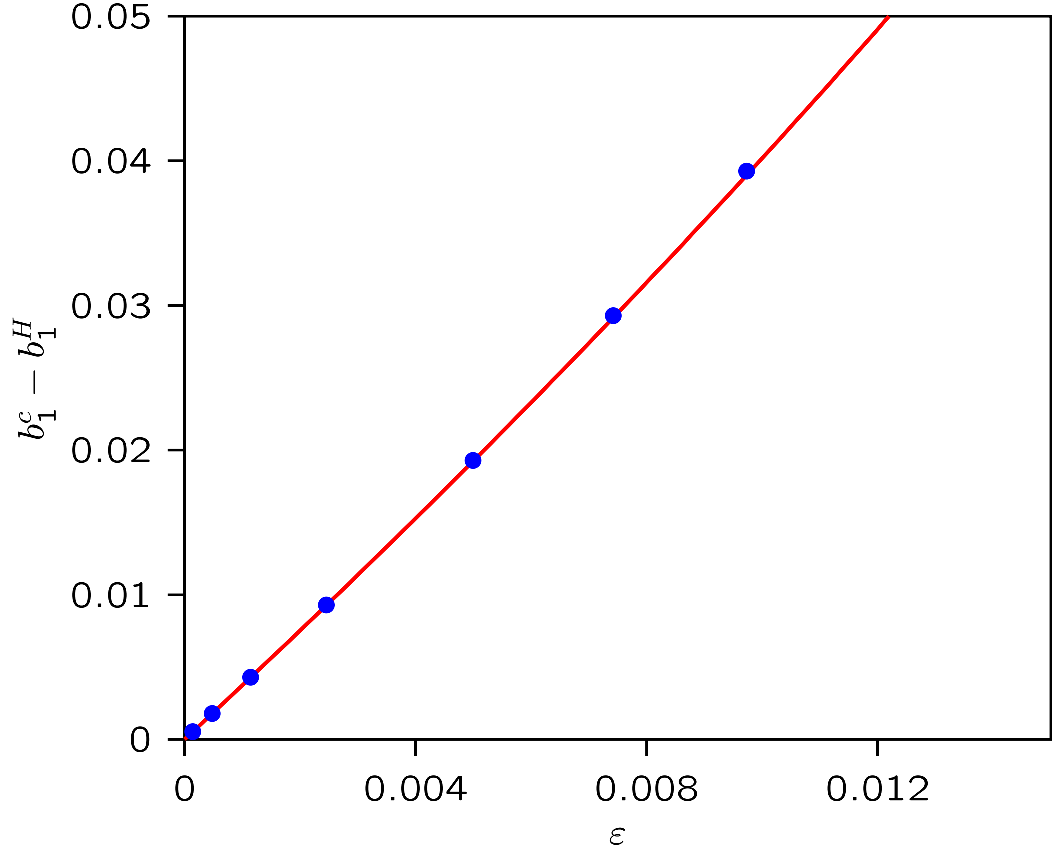

One-parameter diagram $\delta = 0.0001$
for ε with various $b_1 = 4.00125, 4.0025, 4.005$
0.25
0.125
0.0
x_2
4.00125
4.0025
4.005
1.0
0.5
0.0
x_1
0
0.0005
0.001
0.0015
0.002
ε

One-parameter diagram $\delta = 0.0001$

for b_1 with various $\varepsilon = 0.0001, 0.01, 0.1, 1$



Carard two-parameter diagram $\delta = 0.0001$
for ε and b_1



line: asymptotic expansion approximation
dots: parameter diagrams

Conclusions

- At $\varepsilon = 0$ Singular Hopf bifurcation there is a catastrophic transition from a stable equilibrium to a stable limit cycle (Relaxation oscillation)

- Canard An abrupt transition from the relaxation oscillation (large cycle) to a stable smooth limit cycle (small cycle)

- In Poggiale et al. (JoMB 2019) existence of Canard phenomenon has been proven

- Asymptotic or power series expansion in ε gives numerical approximation of perturbed critical manifold and where canard explosion occurs

Literature

BW 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 BW 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.