PLANAR S-SYSTEMS:
CENTER PROBLEM, LIMIT CYCLES, AND BOUNDEDNESS OF SOLUTIONS

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B. Boros, JH, S. Müller and G. Regensburger:
Planar S-systems: Stability and the center problem.
Discrete and Continuous Dynamical Systems **39** (2019) 707–727.

Balázs Boros & JH: *Planar S-systems: Permanence.*
J. Diff. Equations **266** (2019) 3787–3817.

PLANAR S-SYSTEMS

$$\dot{x}_1 = \alpha_1\, x_1^{g_{11}} x_2^{g_{12}} - \beta_1\, x_1^{h_{11}} x_2^{h_{12}}$$
$$\dot{x}_2 = \alpha_2\, x_1^{g_{21}} x_2^{g_{22}} - \beta_2\, x_1^{h_{21}} x_2^{h_{22}}$$

with $\alpha_1, \alpha_2, \beta_1, \beta_2 > 0$ and $g_{11}, g_{12}, g_{21}, g_{22}, h_{11}, h_{12}, h_{21}, h_{22} \in \mathbb{R}$.

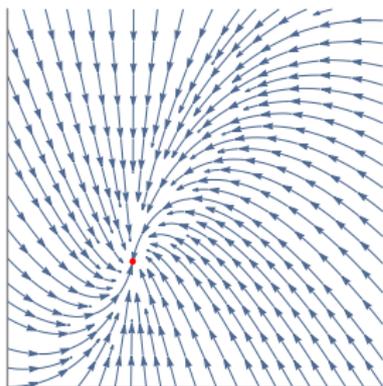ODE on the positive quadrant $\mathbb{R}^2_{>0}$.

S-systems were introduced by Savageau (1969) in the context of biochemical systems theory.
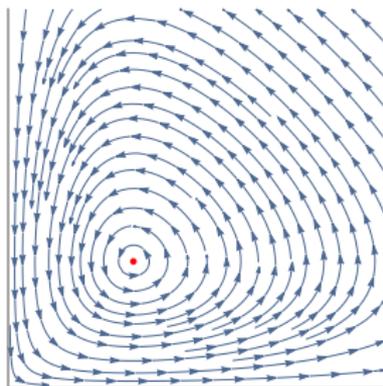(The "S" refers to synergism and saturability.)
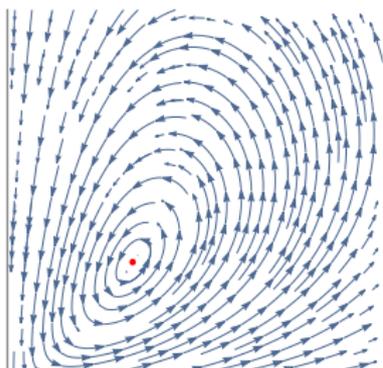
recent review: Voit (2013)

EXAMPLES

$\dot{x} = 1 - x$
$\dot{y} = x - y$

$\dot{x} = x - xy$
$\dot{y} = xy - y$

$\dot{x} = x^{1.4} - xy^{0.61}$
$\dot{y} = xy^{0.61} - y$

$\dot{x} = x^{0.5} - xy^{-1}$
$\dot{y} = xy^{-1} - y$
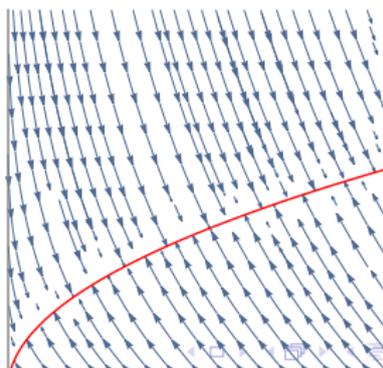
SELKOV (1968)

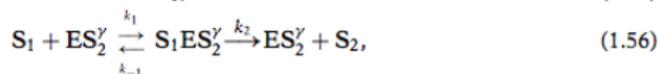a mathematical model of glycolytic oscillations (after simplifications) leads to a planar S-system:

$$\dot{x} = 1 - xy^\gamma$$
$$\dot{y} = \alpha(xy^\gamma - y)$$

Keener & Sneyd (1998)

effect is similar. In the active state, the enzyme catalyzes the production of ADP from ATP as fructose-6-P is phosphorylated. Sel'kov's reaction scheme for this process is as follows: PFK1 (denoted by E) is activated or deactivated by binding or unbinding with γ molecules of ADP (denoted by S_2)

$$\gamma S_2 + E \underset{k_{-3}}{\overset{k_3}{\rightleftarrows}} ES_2^\gamma,$$
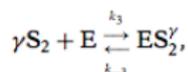
and ATP (denoted S_1) can bind with the activated form of enzyme to produce a product molecule of ADP. In addition, there is assumed to be a steady supply rate of S_1, while product S_2 is irreversibly removed. Thus,

$$\overset{v_1}{\longrightarrow} S_1, \tag{1.55}$$

$$S_1 + ES_2^\gamma \underset{k_{-1}}{\overset{k_1}{\rightleftarrows}} S_1 ES_2^\gamma \overset{k_2}{\longrightarrow} ES_2^\gamma + S_2, \tag{1.56}$$

$$S_2 \overset{v_2}{\longrightarrow}. \tag{1.57}$$

LOTKA'S REACTION

A. Lotka: J. Amer. Chem. Soc., 1920

$$S + X \xrightarrow{k_1} 2X$$

$$X + Y \xrightarrow{k_2} 2Y$$

$$Y \xrightarrow{k_3} P$$
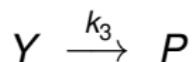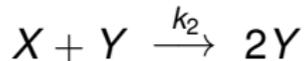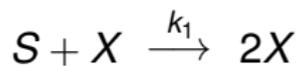
$$\dot{x} = k_1 x - k_2 xy$$
$$\dot{y} = k_2 xy - k_3 y$$

has a first integral

LOTKA'S REACTION / PREDATOR–PREY SYSTEM

$$\dot{x} = ax - bxy$$
$$\dot{y} = cxy - dy$$

LOTKA–FARKAS SYSTEM

$$\dot{x} = k_1 x^r - k_2 x^p y^q$$
$$\dot{y} = k_2 x^p y^q - k_3 y^r$$

... generalized mass action kinetics of the Lotka reaction
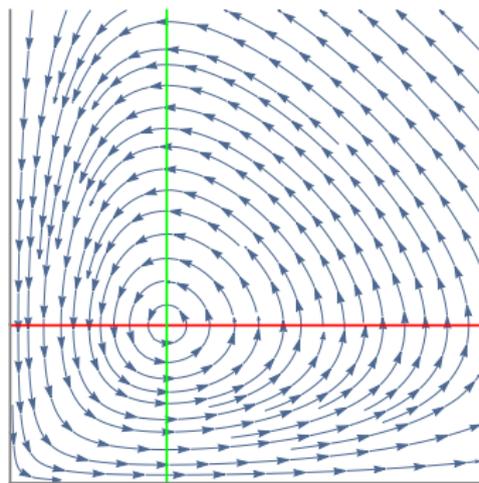
Henrik Farkas and Z. Noszticzius (1985):
Generalized Lotka-Volterra schemes and the construction of
two-dimensional explodator cores and their Liapunov functions via
"critical" Hopf bifurcations. *J. Chem. Soc. Faraday Trans.*

A. Dancsó, H. Farkas, M. Farkas, and G. Szabó (1991):
Investigations into a class of generalized two-dimensional
Lotka-Volterra schemes. *Acta Appl. Math.*

limit cycle via Andronov–Hopf bifurcation

A 3D S-SYSTEM (WITH CYCLIC SYMMETRY)

$$\dot{x}_1 = x_3 x_1 - x_1 x_2 = x_1(-x_2 + x_3)$$
$$\dot{x}_2 = x_1 x_2 - x_2 x_3 = x_2(x_1 - x_3)$$
$$\dot{x}_3 = x_2 x_3 - x_3 x_1 = x_3(-x_1 + x_2)$$
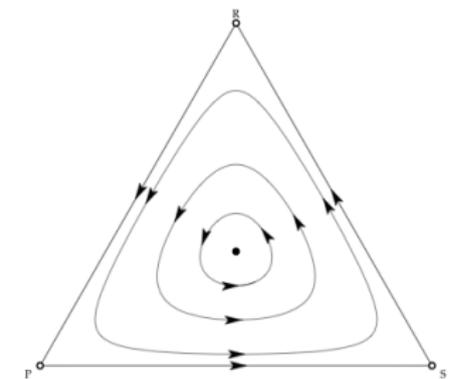
Closed orbits: two constants of motion:

$$x_1 + x_2 + x_3 = C_1$$

$$x_1 x_2 x_3 = C_2$$

rock–scissors–paper game (replicator dynamics)
Ivanova reaction (mass action kinetics)
Hamiltonian triangle

3D S-SYSTEMS

The simplest bi-molecular oscillator (Wilhelm & Heinrich 1995)

$$S_1 + P_1 \xrightarrow{k_1} 2S_1$$
$$S_1 + S_2 \xrightarrow{k_2} S_2 + P_2$$
$$S_2 \xrightarrow{k_3} P_3$$
$$S_1 \xrightarrow{k_4} S_3$$
$$S_3 \xrightarrow{k_5} S_2$$
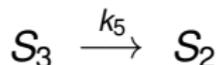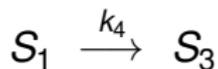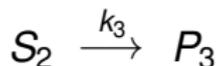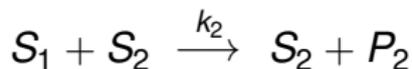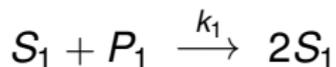
$$\dot{s}_1 = (k_1 p_1 - k_4)s_1 - k_2 s_1 s_2 = s_1(k_1' - k_2 s_2)$$
$$\dot{s}_2 = k_5 s_3 - k_3 s_2$$
$$\dot{s}_3 = k_4 s_1 - k_5 s_3$$

3D S-SYSTEMS: WILHELM & HEINRICH

$$\dot{s}_1 = s_1(k_1' - k_2 s_2)$$
$$\dot{s}_2 = k_5 s_3 - k_3 s_2$$
$$\dot{s}_3 = k_4 s_1 - k_5 s_3$$

2 steady states: $(0, 0, 0)$
$\hat{S}$: $\hat{s}_2 = \frac{k_1'}{k_2}$, $\hat{s}_3 = \frac{k_3 k_1'}{k_5 k_2}$, $\hat{s}_1 = \frac{k_3 k_1'}{k_4 k_2}$ if $k_1' = k_1 p_1 - k_4 > 0$

$\hat{S}$ is stable if $k_1' < k_3 + k_5$
Hopf bifurcation at $k_1' = k_3 + k_5$, supercritical

Hal Smith (2011): $\hat{S}$ is globally asymptotically stable if $k_1' \leq k_3 + k_5$, and a stable limit cycle exists for all $k_1' > k_3 + k_5$

3D S-SYSTEMS: CHAOS

Plesa and Sprott (2026): 8 examples of (presumably) chaotic systems

$$\dot{x} = x^2 - \frac{1}{2}xy \qquad\qquad \dot{x} = xy - \frac{2}{5}xz$$
$$\dot{y} = x^2 - yz \qquad\qquad \dot{y} = x^2 - y$$
$$\dot{z} = y - \frac{9}{10}z \qquad\qquad \dot{z} = xy - 2z$$
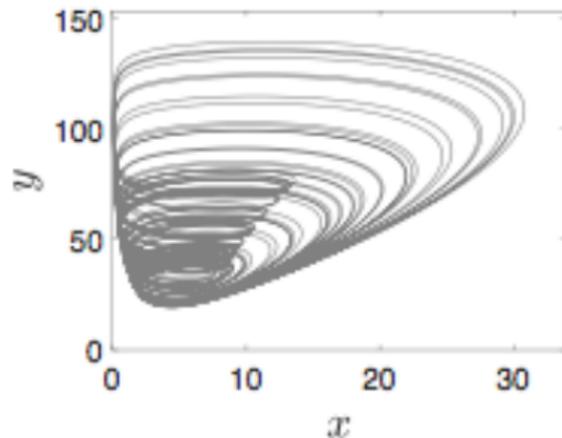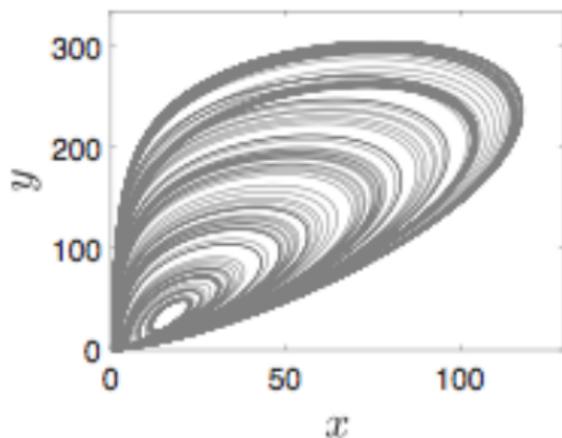
PLANAR S-SYSTEMS

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$$\dot{x}_2 = \alpha_2 \, x_1^{g_{21}} x_2^{g_{22}} - \beta_2 \, x_1^{h_{21}} x_2^{h_{22}}$$

with $\alpha_1, \alpha_2, \beta_1, \beta_2 > 0$ and $g_{11}, g_{12}, g_{21}, g_{22}, h_{11}, h_{12}, h_{21}, h_{22} \in \mathbb{R}$.
ODE on the positive quadrant $\mathbb{R}^2_{>0}$.
We assume that the ODE admits a positive equilibrium (x_1^*, x_2^*), and use the equilibrium to scale the ODE. We obtain

$$\dot{x}_1 = \gamma_1 \left(x_1^{g_{11}} x_2^{g_{12}} - x_1^{h_{11}} x_2^{h_{12}} \right)$$
$$\dot{x}_2 = \gamma_2 \left(x_1^{g_{21}} x_2^{g_{22}} - x_1^{h_{21}} x_2^{h_{22}} \right)$$

where $\gamma_1 = \alpha_1 (x_1^*)^{g_{11}-1} (x_2^*)^{g_{12}}$ and $\gamma_2 = \alpha_2 (x_1^*)^{g_{21}} (x_2^*)^{g_{22}-1}$.
This ODE has the equilibrium $(1, 1)$.

EXPONENTIAL FORM

nonlinear transformation: $x_1 = e^{\gamma_1 u}$, $x_2 = e^{\gamma_2 v}$ leads to

$$\dot{u} = e^{a_1 u + b_1 v} - e^{a_2 u + b_2 v}$$
$$\dot{v} = e^{a_3 u + b_3 v} - e^{a_4 u + b_4 v}$$

defined on $\mathbb{R}^2$, where

$$
\begin{aligned}
a_1 &= \gamma_1(g_{11} - 1), & b_1 &= \gamma_2 g_{12}, \\
a_2 &= \gamma_1(h_{11} - 1), & b_2 &= \gamma_2 h_{12}, \\
a_3 &= \gamma_1 g_{21}, & b_3 &= \gamma_2(g_{22} - 1), \\
a_4 &= \gamma_1 h_{21}, & b_4 &= \gamma_2(h_{22} - 1).
\end{aligned}
$$

This ODE has the equilibrium $(0, 0)$, and the Jacobian there is given by

$$J = \begin{pmatrix} a_1 - a_2 & b_1 - b_2 \\ a_3 - a_4 & b_3 - b_4 \end{pmatrix}$$

In this exponential form, nullclines are straight lines.
And symmetries in the exponents can be exploited.

SYMMETRIES

The family of planar S-systems (in exponential form) is invariant under the symmetry group of the square (**dihedral group** D_4) which consists of the following eight elements (rotations and reflections in $\mathbb{R}^2$):

$$\mathbf{r}_0 = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}, \quad \mathbf{r}_1 = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix}, \quad \mathbf{r}_2 = \begin{pmatrix} -1 & 0 \\ 0 & -1 \end{pmatrix}, \quad \mathbf{r}_3 = \begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix},$$

$$\mathbf{s}_0 = \begin{pmatrix} 1 & 0 \\ 0 & -1 \end{pmatrix}, \quad \mathbf{s}_1 = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}, \quad \mathbf{s}_2 = \begin{pmatrix} -1 & 0 \\ 0 & 1 \end{pmatrix}, \quad \mathbf{s}_3 = \begin{pmatrix} 0 & -1 \\ -1 & 0 \end{pmatrix}$$

Ex: Rotation $\mathbf{r}_1$ by $90°$:

$$\begin{pmatrix} a_1 & a_2 & a_3 & a_4 \\ b_1 & b_2 & b_3 & b_4 \end{pmatrix} \mapsto \begin{pmatrix} -b_4 & -b_3 & -b_1 & -b_2 \\ a_4 & a_3 & a_1 & a_2 \end{pmatrix}$$

GLOBAL STABILITY

$$J = \begin{pmatrix} a_1 - a_2 & b_1 - b_2 \\ a_3 - a_4 & b_3 - b_4 \end{pmatrix}$$

If $a_1 < a_2$, $b_3 < b_4$ and $\det J > 0$ then **O** is globally asymptotically stable.

Proof: use Bendixson–Dulac to exclude closed orbits

If $a_1 > a_2$, $b_3 > b_4$ and $\det J > 0$ then **O** is a global repeller: all nonzero solutions go to ∞.

If $\det J < 0$ then **O** is a saddle: almost all solutions go to ∞.

For other sign patterns of J,

$$\begin{pmatrix} + & * \\ * & - \end{pmatrix}, \begin{pmatrix} - & * \\ * & + \end{pmatrix},$$

global stability is possible, but impossible to characterize.

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For other sign patterns of J,

$$\begin{pmatrix} + & * \\ * & - \end{pmatrix}, \begin{pmatrix} - & * \\ * & + \end{pmatrix},$$

global stability is possible, but impossible to characterize.

THE CENTER PROBLEM

For which a_i, b_i is (0,0) a **center**?
rewrite ODE as differential form

$$(e^{a_3 u + b_3 v} - e^{a_4 u + b_4 v})du = (e^{a_1 u + b_1 v} - e^{a_2 u + b_2 v})dv$$

easy (separable) case: $a_1 = a_2, b_3 = b_4$:

$$(e^{a_3 u} - e^{a_4 u})\, e^{b_4 v}\, du = e^{a_1 u}(e^{b_1 v} - e^{b_2 v})dv$$

multiply with $e^{au + bv}$ and check integrability conditions
$\longrightarrow$ 4 more families of centers

case	condition	constant of motion	integrating factor
S	$a_1 = a_2$ $b_3 = b_4$	$\left[\dfrac{e^{(a_3-a_1)u}}{a_3-a_1} - \dfrac{e^{(a_4-a_1)u}}{a_4-a_1}\right] - \left[\dfrac{e^{(b_1-b_4)v}}{b_1-b_4} - \dfrac{e^{(b_2-b_4)v}}{b_2-b_4}\right]$	$e^{-a_1 u - b_4 v}$
I1	$a_1 = a_3$ $b_1 = b_3$	$+\dfrac{e^{p(u-v)}}{p} + \dfrac{e^{qu}}{q} - \dfrac{e^{rv}}{r}$, where $\begin{cases} p = a_1 - a_2 \\ q = a_4 - a_2 \\ r = b_2 - b_4 \end{cases}$	$e^{-a_2 u - b_4 v}$
I2	$a_1 = a_4$ $b_1 = b_4$	$-\dfrac{e^{p(u+v)}}{p} + \dfrac{e^{qu}}{q} + \dfrac{e^{rv}}{r}$, where $\begin{cases} p = a_1 - a_2 \\ q = a_3 - a_2 \\ r = b_2 - b_3 \end{cases}$	$e^{-a_2 u - b_3 v}$
I3	$a_2 = a_3$ $b_2 = b_3$	$-\dfrac{e^{p(-u-v)}}{p} - \dfrac{e^{qu}}{q} - \dfrac{e^{rv}}{r}$, where $\begin{cases} p = a_1 - a_2 \\ q = a_4 - a_1 \\ r = b_1 - b_4 \end{cases}$	$e^{-a_1 u - b_4 v}$
I4	$a_2 = a_4$ $b_2 = b_4$	$+\dfrac{e^{p(-u+v)}}{p} - \dfrac{e^{qu}}{q} + \dfrac{e^{rv}}{r}$, where $\begin{cases} p = a_1 - a_2 \\ q = a_3 - a_1 \\ r = b_1 - b_3 \end{cases}$	$e^{-a_1 u - b_3 v}$

Replace $\frac{e^{\gamma z}}{\gamma}$ by z whenever $\gamma = 0$. Additionally, $\operatorname{tr} J = a_1 - a_2 + b_3 - b_4 = 0$ (and $\det J > 0$) is required.
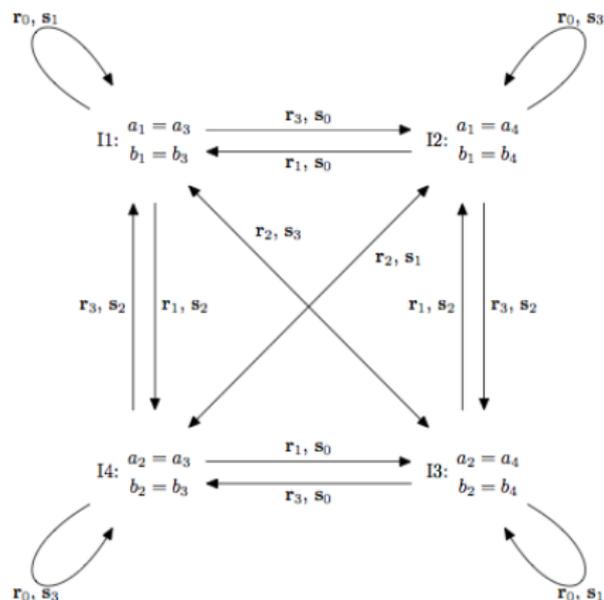
COMPUTING THE FOCAL VALUES (STRUDELGRÖSSE)

coefficients in the Poincaré normal form expansion

at the equilibrium $(0, 0)$:

$$J = \begin{pmatrix} a_1 - a_2 & b_1 - b_2 \\ a_3 - a_4 & b_3 - b_4 \end{pmatrix}$$

$\operatorname{tr} J = a_1 - a_2 + b_3 - b_4 = 0$ (and $\det J > 0$)

$$L_1 = -(b_3 - b_4)\bigg[(a_3 - a_1)(a_4 - a_1) + (a_3 - a_1)(b_4 - b_1) - (a_4 - a_1)(b_3 - b_1)$$

$$-\frac{(a_3 - a_4)(b_3 - b_1)(b_4 - b_1)}{(b_2 - b_1)}\bigg]$$

L_2 is given by a long formula, does not fit on this slide

CENTERS VIA FOCAL VALUES

Theorem (Poincaré, Liapunov)

An equilibrium of an analytic ODE with $\det J > 0$ is a center if and only if $\operatorname{tr} J = 0$ and $L_1 = L_2 = \cdots = 0$.

LIST OF ALL CENTERS OF PLANAR S-SYSTEMS

Solving tr $J = L_1 = L_2 = 0$ leads to 7 cases:

case	parameters	
S	$a_1 = a_2$	$b_3 = b_4$
I1	$a_1 = a_3$	$b_1 = b_3$
I2	$a_1 = a_4$	$b_1 = b_4$
I3	$a_2 = a_4$	$b_2 = b_4$
I4	$a_2 = a_3$	$b_2 = b_3$
R1	$a_1 + b_1 = a_4 + b_4$	$a_2 + b_2 = a_3 + b_3$
R2	$a_1 - b_1 = a_3 - b_3$	$a_2 - b_2 = a_4 - b_4$

Additionally, tr $J = a_1 - a_2 + b_3 - b_4 = 0$ (redundant in case S), and det $J > 0$.
The codimension is 2 for case S, and 3 for the other cases.

THE REMAINING CASES: (R1)

orbitally equivalent to a system of the form

$$
\dot{u} = f(u, v)
$$
$$
\dot{v} = -f(v, u)
$$

This is a **reversible dynamical system**
w.r.t. the reflection $R: (u, v) \mapsto (v, u)$.

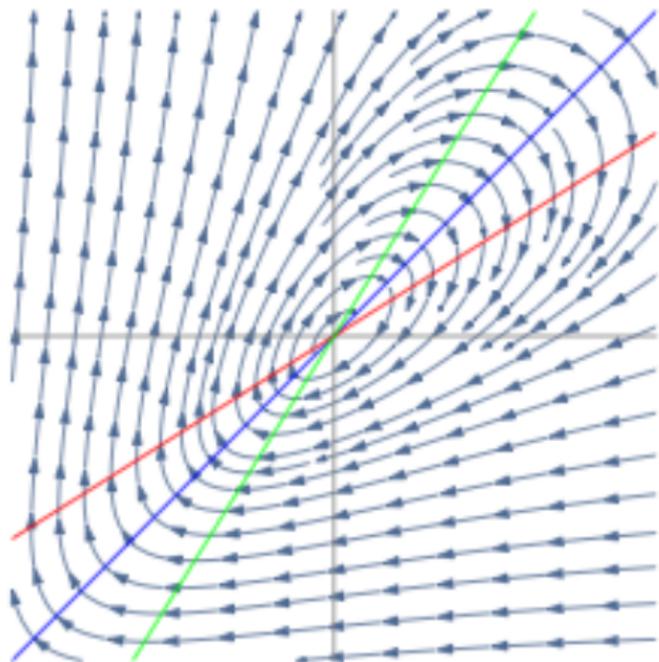orbitally equivalent to a system of the form

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A REVERSIBLE SYSTEM

THE REMAINING CASES: (R2)

Systems (R2) are reversible w.r.t. reflection $(u, v) \mapsto (-v, -u)$

Problem: Since (R1) and (R2) lead to centers, analytic first integrals must exist. We found them only in the intersection of (R1) and (R2) (which is codim 4)

$$(1 + e^{r(u+v)})(e^{qu} + e^{qv})^{-\frac{r}{q}}$$

where $q = a_4 - a_1 = a_2 - a_3 = b_3 - b_2 = b_1 - b_4$
and $r = a_3 - a_1 = a_2 - a_4 = b_2 - b_4 = b_3 - b_1$

integrating factor: $e^{-a_1 u - b_4 v}(e^{qu} + e^{qv})^{-\frac{q+r}{q}}$

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where $q = a_4 - a_1 = a_2 - a_3 = b_3 - b_2 = b_1 - b_4$
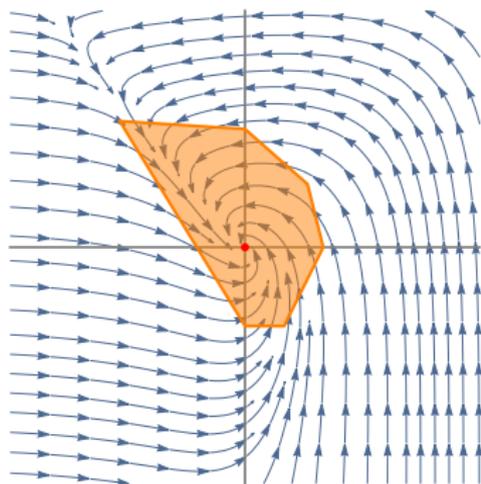and $r = a_3 - a_1 = a_2 - a_4 = b_2 - b_4 = b_3 - b_1$

integrating factor: $e^{-a_1 u - b_4 v}(e^{qu} + e^{qv})^{-\frac{q+r}{q}}$

S-SYSTEMS WITH TWO LIMIT CYCLES

Construct two limit cycles via Andronov–Hopf–Bautin bifurcation

choose parameters with tr $J = 0, L_1 = 0$ and $L_2 \neq 0$
and perturb carefully

PERMANENCE

$$\dot{u} = e^{a_1 u + b_1 v} - e^{a_2 u + b_2 v}$$
$$\dot{v} = e^{a_3 u + b_3 v} - e^{a_4 u + b_4 v}$$

- the system is said to be *permanent* if there exists a compact subset of $\mathbb{R}^2$ that is forward invariant and is a global attractor

- task: characterize a_i, $b_i \in \mathbb{R}$ for which the system is permanent

FROM S-SYSTEMS TO REPLICATOR DYNAMICS

$$\boxed{\begin{aligned} \dot{u} &= e^{a_1 u + b_1 v} - e^{a_2 u + b_2 v} \\ \dot{v} &= e^{a_3 u + b_3 v} - e^{a_4 u + b_4 v} \end{aligned}} \quad \text{in } \mathbb{R}^2$$

$z_i = e^{a_i u + b_i v}$ for $i = 1, 2, 3, 4$

$$\boxed{\dot{z}_i = z_i[a_i(z_1 - z_2) + b_i(z_3 - z_4)] \text{ for } i = 1, 2, 3, 4} \quad \text{in } \mathbb{R}_+^4$$

$x_i = \frac{z_i}{z_1 + z_2 + z_3 + z_4}$ for $i = 1, 2, 3, 4$

$$\boxed{\begin{aligned} \dot{x}_i &= x_i[(Ax)_i - x^\mathsf{T} Ax] \text{ for } i = 1, 2, 3, 4, \\ \text{where } A &= \begin{pmatrix} a_1 & -a_1 & b_1 & -b_1 \\ a_2 & -a_2 & b_2 & -b_2 \\ a_3 & -a_3 & b_3 & -b_3 \\ a_4 & -a_4 & b_4 & -b_4 \end{pmatrix} \end{aligned}} \quad \text{in } \Delta_4^\circ$$

REPLICATOR DYNAMICS

$$\dot{x}_i = x_i[(Ax)_i - x^{\mathsf{T}}Ax] \qquad \text{for } i = 1, 2, 3, 4$$

on the 3d simplex $\Delta_4 = \{x \in \mathbb{R}^4_{\geq 0} \mid x_1 + \cdots + x_4 = 1\}$ with

$$A = \begin{pmatrix} a_1 & -a_1 & b_1 & -b_1 \\ a_2 & -a_2 & b_2 & -b_2 \\ a_3 & -a_3 & b_3 & -b_3 \\ a_4 & -a_4 & b_4 & -b_4 \end{pmatrix}$$

or, equivalently

$$A = \begin{pmatrix} 0 & a_2 - a_1 & b_1 - b_3 & b_4 - b_1 \\ a_2 - a_1 & 0 & b_2 - b_3 & b_4 - b_2 \\ a_3 - a_1 & a_2 - a_3 & 0 & b_4 - b_3 \\ a_4 - a_1 & a_2 - a_4 & b_4 - b_3 & 0 \end{pmatrix}$$

Equilibria at $(\frac{1}{2}, \frac{1}{2}, 0, 0)$ and $(0, 0, \frac{1}{2}, \frac{1}{2})$ and even $\frac{1}{2}(s, s, 1 - s, 1 - s)$

INVARIANT SURFACES INSIDE THE TETRAHEDRON Δ_4

$$\dot{u} = e^{a_1 u + b_1 v} - e^{a_2 u + b_2 v}$$
$$\dot{v} = e^{a_3 u + b_3 v} - e^{a_4 u + b_4 v}$$

- $P_i = (a_i, b_i)$ for $i = 1, 2, 3, 4$

- $\Delta(ijk) = \det(P_j - P_i, P_k - P_i) = 2 \times$ signed area of triangle $P_i P_j P_k$

- $c_1 = \Delta(243)$, $c_2 = \Delta(134)$, $c_3 = \Delta(142)$, $c_4 = \Delta(123)$

$$c_1 = a_3 b_2 - a_2 b_3 + a_2 b_4 - a_4 b_2 + a_4 b_3 - a_3 b_4$$
$$c_2 = a_1 b_3 - a_3 b_1 + a_4 b_1 - a_1 b_4 + a_3 b_4 - a_4 b_3$$
$$c_3 = a_2 b_1 - a_1 b_2 + a_1 b_4 - a_4 b_1 + a_4 b_2 - a_2 b_4$$
$$c_4 = a_1 b_2 - a_2 b_1 + a_3 b_1 - a_1 b_3 + a_2 b_3 - a_3 b_2$$

- $c_1 + c_2 = \det J = -c_3 - c_4$ (> 0 is a permanent system!)

- $c \perp a, b, \mathbf{1}$: $c_1 + c_2 + c_3 + c_4 = 0$

INVARIANT SURFACES INSIDE THE TETRAHEDRON Δ_4

$$\dot{u} = e^{a_1 u + b_1 v} - e^{a_2 u + b_2 v}$$

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- $\Delta(ijk) = \det(P_j - P_i, P_k - P_i) = 2 \times$ signed area of triangle $P_i P_j P_k$
- $c_1 = \Delta(243)$, $c_2 = \Delta(134)$, $c_3 = \Delta(142)$, $c_4 = \Delta(123)$

- $c \perp a, b, \mathbf{1}$: $c_1 + c_2 + c_3 + c_4 = 0$

- $Q(x) = x_1^{c_1} x_2^{c_2} x_3^{c_3} x_4^{c_4}$ is a first integral:

$$\frac{\dot{Q}}{Q} = \sum_i c_i \frac{\dot{x}_i}{x_i} = \sum_i c_i((Ax)_i - x^\mathsf{T} Ax) = c^\mathsf{T} Ax = 0$$
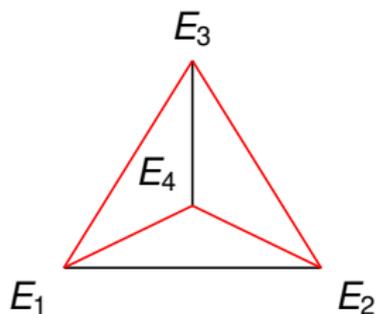
- the planar S-system corresponds to the invariant surface $\{Q = 1\}$

  (since it contains the equilibrium $(u, v) = (0, 0) \sim z = \mathbf{1} \sim x = \frac{1}{4}\mathbf{1}$)
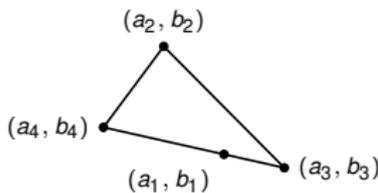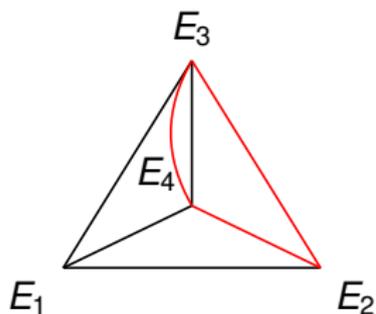
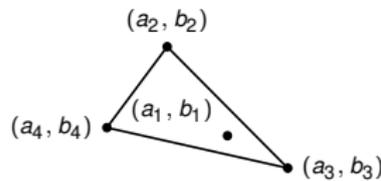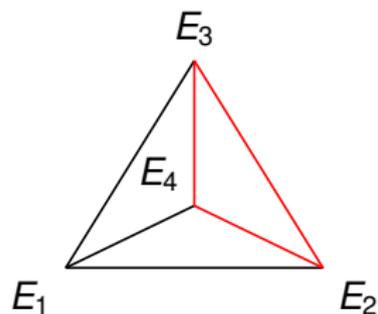$$Q(x) = x_1^{c_1} x_2^{c_2} x_3^{c_3} x_4^{c_4}$$

$\text{sgn}(c_1, c_2, c_3, c_4) = (+, +, -, -)$

$\text{sgn}(c_1, c_2, c_3, c_4) = (+, 0, -, -)$

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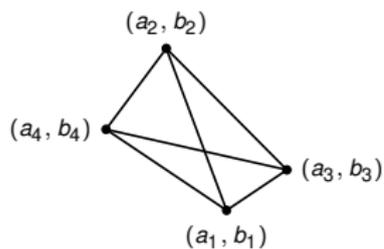
$$Q(x) = x_1^{c_1} x_2^{c_2} x_3^{c_3} x_4^{c_4}$$

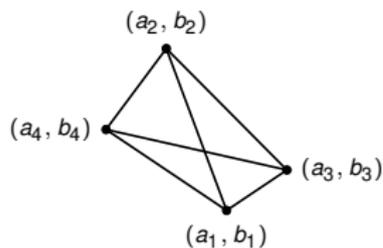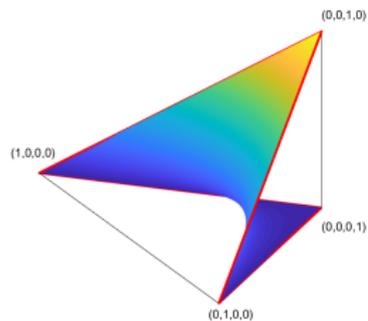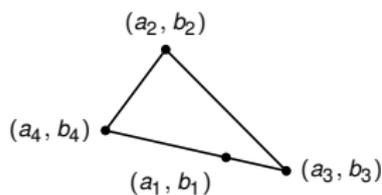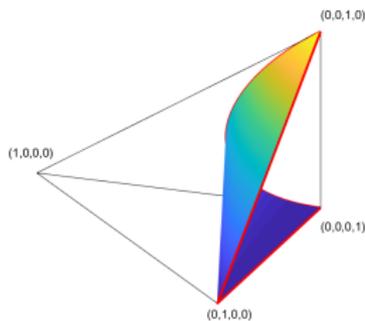$\text{sgn}(c_1, c_2, c_3, c_4) = (+, +, -, -)$ $\qquad$ $\text{sgn}(c_1, c_2, c_3, c_4) = (+, 0, -, -)$ $\qquad$ $\text{sgn}(c_1, c_2, c_3, c_4) = (+, -, -, -)$
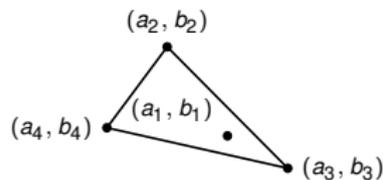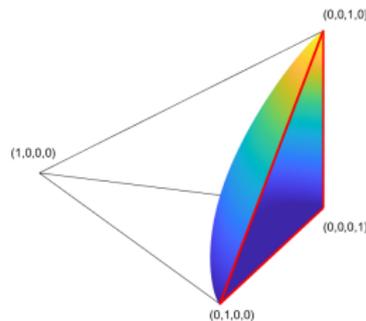
PERMANENCE

To study permanence of the planar S-system we have to study the replicator dynamics on the invariant surface $S = \{x : Q(x) = 1\}$ near the boundary ∂S.

Look at equilibria on ∂S.

Check whether these equilibria can attract interior orbits on S.

REPLICATOR DYNAMICS

$$\dot{x}_i = x_i \left[(Ax)_i - x^\mathsf{T} A x \right] \text{ for } i = 1, \ldots, n$$

with state space $\Delta_n = \{ x \in \mathbb{R}_{\geq 0}^n \mid x_1 + \cdots + x_n = 1 \}$.
(w.l.o.g.) $a_{ii} = 0$ for all $i = 1, \ldots, n$

E_k the kth corner of Δ_n ($x_k = 1$):
For $j \neq k$, the eigenvalue at E_k in the direction E_j is a_{jk}.

An edge equilibrium E_{ij} ($x_i, x_j > 0, x_i + x_j = 1$) exists iff
$\operatorname{sgn} a_{ij} = \operatorname{sgn} a_{ji} \neq 0$.
For $k \neq i, j$, the eigenvalue at E_{ij} in the direction E_k is given by

$$\Gamma_{ij}^k = \left. \frac{\dot{x}_k}{x_k} \right|_{x = E_{ij}} = \frac{a_{ki}a_{ij} + a_{kj}a_{ji} - a_{ij}a_{ji}}{a_{ij} + a_{ji}},$$

$$\Gamma_{12}^3 = \Gamma_{12}^4 = \Gamma_{34}^1 = \Gamma_{34}^2 = 0,$$

$$\Gamma_{13}^k = \frac{1}{(b_1 - b_3) + (a_3 - a_1)} \cdot \begin{cases} (-c_4), & k = 2, \\ (+c_2), & k = 4, \end{cases}$$

$$\Gamma_{23}^k = \frac{1}{(b_2 - b_3) + (a_2 - a_3)} \cdot \begin{cases} (-c_4), & k = 1, \\ (+c_1), & k = 4, \end{cases}$$

$$\Gamma_{24}^k = \frac{1}{(b_4 - b_2) + (a_2 - a_4)} \cdot \begin{cases} (-c_3), & k = 1, \\ (+c_1), & k = 3, \end{cases}$$

$$\Gamma_{14}^k = \frac{1}{(b_4 - b_1) + (a_4 - a_1)} \cdot \begin{cases} (-c_3), & k = 2, \\ (+c_2), & k = 3, \end{cases}$$

REPLICATOR DYNAMICS WITH OUR SPECIAL MATRIX A

Assuming $a_4 \leq a_2 < a_1 \leq a_3$, we have

$$\operatorname{sgn} \Gamma_{13}^2 = - \operatorname{sgn} c_4, \qquad \operatorname{sgn} \Gamma_{13}^4 = + \operatorname{sgn} c_2,$$
$$\operatorname{sgn} \Gamma_{23}^1 = + \operatorname{sgn} c_4, \qquad \operatorname{sgn} \Gamma_{23}^4 = - \operatorname{sgn} c_1,$$
$$\operatorname{sgn} \Gamma_{24}^1 = - \operatorname{sgn} c_3, \qquad \operatorname{sgn} \Gamma_{24}^3 = + \operatorname{sgn} c_1,$$
$$\operatorname{sgn} \Gamma_{14}^2 = + \operatorname{sgn} c_3, \qquad \operatorname{sgn} \Gamma_{14}^3 = - \operatorname{sgn} c_2.$$

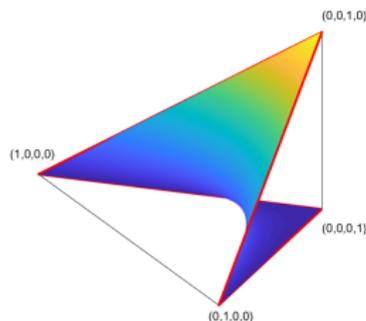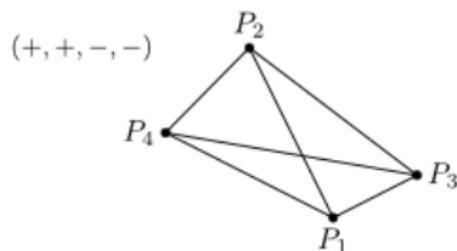# INTERESTING CASE

No edge equilibria on ∂S, cycle along the edges.
This can happen in the quadrangle case (but not in the triangle case!)

$$a_4 \leq a_2 < a_1 \leq a_3,$$
$$b_1 \leq b_3 < b_4 \leq b_2.$$

Heteroclinic cycle along the edges $E_1 \to E_3 \to E_2 \to E_4 \to E_1$ with
eigenvalues $a_4 - a_1 < 0, a_3 - a_1 > 0$ at $E_1, \ldots,$
$b_4 - b_2 < 0, b_4 - b_1 > 0$ at E_4

MAIN TECHNICAL TOOL: HETEROCLINIC CASE

THEOREM (DULAC, 1923)

Consider an ODE on the unit square $[0, 1] \times [0, 1]$ with the boundary being a heteroclinic cycle with outgoing and incoming eigenvalues as shown:
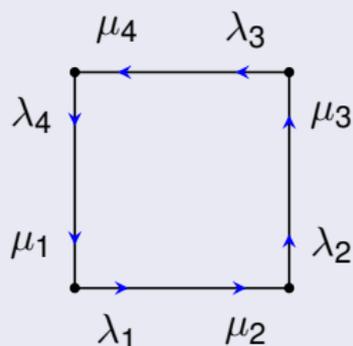
Let $L_\infty = \prod_{i=1}^{4} \lambda_i - \prod_{i=1}^{4} \mu_i$.

Then the heteroclinic cycle is $\begin{cases} \text{repelling} \\ \text{attractive} \end{cases}$ *if* $\begin{cases} L_\infty > 0 \\ L_\infty < 0 \end{cases}$.

PERMANENCE IN THE HETEROCLINIC CASE

$$\dot{u} = e^{a_1 u + b_1 v} - e^{a_2 u + b_2 v}$$
$$\dot{v} = e^{a_3 u + b_3 v} - e^{a_4 u + b_4 v}$$

$$J = \begin{pmatrix} a_1 - a_2 & b_1 - b_2 \\ a_3 - a_4 & b_3 - b_4 \end{pmatrix}$$

THEOREM

Assume $\text{sgn } J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$ and

$$a_4 \leq a_2 < a_1 \leq a_3,$$
$$b_1 \leq b_3 < b_4 \leq b_2.$$

Let $L_\infty = (a_3 - a_1)(b_2 - b_3)(a_2 - a_4)(b_4 - b_1) - (b_1 - b_3)(a_2 - a_3)(b_4 - b_2)(a_4 - a_1)$. Then the following two statements hold.

(I) If $L_\infty > 0$ then the ODE is permanent.

(II) If $L_\infty < 0$ then the ODE is not permanent.

PERMANENCE IN THE ACYCLIC CASE: $J_{11}J_{22} \geq 0$

$$\dot{u} = e^{a_1 u + b_1 v} - e^{a_2 u + b_2 v}$$
$$\dot{v} = e^{a_3 u + b_3 v} - e^{a_4 u + b_4 v}$$

$$J = \begin{pmatrix} a_1 - a_2 & b_1 - b_2 \\ a_3 - a_4 & b_3 - b_4 \end{pmatrix}$$

THEOREM

Assume $J_{11}J_{22} \geq 0$. Then the following are equivalent.

(I) *Permanence.*

(II) *The origin is globally stable.*

(III) $\det J > 0$ *and one of (A), (B1), (B2) below holds.*

(A) $\operatorname{sgn} J = \begin{pmatrix} - & * \\ * & - \end{pmatrix}$

(B1) $\operatorname{sgn} J = \begin{pmatrix} 0 & * \\ * & - \end{pmatrix}$ *and* $\min(a_3, a_4) \leq a_2 = a_1 \leq \max(a_3, a_4)$

(B2) $\operatorname{sgn} J = \begin{pmatrix} - & * \\ * & 0 \end{pmatrix}$ *and* $\min(b_1, b_2) \leq b_4 = b_3 \leq \max(b_1, b_2)$

PERMANENCE IN THE ACYCLIC CASE: $J_{11}J_{22} < 0$

THEOREM

Assume ∂S does not form a heteroclinic cycle and sgn $J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$.

Then permanence is equivalent to $\det J > 0$, $a_4 \leq a_2 < a_1 \leq a_3$, *and one of the following holds:*

- sgn$(c_3, c_4) = (-, -)$

- sgn $c = (+, -, -, 0)$ *or* sgn $c = (-, +, 0, -)$ *and*

$$-\frac{a_1 - a_2}{b_1 - b_2} < \frac{(L+1)^{L+1}}{L^L}, \text{ where } L = \begin{cases} \frac{c_2}{c_3}, & \text{if sgn } c = (+, -, -, 0), \\ \frac{c_1}{c_4}, & \text{if sgn } c = (-, +, 0, -) \end{cases}$$

- sgn $c = (+, 0, -, 0)$ *or* sgn $c = (0, +, 0, -)$ *and*

$$-\frac{a_1 - a_2}{b_1 - b_2} \leq 1 \text{ and } \operatorname{tr} J < 0.$$

ROBUST PERMANENCE

$$\dot{u} = e^{a_1 u + b_1 v} - e^{a_2 u + b_2 v}$$
$$\dot{v} = e^{a_3 u + b_3 v} - e^{a_4 u + b_4 v}$$

$$J = \begin{pmatrix} a_1 - a_2 & b_1 - b_2 \\ a_3 - a_4 & b_3 - b_4 \end{pmatrix}$$

COROLLARY

Assume $J_{22} < 0$. Then the ODE remains permanent after small perturbations of a_i, b_i if and only if $\det J > 0$ and one of (A), (B), (C) holds.

(A) $\operatorname{sgn} J = \begin{pmatrix} - & * \\ * & - \end{pmatrix}$

(B) $\operatorname{sgn} J = \begin{pmatrix} 0 & * \\ * & - \end{pmatrix}$ *and* $\min(a_3, a_4) < a_2 = a_1 < \max(a_3, a_4)$

(C) $\operatorname{sgn} J = \begin{pmatrix} + & * \\ * & - \end{pmatrix}$ *and* $\min(a_3, a_4) < a_2 < a_1 < \min(a_3, a_4)$ *and*
$\operatorname{sgn}(c_3, c_4) = (-, -)$,
and if $\min(b_1, b_2) < b_3 < b_4 < \max(b_1, b_2)$ *then* $L_\infty > 0$

A byproduct: three limit cycles

- We proved the existence of parameters a_i, b_i for which

$$\dot{u} = e^{a_1 u + b_1 v} - e^{a_2 u + b_2 v}$$
$$\dot{v} = e^{a_3 u + b_3 v} - e^{a_4 u + b_4 v}$$

  has at least 3 limit cycles (2 born at the origin, 1 at infinity).

- Fewnomial version of Hilbert's 16th problem:
  What is the maximum number of limit cycles for a planar
  polynomial system having only a few (e.g. 4) monomials?

  Gasull & Santana (2024): 12 limit cycles for systems with 4
  monomials ($12 = 3 \times 4$)

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CONNECTION TO 3D LOTKA–VOLTERRA SYSTEMS

The center families found for planar S-systems correspond to centers found by

Bobieński & Żołądek (2005) in 3d Lotka–Volterra systems:

1) families with invariant planes
2) Darboux: global first integral of the product form
3) Hopf: line of equilibria, with a foliation into 2d leaves, equilibria change stability $\longrightarrow$ family of periodic orbits