Available online at www.sciencedirect.com

ScienceDirect

J. Differential Equations 266 (2019) 3787–3817

Journal of Differential Equations

www.elsevier.com/locate/jde

Planar S-systems: Permanence ☆

Balázs Boros *, Josef Hofbauer

Faculty of Mathematics, University of Vienna, Oskar-Morgenstern-Platz 1, 1090 Vienna, Austria

Received 25 May 2018
Available online 3 October 2018

Abstract

We characterize permanence of planar S-systems. Further, we construct a planar S-system with three limit cycles.

MSC: 34C05; 34C11; 34C14; 34C23; 34C37; 34C45; 80A30

Keywords: Homogeneous Lotka–Volterra systems; Replicator dynamics; Heteroclinic cycle; Limit cycles; Center manifold; Dihedral group

1. Introduction

An S-system is a dynamical system on the positive orthant for which the right hand side is given by differences of power products (monomials) with real exponents. They were introduced by Savageau [11] in the context of biochemical systems theory. In a previous paper [3] we studied planar S-systems, especially the local and global asymptotic stability of the unique positive equilibrium and also the center problem.

In the present paper we characterize (except for some boundary case) the permanence of planar S-systems. This is done by first transforming planar S-systems into a 3-dimensional replicator dynamics.

☆ BB is supported by the Austrian Science Fund (FWF), project P28406.
* Corresponding author.
E-mail addresses: balazs.boros@univie.ac.at (B. Boros), josef.hofbauer@univie.ac.at (J. Hofbauer).

https://doi.org/10.1016/j.jde.2018.09.016
0022-0396/

The results will be illustrated for some special cases: Selkov's model for glycolytic oscillations [12,4] and the Lotka reactions with generalized mass-action kinetics [6,1].

Finally, the obtained results allow us to construct a planar S-system with three limit cycles. This improves the previous studies [6] (one limit cycle) and [3,2] (two limit cycles).

2. Planar S-systems

A planar S-system is given by

$$\begin{aligned}\dot{x}_1 &= \alpha_1 x_1^{g_{11}} x_2^{g_{12}} - \beta_1 x_1^{h_{11}} x_2^{h_{12}},\\ \dot{x}_2 &= \alpha_2 x_1^{g_{21}} x_2^{g_{22}} - \beta_2 x_1^{h_{21}} x_2^{h_{22}}\end{aligned} \tag{1}$$

with $\alpha_1, \alpha_2, \beta_1, \beta_2 \in \mathbb{R}_+$ and $g_{11}, g_{12}, g_{21}, g_{22}, h_{11}, h_{12}, h_{21}, h_{22} \in \mathbb{R}$. Since we allow real exponents, we study the dynamics on the positive quadrant $\mathbb{R}^2_+ = \{(x_1, x_2) \in \mathbb{R}^2 \mid x_1 > 0, x_2 > 0\}$. Our aim in this paper is to characterize the parameters for which the ODE (1) is *permanent*, meaning that there exists a compact subset of $\mathbb{R}^2_+$ that is forward invariant and is a global attractor.

A short calculation shows that there is either 0, 1, or infinitely many positive equilibria, and, if there is no positive equilibrium then the system cannot be permanent. We thus concentrate on the case, when there exists a (not necessarily unique) positive equilibrium (x_1^*, x_2^*). Introducing

$$\gamma_1 = \alpha_1 (x_1^*)^{g_{11}-1} (x_2^*)^{g_{12}} \text{ and } \gamma_2 = \alpha_2 (x_1^*)^{g_{21}} (x_2^*)^{g_{22}-1},$$

we perform the nonlinear transformation

$$u = \frac{1}{\gamma_1} \log \frac{x_1}{x_1^*} \text{ and } v = \frac{1}{\gamma_2} \log \frac{x_2}{x_2^*}.$$

This leads to the ODE

$$\begin{aligned}\dot{u} &= \mathrm{e}^{a_1 u + b_1 v} - \mathrm{e}^{a_2 u + b_2 v},\\ \dot{v} &= \mathrm{e}^{a_3 u + b_3 v} - \mathrm{e}^{a_4 u + b_4 v}\end{aligned} \tag{2}$$

with state space $\mathbb{R}^2$, where

$$\begin{aligned} a_1 &= \gamma_1 (g_{11} - 1), & b_1 &= \gamma_2 g_{12},\\ a_2 &= \gamma_1 (h_{11} - 1), & b_2 &= \gamma_2 h_{12},\\ a_3 &= \gamma_1 g_{21}, & b_3 &= \gamma_2 (g_{22} - 1),\\ a_4 &= \gamma_1 h_{21}, & b_4 &= \gamma_2 (h_{22} - 1).\end{aligned} \tag{3}$$

We say that the ODE (2) is *permanent* if there exists a compact subset of $\mathbb{R}^2$ that is forward invariant and is a global attractor. Clearly, the permanence of the ODE (1) is equivalent to the permanence of the ODE (2) with (3).

The ODE (2) admits the origin as an equilibrium. The Jacobian matrix J at the origin is given by

$$J = \begin{pmatrix} a_1 - a_2 & b_1 - b_2 \\ a_3 - a_4 & b_3 - b_4 \end{pmatrix}. \tag{4}$$

A short calculation shows that if $\det J = 0$ then the set of equilibria is either a line through the origin or the whole $\mathbb{R}^2$. Thus, the system cannot be permanent for $\det J = 0$. To characterize permanence for the ODE (1), it suffices to characterize those $a_1, a_2, a_3, a_4, b_1, b_2, b_3, b_4 \in \mathbb{R}$, for which $\det J \neq 0$ and the ODE (2) is permanent. The aim of this paper is to perform this characterization (except for some boundary case). Crucial for this is the relative position of the four points $P_i = (a_i, b_i)$ for $i = 1, 2, 3, 4$ in the plane. Define the numbers c_1, c_2, c_3, c_4 by

$$\begin{aligned} c_1 &= \Delta(243), \\ c_2 &= \Delta(134), \\ c_3 &= \Delta(142), \\ c_4 &= \Delta(123), \end{aligned} \tag{5}$$

where $\Delta(ijk) = \det(P_j - P_i, P_k - P_i)$ is twice the signed area of the triangle $P_i P_j P_k$. The quantity $\Delta(ijk)$ is thus positive (respectively, negative) if the sequence P_i, P_j, P_k, P_i of points are positively (respectively, negatively) oriented. The quantity $\Delta(ijk)$ is zero if the three points P_i, P_j, P_k lie on a line. Note also that

$$\Delta(ijk) = \Delta(jki) = \Delta(kij) = -\Delta(jik) = -\Delta(ikj) = -\Delta(kji)$$

and $c_1 + c_2 + c_3 + c_4 = 0$.

Now we show how the sign pattern of $c = (c_1, c_2, c_3, c_4)$ is related to the relative position of the four points P_1, P_2, P_3, P_4. There are four qualitatively different situations. (The case $c = (0, 0, 0, 0)$ we ignore, because then the four points P_1, P_2, P_3, P_4 are co-linear, contradicting $\det J \neq 0$.)

(i) When $\operatorname{sgn} c = (+, +, -, -)$, the four points P_1, P_2, P_3, P_4 form a quadrangle with diagonals P_1P_2 and P_3P_4. The geometric interpretation of the equality $\frac{c_1}{2} + \frac{c_2}{2} = \frac{-c_3}{2} + \frac{-c_4}{2}$ is that the area of this quadrangle can be written as the sum of the areas of the triangles $P_2P_4P_3$ and $P_1P_3P_4$, or alternatively as the sum of the areas of the triangles $P_1P_2P_4$ and $P_1P_3P_2$.

(ii) When $\operatorname{sgn} c = (+, -, -, -)$, the three points P_2, P_3, P_4 form a triangle and the point P_1 lies inside. The geometric interpretation of the equality $\frac{c_1}{2} = \frac{-c_2}{2} + \frac{-c_3}{2} + \frac{-c_4}{2}$ is that the area of this triangle can be written as the sum of the areas of the triangles $P_1P_4P_3$, $P_1P_2P_4$, $P_1P_3P_2$.

(iii) When $\operatorname{sgn} c = (+, 0, -, -)$, the three points P_2, P_3, P_4 form a triangle and the point P_1 lies in the edge P_3P_4. The geometric interpretation of the equality $\frac{c_1}{2} = \frac{-c_3}{2} + \frac{-c_4}{2}$ is that the area of this triangle can be written as the sum of the areas of the triangles $P_1P_2P_4$, $P_1P_3P_2$.

(iv) When $\operatorname{sgn} c = (+, 0, -, 0)$, the three points P_2, P_3, P_4 form a triangle and the point P_1 coincides with P_3. Clearly, $\frac{c_1}{2} = \frac{-c_3}{2}$, because the triangles $P_3P_2P_4$ and $P_1P_2P_4$ coincide, and thus, their area are the same.

3. Main results

In this section we list the main results of this paper.

The following simple lemma states that permanence of the ODE (2) is possible only under $\det J > 0$.

Lemma 3.1. *If* $\det J \leq 0$ *then the ODE* (2) *is not permanent.*

Proof. We discussed in Section 2 that the ODE (2) cannot be permanent under $\det J = 0$.

In case $\det J < 0$, the origin is the unique equilibrium, and therefore, would the system be permanent, the index of the origin is $+1$, contradicting $\det J < 0$. Thus, the system cannot be permanent under $\det J < 0$. □

The following three theorems provide an almost complete characterization of permanence of the ODE (2). The first one deals with the easier case when the diagonal entries in the Jacobian matrix at the origin are of the same sign or one of them is zero. The third one deals with the more complicated case when the diagonal entries have opposite nonzero sign. The case of a heteroclinic cycle at infinity needs a separate treatment, this is dealt with in the second of these three theorems. The proofs of the latter two are given in Sections 4 and 5.

Theorem 3.2. *Assume that* $J_{11}J_{22} \geq 0$ *(i.e.,* $(a_1 - a_2)(b_3 - b_4) \geq 0$*). Then the following three statements are equivalent.*

(i) *The ODE* (2) *is permanent.*
(ii) *The origin is globally asymptotically stable for the ODE* (2).
(iii) $\det J > 0$ *and one of (A), (B1), (B2) below holds.*

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

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

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

Proof. First, we prove the implication (i) ⇒ (iii). By Lemma 3.1, permanence implies that $\det J > 0$. After multiplying the vector field by $e^{-a_1 u - b_4 v}$, its divergence is

$$(a_1 - a_2)e^{(a_2-a_1)u+(b_2-b_4)v} + (b_3 - b_4)e^{(a_3-a_1)u+(b_3-b_4)v},$$

which is negative if at least one of $a_1 - a_2$ and $b_3 - b_4$ is negative, zero if $a_1 - a_2 = b_3 - b_4 = 0$, and positive if at least one of $a_1 - a_2$ and $b_3 - b_4$ is positive. The latter two cases cannot lead to a permanent system as the area is invariant or expanding. This leaves the three sign patterns of J given in (A), (B1), (B2). In the latter two cases, the conditions $\min(a_3, a_4) \leq a_2 = a_1 \leq \max(a_3, a_4)$ and $\min(b_1, b_2) \leq b_4 = b_3 \leq \max(b_1, b_2)$ follow from the boundedness of all solutions, see [2, Lemma 5 (b2), (c2), (d2), (e2)].

The implication (iii) ⇒ (ii) follows from [2, Theorem 3].

Finally, the implication (ii) ⇒ (i) is obvious. □

Theorem 3.3. *Assume that* $\det J > 0$ *and further that either (A) or (B) below holds.*

$$(A)\quad \operatorname{sgn} J = \begin{pmatrix} * & - \\ + & * \end{pmatrix} \text{ and } \begin{cases} a_4 \le \min(a_1, a_2) \le \max(a_1, a_2) \le a_3 \\ b_1 \le \min(b_3, b_4) \le \max(b_3, b_4) \le b_2 \end{cases}$$

$$(B)\quad \operatorname{sgn} J = \begin{pmatrix} * & + \\ - & * \end{pmatrix} \text{ and } \begin{cases} a_3 \le \min(a_1, a_2) \le \max(a_1, a_2) \le a_4 \\ b_2 \le \min(b_3, b_4) \le \max(b_3, b_4) \le b_1 \end{cases}$$

In case (A)*, let*

$$L_\infty = (a_3 - a_1)(b_2 - b_3)(a_2 - a_4)(b_4 - b_1) - (b_1 - b_3)(a_2 - a_3)(b_4 - b_2)(a_4 - a_1),$$

while in case (B)*, let*

$$L_\infty = (b_1 - b_3)(a_2 - a_3)(b_4 - b_2)(a_4 - a_1) - (a_3 - a_1)(b_2 - b_3)(a_2 - a_4)(b_4 - b_1).$$

Then the following two statements hold.

(i) If $L_\infty > 0$ *then the ODE* (2) *is permanent.*
(ii) If $L_\infty < 0$ *then the ODE* (2) *is not permanent.*

Theorem 3.4. *Assume that* $J_{11} J_{22} < 0$ *(i.e.,* $(a_1 - a_2)(b_3 - b_4) < 0$*) and at least one of the two conditions*

$$\min(a_3, a_4) \le \min(a_1, a_2) \le \max(a_1, a_2) \le \max(a_3, a_4) \text{ and}$$
$$\min(b_1, b_2) \le \min(b_3, b_4) \le \max(b_3, b_4) \le \max(b_1, b_2)$$

is violated. Then the ODE (2) *is permanent if and only if* $\det J > 0$ *and one of (C1), (C2), (C3), (C4) below holds.*

(C1) $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$, $a_4 \le a_2 < a_1 \le a_3$, *and either of (C1a), (C1b), or (C1c) below holds*

(C1a) $\operatorname{sgn}(c_3, c_4) = (-, -)$

(C1b) $\operatorname{sgn} c = (+, -, -, 0)$ *or* $\operatorname{sgn} c = (-, +, 0, -)$ *and*

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

(C1c) $\operatorname{sgn} c = (+, 0, -, 0)$ *or* $\operatorname{sgn} c = (0, +, 0, -)$ *and*

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

(C2) $\operatorname{sgn} J = \begin{pmatrix} + & + \\ - & - \end{pmatrix}$, $a_3 \le a_2 < a_1 \le a_4$, *and either of (C2a), (C2b), or (C2c) below holds*
(C2a) $\operatorname{sgn}(c_3, c_4) = (-,-)$
(C2b) $\operatorname{sgn} c = (-,+,-,0)$ *or* $\operatorname{sgn} c = (+,-,0,-)$ *and*

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

(C2c) $\operatorname{sgn} c = (0,+,-,0)$ *or* $\operatorname{sgn} c = (+,0,0,-)$ *and*

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

(C3) $\operatorname{sgn} J = \begin{pmatrix} - & - \\ + & + \end{pmatrix}$, $b_1 \le b_4 < b_3 \le b_2$, *and either of (C3a), (C3b), or (C3c) below holds*
(C3a) $\operatorname{sgn}(c_1, c_2) = (+,+)$
(C3b) $\operatorname{sgn} c = (0,+,-,+)$ *or* $\operatorname{sgn} c = (+,0,+,-)$ *and*

$$\frac{b_3 - b_4}{a_3 - a_4} < \frac{(L+1)^{L+1}}{L^L}, \text{ where } L = \begin{cases} \frac{c_4}{c_2}, & \text{if } \operatorname{sgn} c = (0,+,-,+), \\ \frac{c_3}{c_1}, & \text{if } \operatorname{sgn} c = (+,0,+,-) \end{cases}$$

(C3c) $\operatorname{sgn} c = (0,+,-,0)$ *or* $\operatorname{sgn} c = (+,0,0,-)$ *and*

$$\frac{b_3 - b_4}{a_3 - a_4} \le 1 \text{ and } \operatorname{tr} J < 0$$

(C4) $\operatorname{sgn} J = \begin{pmatrix} - & + \\ - & + \end{pmatrix}$, $b_2 \le b_4 < b_3 \le b_1$, *and either of (C4a), (C4b), or (C4c) below holds*
(C4a) $\operatorname{sgn}(c_1, c_2) = (+,+)$
(C4b) $\operatorname{sgn} c = (0,+,+,-)$ *or* $\operatorname{sgn} c = (+,0,-,+)$ *and*

$$-\frac{b_3 - b_4}{a_3 - a_4} < \frac{(L+1)^{L+1}}{L^L}, \text{ where } L = \begin{cases} \frac{c_3}{c_2}, & \text{if } \operatorname{sgn} c = (0,+,+,-), \\ \frac{c_4}{c_1}, & \text{if } \operatorname{sgn} c = (+,0,-,+) \end{cases}$$

(C4c) $\operatorname{sgn} c = (0,+,0,-)$ *or* $\operatorname{sgn} c = (+,0,-,0)$ *and*

$$-\frac{b_3 - b_4}{a_3 - a_4} \le 1 \text{ and } \operatorname{tr} J < 0$$

With Theorems 3.2, 3.3, 3.4, permanence is characterized except in the marginal case $L_\infty = 0$ in Theorem 3.3. The solution of this remaining case requires more sophisticated techniques.

By *robust permanence* of the ODE (2), we mean that the ODE remains permanent after small perturbation of the eight parameters a_i and b_i (for $i = 1, 2, 3, 4$). The following corollary is a characterization of robust permanence, it is an immediate consequence of the above three theorems.

Corollary 3.5. *The ODE* (2) *is robustly permanent if and only if* $\det J > 0$ *and one of (A), (B1), (B2), (B3), (B4), (C1), (C2), (C3), (C4) below holds. (The number* L_∞ *below in (C1), (C2), (C3), (C4) is defined as in the corresponding case in Theorem 3.3.)*

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

(B1) $\operatorname{sgn} J = \begin{pmatrix} 0 & - \\ + & - \end{pmatrix}$ *and* $a_4 < a_2 = a_1 < a_3$

(B2) $\operatorname{sgn} J = \begin{pmatrix} 0 & + \\ - & - \end{pmatrix}$ *and* $a_3 < a_2 = a_1 < a_4$

(B3) $\operatorname{sgn} J = \begin{pmatrix} - & + \\ - & 0 \end{pmatrix}$ *and* $b_2 < b_4 = b_3 < b_1$

(B4) $\operatorname{sgn} J = \begin{pmatrix} - & - \\ + & 0 \end{pmatrix}$ *and* $b_1 < b_4 = b_3 < b_2$

(C1) $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$, $a_4 < a_2 < a_1 < a_3$, $\operatorname{sgn}(c_3, c_4) = (-,-)$,
and if $b_1 < b_3 < b_4 < b_2$ *then* $L_\infty > 0$

(C2) $\operatorname{sgn} J = \begin{pmatrix} + & + \\ - & - \end{pmatrix}$, $a_3 < a_2 < a_1 < a_4$, $\operatorname{sgn}(c_3, c_4) = (-,-)$,
and if $b_2 < b_3 < b_4 < b_1$ *then* $L_\infty > 0$

(C3) $\operatorname{sgn} J = \begin{pmatrix} - & - \\ + & + \end{pmatrix}$, $b_1 < b_4 < b_3 < b_2$, $\operatorname{sgn}(c_1, c_2) = (+,+)$,
and if $a_4 < a_1 < a_2 < a_3$ *then* $L_\infty > 0$

(C4) $\operatorname{sgn} J = \begin{pmatrix} - & + \\ - & + \end{pmatrix}$, $b_2 < b_4 < b_3 < b_1$, $\operatorname{sgn}(c_1, c_2) = (+,+)$,
and if $a_3 < a_1 < a_2 < a_4$ *then* $L_\infty > 0$

4. From S-systems to replicator systems

To prove Theorems 3.3 and 3.4, we embed the two-dimensional ODE (2) into a four-dimensional Lotka–Volterra system. Let $z_i = \mathrm{e}^{a_i u + b_i v}$ for $i = 1, 2, 3, 4$. Then

$$\dot{z}_i = z_i\,[a_i \dot{u} + b_i \dot{v}] = z_i\,[a_i(z_1 - z_2) + b_i(z_3 - z_4)] \text{ for } i = 1, 2, 3, 4, \tag{6}$$

which is a 4-dimensional Lotka–Volterra system with matrix

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

Since the ODE (6) is homogeneous, we can reduce the dimension by projecting the dynamics to the 3-dimensional simplex

$$\Delta_4 = \left\{ x \in \mathbb{R}^4_{\geq 0} \mid x_1 + x_2 + x_3 + x_4 = 1 \right\}.$$

Let

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

Then, after division by the positive factor $z_1 + z_2 + z_3 + z_4$, the ODE (6) leads to

$$\dot{x}_i = x_i \left[(\widetilde{A}x)_i - x^\mathsf{T} \widetilde{A} x\right] \text{ for } i = 1, 2, 3, 4 \tag{7}$$

on the simplex Δ_4, the replicator equation with matrix $\widetilde{A}$, see [8,9]. Adding any multiple of $\mathbf{1} = (1, 1, 1, 1)^\mathsf{T}$ to any column of $\widetilde{A}$ leaves the ODE (7) unchanged, therefore, we can replace the ODE (7) by the replicator equation on the simplex Δ_4 with matrix

$$A = \begin{pmatrix} 0 & a_2 - a_1 & b_1 - b_3 & b_4 - b_1 \\ a_2 - a_1 & 0 & b_2 - b_3 & b_4 - b_2 \\ a_3 - a_1 & a_2 - a_3 & 0 & b_4 - b_3 \\ a_4 - a_1 & a_2 - a_4 & b_4 - b_3 & 0 \end{pmatrix}, \tag{8}$$

i.e.,

$$\dot{x}_i = x_i \left[(Ax)_i - x^\mathsf{T} A x\right] \text{ for } i = 1, 2, 3, 4. \tag{9}$$

Note that besides the corners E_1, E_2, E_3, E_4 of Δ_4, the points $E_{12} = \left(\frac{1}{2}, \frac{1}{2}, 0, 0\right)$ and $E_{34} = \left(0, 0, \frac{1}{2}, \frac{1}{2}\right)$ are equilibria of the ODE (9). Also, each point on the line segment connecting E_{12} and E_{34} is an equilibrium. Further, a short calculation shows that $\det J \neq 0$ implies that there is no other equilibrium in Δ_4°, the relative interior of Δ_4.

Let $c \in \mathbb{R}^4$ be as in (5), or explicitly,

$$\begin{aligned} c_1 &= a_3 b_2 - a_2 b_3 + a_2 b_4 - a_4 b_2 + a_4 b_3 - a_3 b_4, \\ c_2 &= a_1 b_3 - a_3 b_1 + a_4 b_1 - a_1 b_4 + a_3 b_4 - a_4 b_3, \\ c_3 &= a_2 b_1 - a_1 b_2 + a_1 b_4 - a_4 b_1 + a_4 b_2 - a_2 b_4, \\ c_4 &= a_1 b_2 - a_2 b_1 + a_3 b_1 - a_1 b_3 + a_2 b_3 - a_3 b_2. \end{aligned} \tag{10}$$

Note that

$$c_1 + c_2 = + \det J, \tag{11}$$

$$c_3 + c_4 = - \det J \tag{12}$$

and c is perpendicular to the three vectors a, b, and $\mathbf{1}$ (a short calculation shows that $\det J \neq 0$ implies that a, b, and $\mathbf{1}$ are linearly independent). Then $c^\mathsf{T} A = 0$ and hence the function $Q : \Delta_4^\circ \to \mathbb{R}_+$ defined by $Q(x) = \prod_{i=1}^4 x_i^{c_i}$ is a constant of motion for the ODE (9). Indeed, by the choice of c,

$$(Q(x))^\cdot = Q(x) \sum_{i=1}^4 c_i \left[(Ax)_i - x^\mathsf{T} A x\right] = Q(x) \left[c^\mathsf{T} A x - x^\mathsf{T} A x \sum_{i=1}^4 c_i\right] = 0.$$

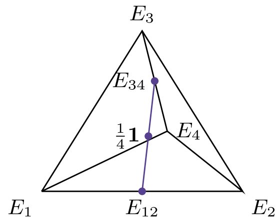

Fig. 1. Each point on the line segment connecting E_{12} and E_{34} is an equilibrium. The planar S-system (2) and the origin of the (u, v)-plane correspond to the surface $\prod_{i=1}^4 x_i^{c_i} = 1$ and $x = \frac{1}{4}\mathbf{1}$ (the midpoint between E_{12} and E_{34}), respectively.

The planar S-system (2) corresponds to the restriction of the ODE (9) to the surface $\{Q = 1\}$. (The origin of the (u, v)-plane is mapped to $z = \mathbf{1}$ and $x = \frac{1}{4}\mathbf{1}$. Further, since $\sum_{i=1}^4 c_i = 0$, we have $Q\left(\frac{1}{4}\mathbf{1}\right) = 1$. See Fig. 1 for an illustration.) The shape of the surface $\{Q = 1\}$ depends on the sign pattern of c. Let

$$\overline{S} = \Delta_4 \cap \{Q = 1\},$$
$$S = \Delta_4^\circ \cap \{Q = 1\},$$
$$\partial S = \overline{S} \setminus S.$$

Note that the planar S-system (2) is permanent if and only if the restriction of the ODE (9) to the surface $\overline{S}$ is *permanent*, meaning there exists a compact subset of S that is forward invariant and attracts every point in S (or, equivalently, ∂S is a repeller in $\overline{S}$).

We illustrate the usefulness of this embedding by proving Theorem 3.3. We state and prove here case (A). Case (B) follows from case (A) by time reversal of the ODE (2), which swaps P_1 with P_2 and P_3 with P_4.

Lemma 4.1. *Assume that* $\det J > 0$ *and further that*

$$\operatorname{sgn} J = \begin{pmatrix} * & - \\ + & * \end{pmatrix} \text{ and } \begin{cases} a_4 \le \min(a_1, a_2) \le \max(a_1, a_2) \le a_3 \\ b_1 \le \min(b_3, b_4) \le \max(b_3, b_4) \le b_2 \end{cases}.$$

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* (2) *is permanent.*
(ii) If $L_\infty < 0$ *then the ODE* (2) *is not permanent (orbits with large initial conditions spiral outwards towards infinity).*

Proof. First note that $L_\infty \neq 0$ implies that all the four points P_1, P_2, P_3, P_4 are distinct. Further, the assumptions $a_4 \le \min(a_1, a_2) \le \max(a_1, a_2) \le a_3$ and $b_1 \le \min(b_3, b_4) \le \max(b_3, b_4) \le b_2$ yield $\operatorname{sgn} c = (+, +, -, -)$, see (5). Then the surface S is given by $\frac{x_1^{|c_1|} x_2^{|c_2|}}{x_3^{|c_3|} x_4^{|c_4|}} = 1$

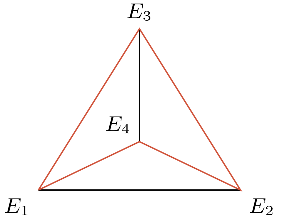

Fig. 2. Under $\operatorname{sgn} c = (+, +, -, -)$, the set ∂S consists of the four edges $\mathcal{F}_{13}$, $\mathcal{F}_{32}$, $\mathcal{F}_{24}$, $\mathcal{F}_{41}$.

and thus, ∂S consists of the four edges $\mathcal{F}_{13}$, $\mathcal{F}_{32}$, $\mathcal{F}_{24}$, $\mathcal{F}_{41}$, see Fig. 2. There is no edge equilibrium and there is a heteroclinic cycle along E_1, E_3, E_2, E_4, E_1. Indeed, on the surface $\overline{S}$, near E_4, the ODE (9) is given by

$$\dot{x}_1 = x_1 \left(b_4 - b_1 + f_1(x_1, x_2) \right),$$
$$\dot{x}_2 = x_2 \left(b_4 - b_2 + f_2(x_1, x_2) \right)$$

with $b_4 - b_1 \geq 0$ and $b_4 - b_2 \leq 0$ (not both zero, because $b_1 < b_2$) being the eigenvalues at E_4 and $|f_i(x_1, x_2)| \to 0$ as $(x_1, x_2) \to (0, 0)$. Similarly near the other corners. By [7, Theorem 3], this heteroclinic cycle is repelling if the product of the outgoing eigenvalues is larger than the product of the incoming eigenvalues along the cycle, i.e., if

$$(a_3 - a_1)(b_2 - b_3)(a_2 - a_4)(b_4 - b_1) - (b_1 - b_3)(a_2 - a_3)(b_4 - b_2)(a_4 - a_1) > 0.$$

Conversely, if $L_\infty < 0$ then the heteroclinic cycle is attracting. □

5. Proof of Theorem 3.4

This section is devoted to prove Theorem 3.4. By Lemma 3.1, permanence of the ODE (2) implies $\det J > 0$. Since $J_{11} J_{22} < 0$ is assumed in Theorem 3.4, all permanent systems fulfil $J_{12} J_{21} < 0$. Thus, we are left with the four sign patterns

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

for the Jacobian matrix J. As it is explained in [2, Subsection 2.2], the family of ODEs (2) is invariant under the symmetry group of the square (i.e., the dihedral group D_4) which consists of the rotations $\mathbf{r}_0$ (by 0°), $\mathbf{r}_1$ (by +90°), $\mathbf{r}_2$ (by +180°), $\mathbf{r}_3$ (by +270°) and the reflections $\mathbf{s}_0$ (along the u-axis), $\mathbf{s}_1$ (along the $u = v$ line), $\mathbf{s}_2$ (along the v-axis), $\mathbf{s}_3$ (along the $u = -v$ line). The list in [2, Subsection 2.2] reveals how the a_i and b_i are mapped under these eight operations. Fig. 3 illustrates how the above mentioned four sign patterns of J are transformed into each other. The vector (c_1, c_2, c_3, c_4) is mapped by the elements of the dihedral group D_4 as

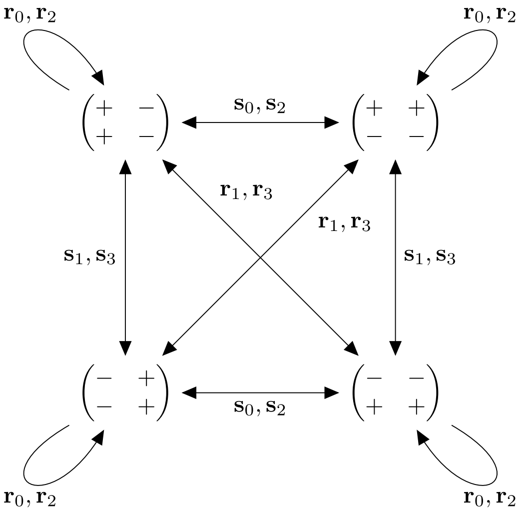

Fig. 3. How the elements of the dihedral group D_4 transform the sign pattern of the Jacobian matrix J.

$$\begin{aligned}
&(c_1,c_2,c_3,c_4) \overset{\mathbf{r}_0}{\mapsto} (c_1,c_2,c_3,c_4), && (c_1,c_2,c_3,c_4) \overset{\mathbf{s}_0}{\mapsto} (c_1,c_2,c_4,c_3),\\
&(c_1,c_2,c_3,c_4) \overset{\mathbf{r}_1}{\mapsto} (-c_4,-c_3,-c_1,-c_2), && (c_1,c_2,c_3,c_4) \overset{\mathbf{s}_1}{\mapsto} (-c_3,-c_4,-c_1,-c_2),\\
&(c_1,c_2,c_3,c_4) \overset{\mathbf{r}_2}{\mapsto} (c_2,c_1,c_4,c_3), && (c_1,c_2,c_3,c_4) \overset{\mathbf{s}_2}{\mapsto} (c_2,c_1,c_3,c_4),\\
&(c_1,c_2,c_3,c_4) \overset{\mathbf{r}_3}{\mapsto} (-c_3,-c_4,-c_2,-c_1), && (c_1,c_2,c_3,c_4) \overset{\mathbf{s}_3}{\mapsto} (-c_4,-c_3,-c_2,-c_1).
\end{aligned}$$

Using these symmetries, once we prove case (C1) in Theorem 3.4, the cases (C2), (C3), and (C4) follow by applying $\mathbf{s}_0$ or $\mathbf{s}_2$, $\mathbf{r}_1$ or $\mathbf{r}_3$, and $\mathbf{s}_1$ or $\mathbf{s}_3$, respectively.

Thus, from now on we mainly focus on characterizing permanence under $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$. Since we will make use of the rotation $\mathbf{r}_2$, we mention here that the ODE (2) is transformed by $\mathbf{r}_2$ into

$$\begin{aligned}
\dot{u} &= \mathrm{e}^{-a_2u-b_2v} - \mathrm{e}^{-a_1u-b_1v},\\
\dot{v} &= \mathrm{e}^{-a_4u-b_4v} - \mathrm{e}^{-a_3u-b_3v}.
\end{aligned}$$

Further, the rotation $\mathbf{r}_2$ maps (P_1,P_2,P_3,P_4) to $(-P_2,-P_1,-P_4,-P_3)$, hence, the tuple (c_1,c_2,c_3,c_4) goes to the tuple (c_2,c_1,c_4,c_3) (as already listed above).

The following lemma gives a necessary condition for the ODE (2) with $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$ to be permanent.

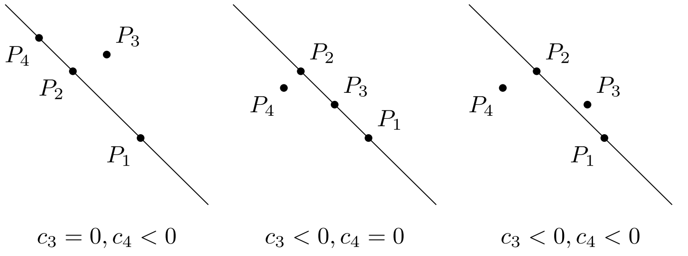

Fig. 4. Illustration of the proof of the claim (13).

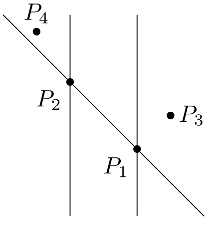

Fig. 5. Illustration of the proof that $c_3 > 0$ implies $c_1 < 0$ and $c_2 > 0$.

Lemma 5.1. *Assume that* $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$ *and* $\det J > 0$. *Then permanence of the ODE* (2) *implies*

(i) $a_4 \le a_2 < a_1 \le a_3$ *and*
(ii) $c_3 \le 0$, $c_4 \le 0$, *and* $(c_3, c_4) \ne (0, 0)$.

Proof. The inequalities $a_2 < a_1$ and $a_4 < a_3$ readily follow from the assumption on the sign pattern of the Jacobian matrix.

Next, we prove that $a_1 \le a_3$. Assume by contradiction that $a_3 < a_1$. Then all the non-diagonal entries in the first column of A in the ODE (9) are negative, and therefore the corner $E_1 = (1, 0, 0, 0)$ is asymptotically stable. We claim that

$$\text{there is both a positive and a negative number among } c_2, c_3, c_4. \tag{13}$$

Once we show that the claim (13) indeed holds, it follows that $E_1 \in \partial S$. This together with the asymptotic stability of E_1 contradicts the permanence of the ODE (2). Thus, $a_1 \le a_3$ follows. We now prove the claim (13). By equation (12), if one of c_3 and c_4 is positive, the other must be negative. Observe that c_3 and c_4 cannot both be zero, because then $\det J = 0$ by equation (12). We argue that each of $\operatorname{sgn}(c_3, c_4) = (0, -)$, $\operatorname{sgn}(c_3, c_4) = (-, 0)$, and $\operatorname{sgn}(c_3, c_4) = (-, -)$ implies $c_2 > 0$. Indeed, these follow immediately from $a_4 < a_3 < a_1$ and the geometric definition (5) of c_2, c_3, c_4, see Fig. 4. The claim (13) is therefore proven.

The inequality $a_4 \le a_2$ follows in a similar way: $a_2 < a_4$ would imply that $E_2 = (0, 1, 0, 0)$ is asymptotically stable (and, one can show that $E_2 \in \partial S$). Alternatively, using the rotation $\mathbf{r}_2$ and the just proved fact that permanence implies $a_1 \le a_3$, one immediately finds that permanence implies $-a_2 \le -a_4$. Or, equivalently, $a_4 \le a_2$. This concludes the proof of (i).

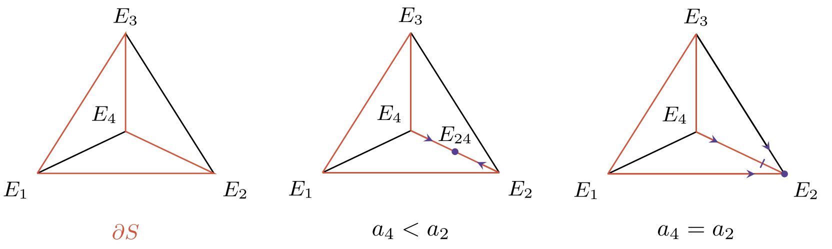

Fig. 6. Under $\operatorname{sgn} c = (-, +, +, -)$, the set ∂S (left panel), the asymptotically stable equilibrium E_{24} (middle panel), and the asymptotically stable equilibrium E_2 (right panel).

Assume from now on that $a_4 \le a_2 < a_1 \le a_3$. As we already mentioned, $c_3 = c_4 = 0$ would imply that $\det J = 0$. Thus, $(c_3, c_4) \ne (0, 0)$.

Next, we prove that $c_3 \le 0$. Assume by contradiction that $c_3 > 0$. Then, by equation (12), $c_4 < 0$. Further, $c_1 < 0$ and $c_2 > 0$ follow immediately, see Fig. 5. Thus, $\operatorname{sgn} c = (-, +, +, -)$, and hence, the set ∂S is the union of the four edges $\mathcal{F}_{12}$, $\mathcal{F}_{24}$, $\mathcal{F}_{43}$, $\mathcal{F}_{31}$, see the left panel in Fig. 6. As can be read from Fig. 5, we have $b_2 < b_4$.

If $a_4 < a_2$ also holds, there exists an equilibrium E_{24} on the edge $\mathcal{F}_{24}$, see the middle panel in Fig. 6. By the equations (27) in Appendix B,

$$\operatorname{sgn} \Gamma^1_{24} = -\operatorname{sgn} c_3 = -1,$$
$$\operatorname{sgn} \Gamma^3_{24} = +\operatorname{sgn} c_1 = -1,$$

i.e., both of the external eigenvalues at E_{24} are negative. Thus, E_{24} is asymptotically stable, contradicting that the flow on S is permanent.

To obtain a contradiction, it is left to show that the flow on S is not permanent when $a_4 = a_2$. The eigenvalues at E_2 in the directions E_1, E_3, and E_4 are negative, negative, and zero, respectively. Further, the flow on the edge $\mathcal{F}_{24}$ goes from E_4 to E_2. See the right panel in Fig. 6.

Therefore, the stable manifold at E_2 is 2-dimensional (and is contained in the facet $\mathcal{F}_{123}$), the center manifold at E_2 is 1-dimensional (and is contained in the edge $\mathcal{F}_{24}$), and since the flow on the edge $\mathcal{F}_{24}$ goes from E_4 to E_2, E_2 is attracting on the center manifold. By the reduction principle (see [10, Theorem 5.2]), E_2 is asymptotically stable in Δ_4, contradicting that the flow on S is permanent. Therefore, we conclude that permanence implies $c_3 \le 0$.

Finally, proving that c_4 is also non-positive can be done in a similar way, but it is more elegant to apply the rotation $\mathbf{r}_2$: it maps the tuple (c_1, c_2, c_3, c_4) to the tuple (c_2, c_1, c_4, c_3). This concludes the proof of (ii). □

The following lemma reveals further connections between the signs of c_1, c_2, c_3, c_4.

Lemma 5.2. *Assume that* $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$, $\det J > 0$, *and* $a_4 \le a_2 < a_1 \le a_3$. *Then*

(i) $c_3 = 0$ *and* $c_4 < 0$ *imply* $c_1 \le 0$ *and* $c_2 > 0$,
(ii) $c_3 < 0$ *and* $c_4 = 0$ *imply* $c_1 > 0$ *and* $c_2 \le 0$.

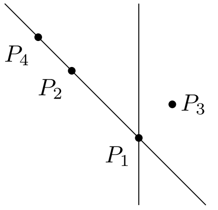

Fig. 7. Illustration of the proof that $c_3 = 0$ and $c_4 < 0$ imply $c_1 \leq 0$ and $c_2 > 0$.

Proof. Under $c_3 = 0$ and $c_4 < 0$, the configuration of the points P_1, P_2, P_3, P_4 is as shown in Fig. 7. Using (5), one immediately obtains $c_1 \leq 0$ (with equality if and only if $a_2 = a_4$ (or, equivalently, $P_2 = P_4$)) and $c_2 > 0$. This concludes the proof of (i).

One can prove (ii) in a similar way. Alternatively, one may apply the rotation $\mathbf{r}_2$, it maps the tuple (c_1, c_2, c_3, c_4) to the tuple (c_2, c_1, c_4, c_3). Thus, the statement (ii) follows from (i). $\square$

By the inequality (11) and Lemmata 5.1 and 5.2, there are only 9 possible sign patterns of c that a permanent ODE (2) with $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$ can lead to, see Fig. 8. See Fig. 9 for the relative positions of the four points P_1, P_2, P_3, P_4 in the 9 cases.

If $\operatorname{sgn} c = (+, +, -, -)$ then the surface S is given by $\frac{x_1^{|c_1|} x_2^{|c_2|}}{x_3^{|c_3|} x_4^{|c_4|}} = 1$ and thus, ∂S consists of the four edges $\mathcal{F}_{14}$, $\mathcal{F}_{42}$, $\mathcal{F}_{23}$, $\mathcal{F}_{31}$. The four points P_1, P_2, P_3, P_4 form a quadrangle with diagonals $P_1 P_2$ and $P_3 P_4$.

If $\operatorname{sgn} c = (+, -, -, -)$ then the surface S is given by $\frac{x_1^{|c_1|}}{x_2^{|c_2|} x_3^{|c_3|} x_4^{|c_4|}} = 1$ and thus, ∂S consists of the three edges $\mathcal{F}_{23}$, $\mathcal{F}_{34}$, $\mathcal{F}_{42}$. The three points P_2, P_3, P_4 form a triangle, and P_1 lies inside.

If $\operatorname{sgn} c = (+, 0, -, -)$ then the surface S is given by $\frac{x_1^{|c_1|}}{x_3^{|c_3|} x_4^{|c_4|}} = 1$ and thus, ∂S consists of the two edges $\mathcal{F}_{42}$, $\mathcal{F}_{23}$ and the curve

$$\mathcal{C}_{34}^1 = \{x \in \Delta_4 \mid x_2 = 0 \text{ and } x_1^{|c_1|} = x_3^{|c_3|} x_4^{|c_4|}\} \subseteq \mathcal{F}_{134},$$

which connects E_3 and E_4. The three points P_2, P_3, P_4 form a triangle, and P_1 lies inside the edge $P_3 P_4$.

If $\operatorname{sgn} c = (-, +, -, -)$ then the surface S is given by $\frac{x_2^{|c_2|}}{x_1^{|c_1|} x_3^{|c_3|} x_4^{|c_4|}} = 1$ and thus, ∂S consists of the three edges $\mathcal{F}_{13}$, $\mathcal{F}_{34}$, $\mathcal{F}_{41}$. The three points P_1, P_3, P_4 form a triangle, and P_2 lies inside.

If $\operatorname{sgn} c = (0, +, -, -)$ then the surface S is given by $\frac{x_2^{|c_2|}}{x_3^{|c_3|} x_4^{|c_4|}} = 1$ and thus, ∂S consists of the two edges $\mathcal{F}_{41}$, $\mathcal{F}_{13}$ and the curve

$$\mathcal{C}_{34}^2 = \{x \in \Delta_4 \mid x_1 = 0 \text{ and } x_2^{|c_2|} = x_3^{|c_3|} x_4^{|c_4|}\} \subseteq \mathcal{F}_{234},$$

which connects E_3 and E_4. The three points P_1, P_3, P_4 form a triangle, and P_2 lies inside the edge $P_3 P_4$.

If $\operatorname{sgn} c = (+, -, -, 0)$ then the surface S is given by $\frac{x_1^{|c_1|}}{x_2^{|c_2|} x_3^{|c_3|}} = 1$ and thus, ∂S consists of the two edges $\mathcal{F}_{34}$, $\mathcal{F}_{42}$ and the curve

$$\mathcal{C}_{23}^1 = \{x \in \Delta_4 \mid x_4 = 0 \text{ and } x_1^{|c_1|} = x_2^{|c_2|} x_3^{|c_3|}\} \subseteq \mathcal{F}_{123},$$

which connects E_2 and E_3. The three points P_2, P_3, P_4 form a triangle, and P_1 lies inside the edge $P_2 P_3$.

If $\operatorname{sgn} c = (+, 0, -, 0)$ then the surface S is given by $x_1 = x_3$, i.e., S is the triangle with vertices E_2, E_4, $E_m = \frac{1}{2} E_1 + \frac{1}{2} E_3$. The three points P_2, P_3, P_4 form a triangle, and P_1 coincides with P_3.

If $\operatorname{sgn} c = (-, +, 0, -)$ then the surface S is given by $\frac{x_2^{|c_2|}}{x_1^{|c_1|} x_4^{|c_4|}} = 1$ and thus, ∂S consists of the two edges $\mathcal{F}_{43}$, $\mathcal{F}_{31}$ and the curve

$$\mathcal{C}_{14}^2 = \{x \in \Delta_4 \mid x_3 = 0 \text{ and } x_2^{|c_2|} = x_1^{|c_1|} x_4^{|c_4|}\} \subseteq \mathcal{F}_{124},$$

which connects E_1 and E_4. The three points P_1, P_3, P_4 form a triangle, and P_2 lies inside the edge $P_1 P_4$.

If $\operatorname{sgn} c = (0, +, 0, -)$ then the surface S is given by $x_2 = x_4$, i.e., S is the triangle with vertices E_1, E_3, $E_m = \frac{1}{2} E_2 + \frac{1}{2} E_4$. The three points P_1, P_3, P_4 form a triangle, and P_2 coincides with P_4.

To prove Theorem 3.4 (C1), our task is to investigate permanence of the ODE (2) under the 9 sign patterns of c listed in Fig. 8. Due to the next lemma, none of the corners of the simplex Δ_4 can attract an orbit from S.

Lemma 5.3. *Assume that* $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$, $\det J > 0$, *and* $a_4 \le a_2 < a_1 \le a_3$. *Consider any of the* 9 *cases in Fig. 8. Then, for each* $i \in \{1, 2, 3, 4\}$, *if* $E_i \in \partial S$, *it cannot attract an orbit from* S.

Proof. If $a_4 < a_2$ then the eigenvalue at E_2 in the direction E_4 is positive. Thus, by Lemma A.2, E_2 cannot attract an orbit from Δ_4°, and hence, from S.

If $a_4 = a_2$ and $E_2 \in \partial S$ then $c_3 < 0$ (see Fig. 8). Since $c_3 = \Delta(142)$ (see (5)), we obtain $b_4 < b_2$ (see the left panel in Fig. 10). The eigenvalues at E_2 in the directions E_1, E_3, and E_4 are negative, negative, and zero, respectively. Since $b_4 < b_2$, the flow on the edge $\mathcal{F}_{24}$ goes from E_2 to E_4. See the right panel in Fig. 10. Therefore, the stable manifold at E_2 is 2-dimensional (and is contained in the facet $\mathcal{F}_{123}$), the center manifold at E_2 is 1-dimensional (and is contained in the edge $\mathcal{F}_{24}$), and since the flow on the edge $\mathcal{F}_{24}$ goes from E_2 to E_4, E_2 is repelling on the center manifold. By the reduction principle (see [10, Theorem 5.2]), E_2 is topologically a saddle in Δ_4, and hence, cannot attract any orbit from the interior of Δ_4. Therefore, we conclude that the statement of the lemma holds for the corner E_2.

By the application of the rotation $\mathbf{r}_2$, we immediately obtain that the statement of the lemma holds also for E_1.

Since $b_3 < b_4$, the eigenvalue at E_3 (respectively, E_4) in the direction E_4 (respectively, E_3) is positive. Thus, by Lemma A.2, none of E_3 and E_4 can attract an orbit from Δ_4°, and hence, from S. □

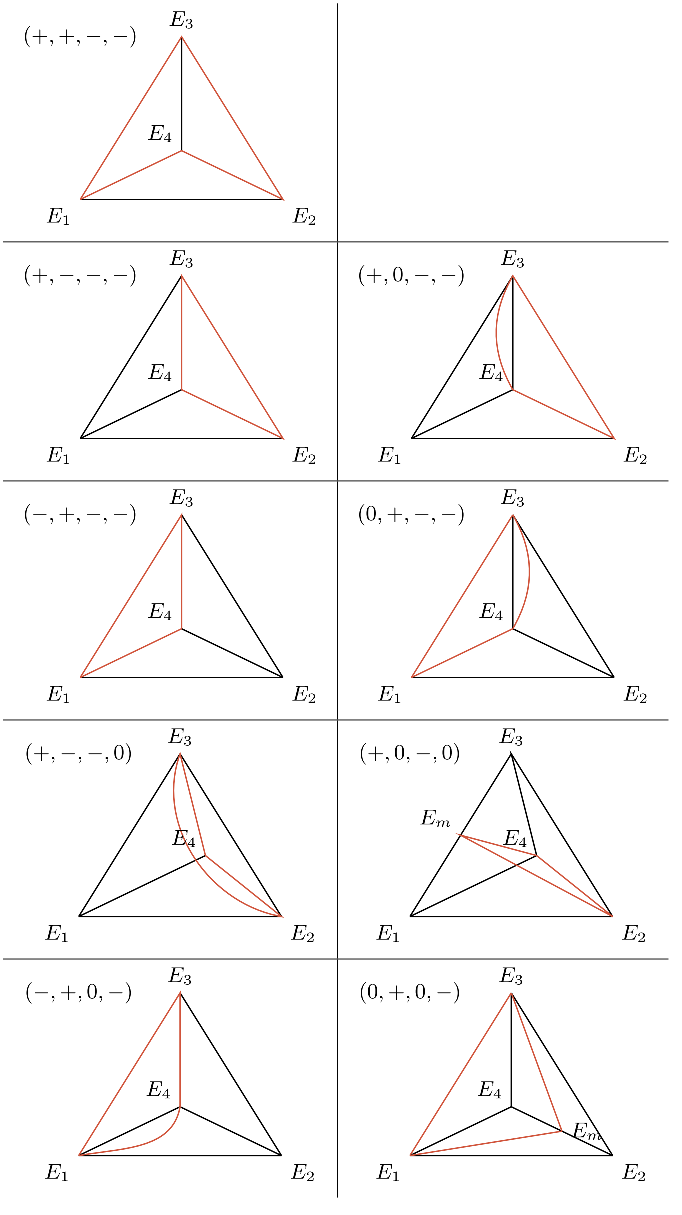

Fig. 8. The 9 sign patterns of c and the corresponding ∂S (red) that a permanent ODE (2) with $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$ can lead to. (For interpretation of the colours in the figure(s), the reader is referred to the web version of this article.)

Next, we describe the behaviour on the facets of the tetrahedron Δ_4. We are especially interested in the behaviour around the edge equilibria E_{12} and E_{34}.

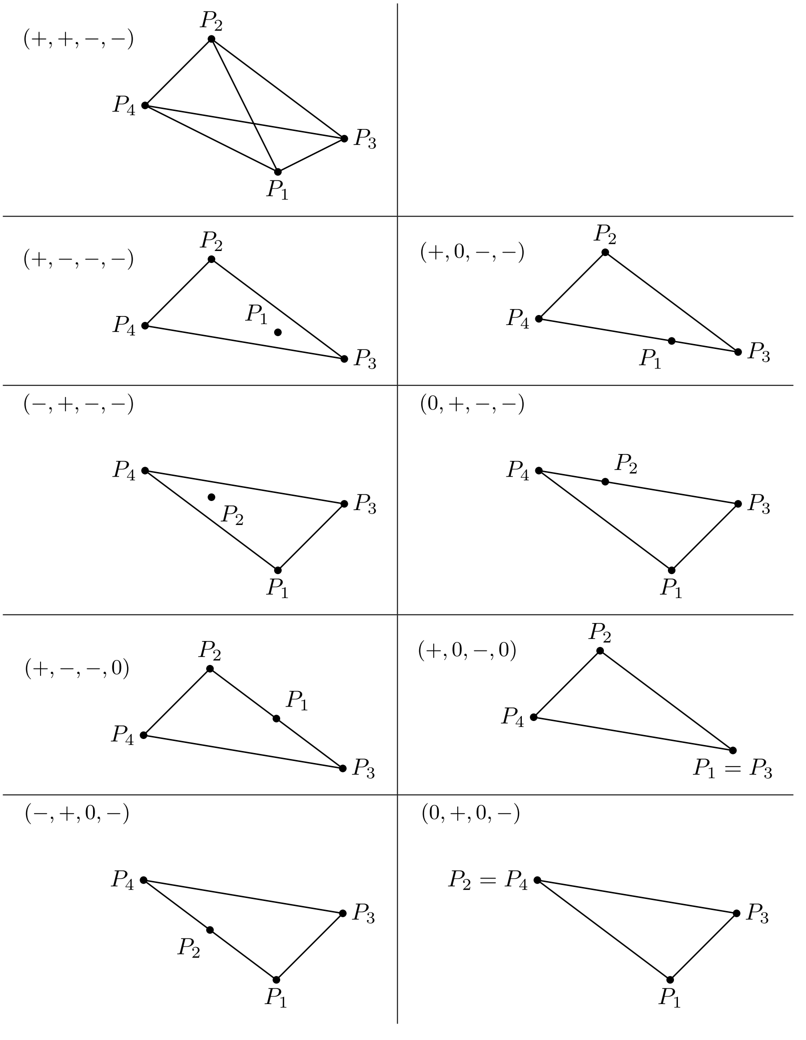

Fig. 9. The 9 sign patterns of c and the corresponding relative positions of the four points P_1, P_2, P_3, P_4 that a permanent ODE (2) with $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$ can lead to.

Lemma 5.4. *The following four statements hold true.*

(i) If $c_1 \neq 0$, there is no equilibrium in the open facet $\mathcal{F}^\circ_{234}$ and there, in a neighbourhood of E_{34}, we have $\operatorname{sgn} \dot{x}_2 = \operatorname{sgn}(-c_1) \operatorname{sgn}(b_4 - b_3)$.

(ii) If $c_2 \neq 0$, there is no equilibrium in the open facet $\mathcal{F}^\circ_{134}$ and there, in a neighbourhood of E_{34}, we have $\operatorname{sgn} \dot{x}_1 = \operatorname{sgn}(-c_2) \operatorname{sgn}(b_4 - b_3)$.

(iii) If $c_3 \neq 0$, there is no equilibrium in the open facet $\mathcal{F}^\circ_{124}$ and there, in a neighbourhood of E_{12}, we have $\operatorname{sgn} \dot{x}_4 = \operatorname{sgn}(+c_3) \operatorname{sgn}(a_2 - a_1)$.

(iv) If $c_4 \neq 0$, there is no equilibrium in the open facet $\mathcal{F}^\circ_{123}$ and there, in a neighbourhood of E_{12}, we have $\operatorname{sgn} \dot{x}_3 = \operatorname{sgn}(+c_4) \operatorname{sgn}(a_2 - a_1)$.

Proof. First, we prove (i). The dynamics on the facet $\mathcal{F}_{234}$ is given by the replicator dynamics with matrix

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

and variable $\widetilde{x} = (x_2, x_3, x_4)$. We claim that the function $V : \mathcal{F}_{234}^{\circ} \to \mathbb{R}$, defined by

$$V(x_2, x_3, x_4) = (b_4 - b_3) \log x_2 + (b_2 - b_4) \log x_3 + (b_3 - b_2) \log x_4,$$

is a Lyapunov function. Indeed,

$$(V(\widetilde{x}))^{\cdot} = (b_4 - b_3)(B\widetilde{x})_2 + (b_2 - b_4)(B\widetilde{x})_3 + (b_3 - b_2)(B\widetilde{x})_4 = x_2(-c_1).$$

Thus, there is no equilibrium in $\mathcal{F}_{234}^{\circ}$, and in a neighbourhood of E_{34} in $\mathcal{F}_{234}^{\circ}$, we have $\operatorname{sgn} \dot{x}_2 = \operatorname{sgn}(-c_1) \operatorname{sgn}(b_4 - b_3)$.

One can prove (ii), (iii), and (iv) in a similar way. However, it is more elegant to say that (ii), (iii), and (iv) follow from (i) by the application of the rotations $\mathbf{r}_2$, $\mathbf{r}_3$, and $\mathbf{r}_1$, respectively. □

Using (among other things) the previous lemma, we now show that none of the edge equilibria can attract an orbit from S.

Lemma 5.5. *Assume that* $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$, $\det J > 0$, *and* $a_4 \leq a_2 < a_1 \leq a_3$. *Consider any of the* 9 *cases in Fig. 8. Then, for each* $i, j \in \{1, 2, 3, 4\}$ *with* $i \neq j$, *if* $\mathcal{F}_{ij} \subseteq \partial S$ *and* E_{ij} *exists, it cannot attract an orbit from* S.

Proof. By Fig. 8, if $\mathcal{F}_{13} \subseteq \partial S$ then $c_2 > 0$ and $c_4 < 0$. Thus, if E_{13} exists, both of the external eigenvalues Γ_{13}^2 and Γ_{13}^4 are positive, see the equations (27). Thus, by Lemma A.2, E_{13} cannot attract an orbit from Δ_4°, and hence, from S.

By Fig. 8, if $\mathcal{F}_{24} \subseteq \partial S$ then $c_1 > 0$ and $c_3 < 0$. Thus, if E_{24} exists, both of the external eigenvalues Γ_{24}^1 and Γ_{24}^3 are positive, see the equations (27). Thus, by Lemma A.2, E_{24} cannot attract an orbit from Δ_4°, and hence, from S. (Alternatively, one could prove the statement for E_{24} by applying the rotation $\mathbf{r}_2$ to the statement for E_{13}.)

By Fig. 8, if $\mathcal{F}_{14} \subseteq \partial S$ then $c_2 > 0$. Since $c_2 = \Delta(134)$ (see (5)), we obtain $b_1 < b_4$ (see the left panel in Fig. 11). Since $a_4 < a_1$ also holds, the flow on $\mathcal{F}_{14}$ goes from E_4 to E_1 and there is no equilibrium in $\mathcal{F}_{14}^{\circ}$.

By Fig. 8, if $\mathcal{F}_{23} \subseteq \partial S$ then $c_1 > 0$. Since $c_1 = \Delta(243)$ (see (5)), we obtain $b_3 < b_2$ (see the right panel in Fig. 11). Since $a_2 < a_3$ also holds, the flow on $\mathcal{F}_{23}$ goes from E_3 to E_2 and there is no equilibrium in $\mathcal{F}_{23}^{\circ}$. (Alternatively, one could prove the non-existence of E_{23} by applying the rotation $\mathbf{r}_2$ to the non-existence of E_{14}.)

The edge $\mathcal{F}_{12}$ is not part of ∂S in any of the 9 cases in Fig. 8.

Assume now that $\mathcal{F}_{34} \subseteq \partial S$. Since $b_4 - b_3 > 0$, the edge equilibrium E_{34} is stable within the edge $\mathcal{F}_{34}$, with eigenvalue $-\frac{b_4 - b_3}{2} < 0$, see Appendix A. Both of the external eigenvalues Γ_{34}^1 and Γ_{34}^2 are zero. This follows from the general formula in Appendix B, but also from the

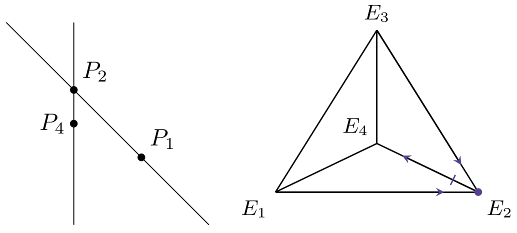

Fig. 10. Illustration of the proof that $a_4 = a_2$ and $c_3 < 0$ imply $b_4 < b_2$ (left panel) and no orbit from the interior of Δ_4 can converge to E_2 (right panel).

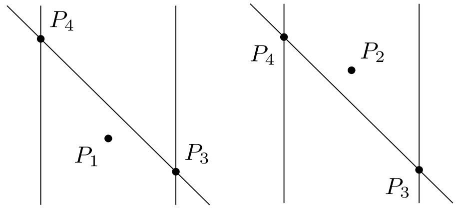

Fig. 11. Illustration of the proof of the facts that $c_2 > 0$ implies $b_1 < b_4$ (left panel) and $c_1 > 0$ implies $b_3 < b_2$ (right panel).

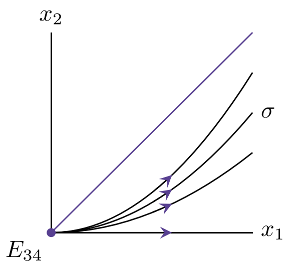

Fig. 12. The flow on the center manifold at E_{34} near $\mathcal{F}_{134}$.

existence of the line of equilibria $\left(\frac{\varepsilon}{2}, \frac{\varepsilon}{2}, \frac{1-\varepsilon}{2}, \frac{1-\varepsilon}{2}\right)$ for $0 \le \varepsilon \le 1$. Therefore, the stable manifold at E_{34} is 1-dimensional (and is contained in the edge $\mathcal{F}_{34}$) and there is a (not necessarily unique) 2-dimensional center manifold through E_{34}, transversal to the edge $\mathcal{F}_{34}$, and containing the equilibria $\left(\frac{\varepsilon}{2}, \frac{\varepsilon}{2}, \frac{1-\varepsilon}{2}, \frac{1-\varepsilon}{2}\right)$ for small $\varepsilon > 0$.

Now assume further that $\operatorname{sgn}(c_1, c_2) = (+, -)$. The invariant surfaces $\{Q = d\}$ can be expressed as $x_2 = \left(d x_1^{-c_1} x_3^{-c_3} x_4^{-c_4}\right)^{\frac{1}{c_2}}$, which is approximately $d' x_1^{-\frac{c_1}{c_2}}$ near E_{34}. Since, by the inequality (11), we have $-\frac{c_1}{c_2} > 1$, the invariant surfaces $\{Q = d\}$ are tangent to the facet $\mathcal{F}_{134}$ at E_{34}. On the facet $\mathcal{F}^\circ_{134}$ near E_{34}, by Lemma 5.4 (ii), we have $\operatorname{sgn} \dot{x}_1 = \operatorname{sgn}(-c_2) \operatorname{sgn}(b_4 - b_3)$, which is positive. The invariant surfaces $\{Q = d\}$ intersect the 2-dimensional center manifold in a family of curves tangent to the facet $\mathcal{F}_{134}$. Then, by continuity, $\dot{x}_1 > 0$ holds on these curves near E_{34} (because the only equilibria in Δ°_4 are on the line segment from E_{12} to E_{34}), in particular, $\dot{x}_1 > 0$ on the intersection σ of S with the center manifold. Hence, the flow on σ moves away from E_{34} (see Fig. 12). Then, by the reduction principle (see [10, Theorem 5.2]), applied to the 2-dimensional flow on $\overline{S}$, E_{34} is topologically a saddle in $\overline{S}$, and hence, does not attract

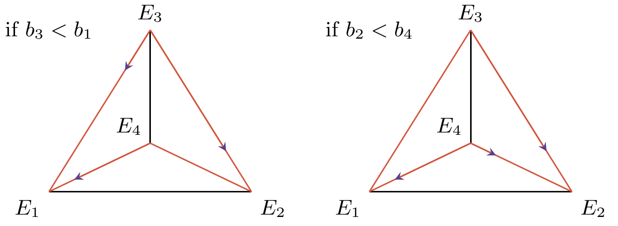

Fig. 13. Under the assumptions of Lemma 5.8, ∂S does not form a heteroclinic cycle.

any orbit from S. To arrive at the same conclusion in case $\mathrm{sgn}(c_1, c_2) = (-, +)$, one can apply the rotation $\mathbf{r}_2$. □

The following theorem is a special case of [5, Theorem 3.1].

Theorem 5.6. *Consider the ODE* (9) *restricted to* $\overline{S}$ *with* $\det J > 0$. *If*

(i) there are only finitely many equilibria in ∂S,
(ii) no equilibrium in ∂S *attracts an orbit from* S, *and*
(iii) ∂S *does not form a heteroclinic cycle (between the equilibria in* ∂S*)*

then the ODE (9) *restricted to* $\overline{S}$ *is permanent.*

The following lemma is obvious.

Lemma 5.7. *Fix* $i, j \in \{1, 2, 3, 4\}$ *with* $i \neq j$. *Then the following two statements hold.*

(i) If $P_i \neq P_j$ *then there is at most one equilibrium in the edge* $\mathcal{F}_{ij}^{\circ}$.
(ii) If $P_i = P_j$ *then* $c_k = 0$ *for all* $k \in \{1, 2, 3, 4\} \setminus \{i, j\}$.

The next lemma covers the case $\mathrm{sgn}\, c = (+, +, -, -)$, i.e., the situation in the 1st row in Fig. 8, the quadrangle case. It is permanent.

Lemma 5.8. *Assume* $\mathrm{sgn}\, J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$, $\det J > 0$, *and that* $a_4 \leq a_2 < a_1 \leq a_3$ *and* $\mathrm{sgn}\, c = (+, +, -, -)$. *Further, assume that at least one of the two inequalities* $b_1 \leq b_3$ *and* $b_4 \leq b_2$ *is violated. Then the ODE* (2) *is permanent.*

Proof. We apply Theorem 5.6. By Lemma 5.7, there are only finitely many equilibria on ∂S. By Lemmata 5.3 and 5.5, no boundary equilibrium attracts an orbit from S. As can be read from Fig. 13, neither in case $b_3 < b_1$ nor in case $b_2 < b_4$ the boundary of ∂S forms a heteroclinic cycle. □

The next lemma covers the cases, where $\mathrm{sgn}\, c$ is one of $(+, -, -, -)$, $(+, 0, -, -)$, $(-, +, -, -)$, $(0, +, -, -)$, i.e., the situations in the 2nd and 3rd rows in Fig. 8. They are all permanent. Lemmata 5.8 and 5.9 together conclude the proof of the fact that $\mathrm{sgn}(c_3, c_4) = (-, -)$ implies permanence, it is the case (C1a) in Theorem 3.4.

Lemma 5.9. *Assume* $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$, $\det J > 0$, *and that* $a_4 \le a_2 < a_1 \le a_3$. *Further, assume that* $\operatorname{sgn}(c_3, c_4) = (-, -)$ *and* $\operatorname{sgn}(c_1, c_2) \neq (+, +)$. *Then the ODE* (2) *is permanent.*

Proof. By the inequality (11) and the assumption $\operatorname{sgn}(c_1, c_2) \neq (+, +)$, $\operatorname{sgn}(c_1, c_2)$ is one of $(+, -)$, $(+, 0)$, $(-, +)$, $(0, +)$.

To prove permanence in case $\operatorname{sgn} c = (+, -, -, -)$, we apply Theorem 5.6. By Lemma 5.7, there are only finitely many equilibria on ∂S. By Lemmata 5.3 and 5.5, no boundary equilibrium attracts an orbit from S. Since there exists an edge equilibrium on ∂S, namely E_{34}, ∂S does not form a heteroclinic cycle.

To prove permanence in case $\operatorname{sgn} c = (-, +, -, -)$, one can argue similarly as in the above paragraph. Alternatively, one may apply the rotation $\mathbf{r}_2$ to the previous case.

Next, we prove permanence in case $\operatorname{sgn} c = (+, 0, -, -)$. Then ∂S consists of the two edges $\mathcal{F}_{42}$, $\mathcal{F}_{23}$ and the curve

$$\mathcal{C}^1_{34} = \{x \in \Delta_4 \mid x_2 = 0 \text{ and } x_1^{|c_1|} = x_3^{|c_3|} x_4^{|c_4|}\} \subseteq \mathcal{F}_{134},$$

which connects E_3 and E_4. Note that $a_1 = a_3$ is not possible, because $c_2 = 0$ and $c_4 \neq 0$. Since $a_4 < a_1 < a_3$ together with $b_3 < b_4$ and $c_2 = 0$ (i.e., the three points P_1, P_3, P_4 lie on a line) imply that $b_3 < b_1 < b_4$, see the left panel in Fig. 14. Thus, the sign of the matrix corresponding to the facet $\mathcal{F}_{134}$ is

$$\begin{pmatrix} 0 & + & + \\ + & 0 & + \\ - & + & 0 \end{pmatrix}.$$

Hence, E_3 is repelling both in the direction of E_1 and of E_4, and, similarly, E_4 is repelling both in the direction of E_1 and of E_3. Thus, the flow on $\mathcal{C}^1_{34}$ goes away both from E_3 and from E_4. Furthermore, there is no equilibrium on $\mathcal{F}_{14}$, the flow goes from E_4 to E_1, and there exists an equilibrium E_{13} on the edge $\mathcal{F}_{13}$. Using $c_2 = 0$, a short calculation shows that there is a line of equilibria connecting E_{13} and E_{34}, and this line intersects $\mathcal{C}^1_{34}$ at a unique equilibrium E^1_{34}. (All equilibria in $\mathcal{F}^\circ_{134}$ lie on this line.) See the right panel in Fig. 14 for the dynamics on the facet $\mathcal{F}_{134}$. The external eigenvalue at E_{13} in the direction E_2 is positive (because $\operatorname{sgn} \Gamma^2_{13} = -\operatorname{sgn} c_4 = +1$), while the external eigenvalue at E_{34} in the direction E_2 is zero, see Appendix B. It is a general fact that the eigenvalue in the direction of E_2 changes linearly from Γ^2_{34} to Γ^2_{13} while travelling on the line of equilibria from E_{34} to E_{13}. Thus, the external eigenvalue at E^1_{34} is positive, and hence, E^1_{34} is not saturated. Therefore, by Lemma A.2, it cannot attract an orbit from Δ°_4, and hence, from S. Permanence in case $\operatorname{sgn} c = (+, 0, -, -)$ then follows immediately from Theorem 5.6.

To prove permanence in case $\operatorname{sgn} c = (0, +, -, -)$, one can argue similarly as in the above paragraph. Alternatively, one may apply the rotation $\mathbf{r}_2$ to the previous case. □

The next lemma covers the cases, where $\operatorname{sgn} c$ is one of $(+, -, -, 0)$ and $(-, +, 0, -)$, i.e., the situations in the left panels in the 4th and 5th rows in Fig. 8. It is the case (C1b) in Theorem 3.4.

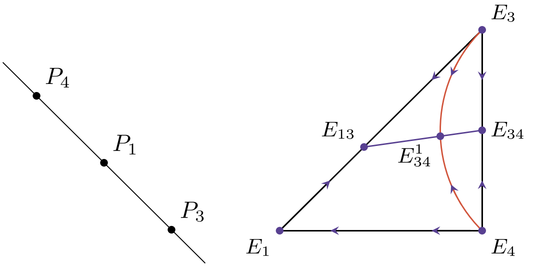

Fig. 14. The relative position of the three points P_1, P_3, P_4 and the behaviour on the facet $\mathcal{F}_{134}$ when $\operatorname{sgn} c = (+, 0, -, -)$ and $a_4 \le a_2 < a_1 \le a_3$.

Lemma 5.10. *Assume* $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$*,* $\det J > 0$*, and that* $a_4 \le a_2 < a_1 \le a_3$ *and either* $\operatorname{sgn} c = (+, -, -, 0)$ *or* $\operatorname{sgn} c = (-, +, 0, -)$*. Then the ODE (2) is permanent if and only if*

$$-\frac{a_1 - a_2}{b_1 - b_2} < \frac{(L+1)^{L+1}}{L^L}, \quad \textit{where } L = \begin{cases} \frac{c_2}{c_3}, & \textit{if } \operatorname{sgn} c = (+, -, -, 0), \\ \frac{c_1}{c_4}, & \textit{if } \operatorname{sgn} c = (-, +, 0, -). \end{cases} \tag{14}$$

Proof. Assume first that $\operatorname{sgn} c = (+, -, -, 0)$. Then ∂S consists of the two edges $\mathcal{F}_{34}$, $\mathcal{F}_{42}$ and the curve

$$\mathcal{C}^1_{23} = \{x \in \Delta_4 \mid x_4 = 0 \text{ and } x_1^{|c_1|} = x_2^{|c_2|} x_3^{|c_3|}\} \subseteq \mathcal{F}_{123},$$

which connects E_2 and E_3. Note that $a_1 = a_3$ is not possible, because $c_4 = 0$ and $c_2 \ne 0$. Since $a_2 < a_1 < a_3$ together with $b_1 < b_2$ and $c_4 = 0$ (i.e., the three points P_1, P_2, P_3 lie on a line) imply that $b_3 < b_1 < b_2$, see the upper left panel in Fig. 15. Thus, the sign of the matrix corresponding to the triangle $\mathcal{F}_{123}$ is

$$\begin{pmatrix} 0 & - & + \\ - & 0 & + \\ + & - & 0 \end{pmatrix}.$$

Hence, E_1 is a saddle, E_2 is an attractor, and E_3 is a repeller. Thus, the flow on $\mathcal{C}^1_{23}$ goes away from E_3 and goes towards E_2. Furthermore, there is no equilibrium on $\mathcal{F}_{23}$, the flow goes from E_3 to E_2, and there exist equilibria E_{13} and E_{12} on the edges $\mathcal{F}_{13}$ and $\mathcal{F}_{12}$, respectively. Using $c_4 = 0$, a short calculation shows that there is a line of equilibria $\mathcal{E}$ connecting E_{12} and E_{13}. (All equilibria in $\mathcal{F}^\circ_{123}$ lie on $\mathcal{E}$.) The line $\mathcal{E}$ intersects $\mathcal{C}^1_{23}$ at either 0, 1, or 2 points. See Fig. 15 for the dynamics on the facet $\mathcal{F}_{123}$ in these three cases.

If the intersection of $\mathcal{E}$ and $\mathcal{C}^1_{23}$ is empty then, by Theorem 5.6, permanence of the ODE (9) follows. On the other hand, if $\mathcal{E}$ and $\mathcal{C}^1_{23}$ intersect each other, say at E^1_{23}, then the system is not permanent. Indeed, in this case the external eigenvalue at E^1_{23} in the direction E_4 is negative, since it is a convex combination of $\Gamma^4_{12} = 0$ and Γ^4_{13}, the latter being negative (because, by (27), $\operatorname{sgn} \Gamma^4_{13} = + \operatorname{sgn} c_2 = -1$). Applying the Stable Manifold Theorem to the flow restricted to $\overline{S}$, there exists at least one orbit in S that converges to E^1_{23}. Thus, the ODE (2) is permanent if and only if $\mathcal{C}^1_{23}$ does not intersect $\mathcal{E}$. The latter is equivalent to

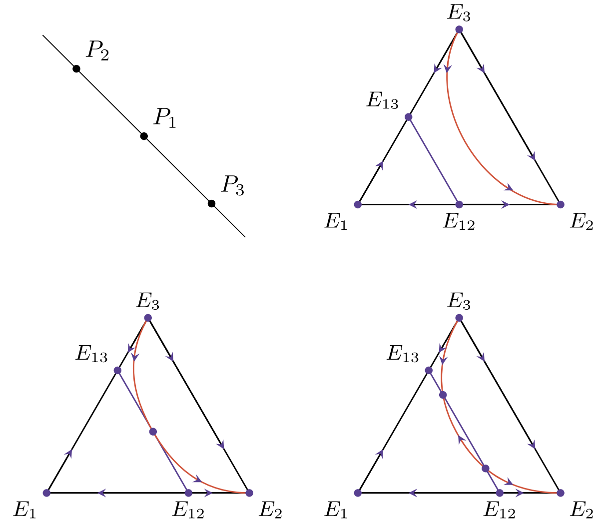

Fig. 15. The relative position of the three points P_1, P_2, P_3 and the three possible behaviours on the facet $\mathcal{F}_{123}$ when $\operatorname{sgn} c = (+, -, -, 0)$ and $a_4 \le a_2 < a_1 \le a_3$.

$$x_1^{c_1} x_2^{c_2} x_3^{c_3} \neq 1 \text{ for all } x \in \mathcal{E},$$

or

$$c_1 \log x_1 + c_2 \log x_2 + c_3 \log x_3 \neq 0 \text{ for all } x \in \mathcal{E}. \tag{15}$$

With $\lambda = \frac{b_1 - b_3}{a_3 - a_1 + b_1 - b_3}$, we have $E_{13} = (\lambda, 0, 1-\lambda, 0)$. Since $E_{12} = \left(\frac{1}{2}, \frac{1}{2}, 0, 0\right)$, the statement (15) is equivalent to $g(\varepsilon) \neq 0$ for all $0 < \varepsilon < 1$, where

$$g(\varepsilon) = c_1 \log\left(\varepsilon\lambda + \frac{1-\varepsilon}{2}\right) + c_2 \log\left(\frac{1-\varepsilon}{2}\right) + c_3 \log\left(\varepsilon(1-\lambda)\right). \tag{16}$$

Since $g(\varepsilon) \to +\infty$ as $\varepsilon \to 0$ or 1, this is equivalent to $g(\varepsilon) > 0$ for all $0 < \varepsilon < 1$. A short calculation shows that g attains its minimum at $\varepsilon^* = \frac{c_3}{c_3 + 2\lambda c_2}$. Note that

$$g(\varepsilon^*) = c_3 \log \frac{1-\lambda}{\lambda} + \log \frac{(-c_2)^{c_2}(-c_3)^{c_3}}{(-c_2 - c_3)^{c_2 + c_3}}.$$

Since $-\frac{a_1 - a_2}{b_1 - b_2} = -\frac{a_1 - a_3}{b_1 - b_3} = \frac{1-\lambda}{\lambda}$, the fact $g(\varepsilon^*)$ is positive is equivalent to the upper case in (14).

To prove the statement in case $\operatorname{sgn} c = (-, +, 0, -)$, one can argue similarly. Alternatively, one may apply the rotation $\mathbf{r}_2$ to the case $\operatorname{sgn} c = (+, -, -, 0)$. $\square$

Note that the function $(0, \infty) \ni L \mapsto \frac{(L+1)^{L+1}}{L^L} \in (1, \infty)$ is monotonically increasing. Since for $\operatorname{sgn} c = (+, -, -, 0)$ (respectively, for $\operatorname{sgn} c = (-, +, 0, -)$), we have $L = \frac{c_2}{c_3} = \frac{\Delta(341)}{\Delta(214)} =$

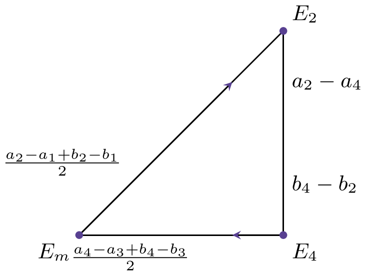

Fig. 16. The flow in the triangle $x_1 = x_3$ in case $P_1 = P_3$.

$\frac{a_1-a_2}{a_3-a_1}$ (respectively, $L = \frac{c_1}{c_4} = \frac{\Delta(243)}{\Delta(123)} = \frac{a_1-a_2}{a_2-a_4}$), the condition (14) holds whenever P_1 (respectively, P_2) is close enough to P_3 (respectively, to P_4). Further, the condition (14) holds whenever the slope of P_1P_2 is at most -1.

The next lemma covers the cases, where $\operatorname{sgn} c$ is one of $(+, 0, -, 0)$ and $(0, +, 0, -)$, i.e., the situations in the right panels in the 4th and 5th rows in Fig. 8. It is the case (C1c) in Theorem 3.4. Once this lemma is proven, it also concludes the proof of Theorem 3.4.

Lemma 5.11. *Assume* $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$, $\det J > 0$, *and that* $a_4 \le a_2 < a_1 \le a_3$ *and* $\operatorname{sgn} c$ *is either* $(+, 0, -, 0)$ *or* $(0, +, 0, -)$. *Then the ODE* (2) *is permanent if and only if* $a_1 - a_2 + b_1 - b_2 \le 0$ *and* $\operatorname{tr} J < 0$.

Proof. We first prove the case $\operatorname{sgn} c = (+, 0, -, 0)$. Note that then $c_1 = -c_3$, $a_1 = a_3$, and $b_1 = b_3$. The surface $\overline{S}$ is thus the triangle $\{x \in \Delta_4 \mid x_1 = x_3\}$. The dynamics on $\overline{S}$ is given by the replicator dynamics for the strategies $\frac{1}{2}E_1 + \frac{1}{2}E_3$, E_2, E_4 with matrix

$$\begin{pmatrix} 0 & a_2 - a_1 & b_4 - b_1 \\ \frac{a_2-a_1+b_2-b_1}{2} & 0 & b_4 - b_2 \\ \frac{a_4-a_3+b_4-b_3}{2} & a_2 - a_4 & 0 \end{pmatrix}. \tag{17}$$

Let $E_m = \frac{1}{2}E_1 + \frac{1}{2}E_3$. See Fig. 16.

We now show that $a_1 - a_2 + b_1 - b_2 > 0$ implies that E_m is asymptotically stable, contradicting permanence. Indeed, a short calculation shows that $a_1 - a_2 + b_1 - b_2 > 0$, $b_1 - b_2 < 0$, $b_3 - b_4 < 0$ and $\det J > 0$ imply that $a_3 - a_4 + b_3 - b_4 > 0$, and hence, both of the eigenvalues at E_m in $\overline{S}$ are negative.

From now on, we assume that $a_1 - a_2 + b_1 - b_2 \le 0$. Thus, there is no equilibrium on the edge $\mathcal{F}_{2m}$ and the flow goes from E_m to E_2. We claim that

$$E_m \text{ does not attract an orbit from } S. \tag{18}$$

Suppose on the contrary that E_m attracts an orbit from S. Then both eigenvalues must be less than or equal to zero. Thus, $a_2 - a_1 + b_2 - b_1 = 0$ and $a_4 - a_3 + b_4 - b_3 \le 0$. As a short calculation shows, $\det J \ne 0$ implies that at least one eigenvalue at E_m is nonzero. Hence, $a_4 - a_3 + b_4 - b_3 < 0$. The center manifold at E_m is thus 1-dimensional (and is contained in $\mathcal{F}_{m2}$). By the reduction principle (see [10, Theorem 5.2]), E_m is topologically a saddle and cannot attract any orbit from S. This contradiction proves the claim (18).

If there exists an equilibrium E_{24} on the edge $\mathcal{F}_{24}$ (i.e., $a_4 < a_2$ and $b_2 < b_4$), it cannot attract any orbit from the interior, see Lemma 5.5. (Note that $P_2 = P_4$ would contradict $c_1 \neq 0$.) Note also that $b_2 < b_4$ implies $\operatorname{tr} J < 0$. Indeed,

$$\operatorname{tr} J = a_1 - a_2 + b_3 - b_4 < a_1 - a_2 + b_1 - b_2 \leq 0.$$

If there exists an equilibrium E_{m4} on the edge $\mathcal{F}_{m4}$ (i.e., $a_4 - a_3 + b_4 - b_3 > 0$), the eigenvalue Γ^2_{m4} in $\overline{S}$, by (26) applied to (17), has the same sign as $-c_3$, and thus, is positive. Therefore, E_{m4} (if it exists at all) cannot attract any orbit from the interior. Note also that $a_4 - a_3 + b_4 - b_3 > 0$ implies $\operatorname{tr} J < 0$. Indeed,

$$\operatorname{tr} J = a_1 - a_2 + b_3 - b_4 < a_1 - a_2 + a_4 - a_3 = a_4 - a_2 < 0.$$

None of E_m, E_2, E_4 can attract an orbit from S (by the claim (18) and Lemma 5.3). By Theorem 5.6, permanence follows if at least one of E_{24} and E_{m4} exists.

It remains to characterize permanence when none of E_{24} and E_{m4} exists. This leads to a heteroclinic cycle along E_m, E_2, E_4, E_m, as in the rock–paper–scissors game. Let us define L_∞ by

$$L_\infty = \frac{a_2 - a_1 + b_2 - b_1}{2}(a_2 - a_4)(b_4 - b_1) + \frac{a_4 - a_3 + b_4 - b_3}{2}(a_2 - a_1)(b_4 - b_2).$$

(Note that L_∞ is the determinant of (17).) With this, if $L_\infty > 0$ then ∂S is repelling (i.e., the ODE (2) is permanent), and if $L_\infty < 0$ then ∂S is attracting (i.e., the ODE (2) is not permanent), see [7, Theorem 3]. A short calculation shows that $L_\infty = -\frac{c_1}{2} \operatorname{tr} J$. If $\operatorname{tr} J = 0$ then the system is not permanent, because we have a global center (see [13, Theorem 6], [2, Theorem 7], [9, Theorem 7.7.2], [8, Exercise 16.5.5(e)]).

To prove the statement in the case $\operatorname{sgn} c = (0, +, 0, -)$ one can argue similarly. However, it is more elegant to apply the rotation $\mathbf{r}_2$ to the case $\operatorname{sgn} c = (+, 0, -, 0)$ (the rotation $\mathbf{r}_2$ leaves both $a_1 - a_2 + b_1 - b_2$ and $\operatorname{tr} J$ invariant). □

We remark that whenever the ODE (2) with the assumptions of Lemma 5.11 is permanent, the origin is globally asymptotically stable. This follows from the classification of the replicator dynamics on the triangle Δ_3, see [13,8,9].

6. Examples

We illustrate some of our results via two examples. The first one is actually a special case of the second one.

6.1. Selkov's glycolytic oscillation

Selkov [12] considered the planar S-system

$$\begin{aligned} \dot{x} &= 1 - xy^\gamma, \\ \dot{y} &= k(xy^\gamma - y) \end{aligned} \tag{19}$$

with $k > 0$ and $\gamma \in \mathbb{R}$ as a model for glycolytic oscillations. One can rewrite it as the ODE (2) with

$$\begin{aligned} a_1 &= -1, & b_1 &= 0, \\ a_2 &= 0, & b_2 &= k\gamma, \\ a_3 &= 1, & b_3 &= k(\gamma-1), \\ a_4 &= 0, & b_4 &= 0. \end{aligned}$$

Then the Jacobian of the ODE (2) at the origin is given by

$$J = \begin{pmatrix} -1 & -k\gamma \\ 1 & k(\gamma-1) \end{pmatrix},$$

while $c = k(\gamma, 1-\gamma, \gamma, -1-\gamma)$. Thus, for $\gamma < 1$ (respectively, for $\gamma = 1$) permanence follows from case (A) (respectively, from case (B2)) in Theorem 3.2. For $\gamma > 1$, the system is not permanent, because based on $\operatorname{sgn} J$ it falls under case (C3) in Theorem 3.4, but $\operatorname{sgn}(c_1, c_2) = (+,-) \notin \{(+,+), (0,+), (+,0)\}$. In the ODE (8), the corner E_4 is asymptotically stable and in the ODE (19), some orbits go to infinity along the x-axis. For $\gamma \le 1 + \frac{1}{k}$, the origin is asymptotically stable, it undergoes a supercritical Andronov–Hopf bifurcation at $\gamma = 1 + \frac{1}{k}$, see [12,1,4]. It is shown that the ODE (19) can have at most one limit cycle and it is an open question, whether this limit cycle disappears in a heteroclinic bifurcation at some value $\widehat{\gamma}(k)$ and for $\gamma > \widehat{\gamma}(k)$ all orbits (except the unique positive equilibrium) escape to infinity, see [4].

6.2. *The Lotka reactions with generalized mass-action kinetics*

Dancsó et al. [6] studied the Lotka reactions with generalized mass-action kinetics. Here we consider the special case

$$\begin{aligned} \dot{x} &= x^\alpha - xy^\beta, \\ \dot{y} &= k(xy^\beta - y) \end{aligned} \tag{20}$$

with $k > 0$ and $\alpha, \beta \in \mathbb{R}$. In [1], we showed that the unique positive equilibrium of the ODE (20) is globally asymptotically stable for all $k > 0$ if and only if

$$\alpha \le 1, \beta \le 1, (\alpha, \beta) \ne (1,1), \text{ and } \alpha\beta > \alpha - 1,$$

while it is globally asymptotically stable for $k = 1$ if and only if either

$$\begin{aligned} &\alpha \le 1, \beta \le 1, (\alpha, \beta) \ne (1,1), \text{ and } \alpha\beta > \alpha - 1 \text{ or} \\ &1 < \alpha \le \frac{3}{2} \text{ and } \alpha - 1 \le \beta \le 2 - \alpha. \end{aligned}$$

Now we characterize permanence for fixed $k > 0$ and $\alpha, \beta \in \mathbb{R}$ (in particular for $k = 1$ and α, $\beta \in \mathbb{R}$). Further, based on this, we characterize those exponents $\alpha, \beta \in \mathbb{R}$ for which permanence holds for all $k > 0$.

One can rewrite the ODE (20) as the ODE (2) with

$$\begin{aligned} a_1 &= \alpha - 1, & b_1 &= 0, \\ a_2 &= 0, & b_2 &= k\beta, \\ a_3 &= 1, & b_3 &= k(\beta - 1), \\ a_4 &= 0, & b_4 &= 0. \end{aligned} \tag{21}$$

Then the Jacobian of the ODE (2) at the origin is given by

$$J = \begin{pmatrix} \alpha - 1 & -k\beta \\ 1 & k(\beta - 1) \end{pmatrix},$$

while $c = k(\beta, (\alpha - 1)(\beta - 1), -(\alpha - 1)\beta, \alpha - 1 - \beta)$.

Proposition 1. *The following three statements hold*

(i) The ODE (2) *with* (21) *is permanent if and only if either*

$$\begin{aligned} &\alpha \le 1, \beta \le 1, (\alpha, \beta) \ne (1, 1), \text{ and } \alpha\beta > \alpha - 1, \\ &1 < \alpha < 2 \text{ and } \alpha - 1 < \beta < 1, \text{ or} \\ &1 < \alpha < 2, \beta = \alpha - 1, \text{ and } k > \beta(1 - \beta)^{\frac{1-\beta}{\beta}}. \end{aligned}$$

(ii) The ODE (2) *with* (21) *is permanent for $k = 1$ if and only if either*

$$\begin{aligned} &\alpha \le 1, \beta \le 1, (\alpha, \beta) \ne (1, 1), \text{ and } \alpha\beta > \alpha - 1 \text{ or} \\ &1 < \alpha < 2 \text{ and } \alpha - 1 \le \beta < 1. \end{aligned}$$

(iii) The ODE (2) *with* (21) *is permanent for all $k > 0$ if and only if either*

$$\begin{aligned} &\alpha \le 1, \beta \le 1, (\alpha, \beta) \ne (1, 1), \text{ and } \alpha\beta > \alpha - 1 \text{ or} \\ &1 < \alpha < 2 \text{ and } \alpha - 1 < \beta < 1. \end{aligned}$$

Proof. Clearly, (ii) and (iii) follow from (i). Thus, it remains to prove (i).

If $\alpha \ge 1$ and $\beta \ge 1$ then there is no negative entry on the diagonal of J, so the system is not permanent, see Theorem 3.2.

If $\alpha \le 1$, $\beta \le 1$, and $(\alpha, \beta) \ne (1, 1)$ then there is no positive entry on the diagonal of J (and at least one diagonal entry is negative), and the system falls under one of the cases (A), (B1), (B2) in Theorem 3.2 (iii). Hence, the system is permanent.

For all other pairs (α, β), the assumptions of Theorem 3.4 hold. If $\alpha < 1$ and $\beta > 1$ then the system falls under case (C3) and is not permanent, because $c_2 < 0$.

If $\alpha > 1$ and $\beta < 1$ then the system falls under case (C1) in Theorem 3.4. To have $\det J > 0$, we need $\beta > 0$. Therefore, $\operatorname{sgn}(c_1, c_2, c_3) = (+, -, -)$. Further, $c_4 \le 0$ if and only if $\beta \ge \alpha - 1$.

When $\beta > \alpha - 1$, the system is permanent as it falls under case (C1a). When $\beta = \alpha - 1$, the system is permanent if and only if $k > \beta(1-\beta)^{\frac{1-\beta}{\beta}}$, see case (C1b). $\square$

We now describe the behaviour in the strip $1 < \alpha < 2$ and $\alpha - 1 < \beta$ under $k = 1$. At the line $\beta = 2 - \alpha$, a supercritical Andronov–Hopf bifurcation occurs, a stable limit cycle appears for β slightly larger than $2 - \alpha$, see [1]. Because of permanence, an asymptotically stable limit cycle must exist for all $2 - \alpha < \beta < 1$. At $\beta = 1$, $\operatorname{sgn} J = \begin{pmatrix} + & - \\ + & 0 \end{pmatrix}$, the divergence is positive, therefore, no closed orbit exists. Since $\operatorname{sgn} c = (+, 0, -, -)$, ∂S consists of the two edges $\mathcal{F}_{32}$, $\mathcal{F}_{24}$ and the curve $\mathcal{C}^1_{43}$, it is a heteroclinic cycle. The equilibrium $(1, 1)$ is a global repeller and the heteroclinic cycle is the global attractor. Therefore, the stable limit cycle for $\beta < 1$ merges with the heteroclinic cycle at $\beta = 1$. For $\beta > 1$, Theorem 3.3 applies, $L_\infty < 0$ (note that one of the outgoing eigenvalues is zero: $b_1 = b_4$, so at E_4 in the direction E_1), and therefore ∂S is strongly attracting. The equilibrium $(1, 1)$ is a global repeller, since the divergence is positive.

7. Three limit cycles

In the papers [6] and [3,2], examples of planar S-systems with one and two limit cycles were constructed around the equilibrium, respectively. Based on the findings of the present paper, we can construct one more limit cycle, one that is created near infinity.

Consider the ODE (2) with

$$\begin{aligned} a_1 &= 0, & b_1 &= 0, \\ a_2 &= -8, & b_2 &= 35, \\ a_3 &= 10, & b_3 &= 20, \\ a_4 &= -20, & b_4 &= 28. \end{aligned} \tag{22}$$

Then $\operatorname{tr} J = 0$ and $\det J > 0$. As in [2, Section 4.3], the first focal value, L_1, is given by

$$L_1 = -\frac{\pi}{8} \frac{(b_3 - b_4)\,[Db_2 - (a_3 - a_4)b_3 b_4]}{b_2 \sqrt{\det J}},$$

where

$$D = a_3 a_4 + a_3 b_4 - a_4 b_3.$$

Then, with the substitutions (22), we have $D = 480$, $L_1 = 0$, and the second focal value, L_2, is positive, according to the formula derived in [2, Section 4.3]. Further, from the definition in case (A) in Theorem 3.3, $L_\infty = 0$ (i.e., we do not know the behaviour near infinity).

Next, we perturb b_2 to a slightly smaller value $35 - \varepsilon$ (with $\varepsilon > 0$ small). As a result,

$$\begin{aligned} &\operatorname{tr} J = 0, \\ &L_1 = -\frac{\pi}{(35-\varepsilon)\sqrt{986}} D\varepsilon < 0, \\ &L_2 > 0 \end{aligned} \tag{23}$$

and

$$L_\infty = -a_2 D\varepsilon > 0. \tag{24}$$

From (23) we get a Bautin bifurcation (see [10, Section 8.3]) near the origin and an unstable limit cycle Γ_1 is created. The origin is now asymptotically stable. From (24), the system is permanent, see Theorem 3.3. Thus for large initial points, the solutions spiral inwards. By the Poincaré–Bendixson theorem, its ω-limit set is nonempty and either contains an equilibrium (which is not possible, since the only equilibrium is the origin and it is surrounded by Γ_1), or is a periodic orbit, call it Γ_∞. This Γ_∞ must surround an equilibrium, i.e., the origin, and must be attracting at least from the outside, so it is different from Γ_1.

Finally, after fixing $\varepsilon > 0$ with the above behaviour, we perturb for example a_2 to $a_2 - \mu$. Then $\mu = \operatorname{tr} J$ and an Andronov–Hopf bifurcation occurs at $\mu = 0$. It is supercritical, since $L_1 < 0$. So for $\mu > 0$, the origin is unstable, and a small stable limit cycle Γ_0 is created.

Thus this system has (at least) two stable limit cycles (if Γ_∞ is repelling towards the interior then there will be some other limit cycle attracting from both sides), and at least one unstable one.

Appendix A. Replicator dynamics

In this section, we collect some general facts about the replicator dynamics, i.e., about the ODE

$$\dot{x}_i = x_i\left[(Ax)_i - x^\mathsf{T} Ax\right] \text{ for } i = 1, \dots, n \tag{25}$$

with (the $n-1$-dimensional) state space $\Delta_n = \{x \in \mathbb{R}^n_{\geq 0} \mid x_1 + \cdots + x_n = 1\}$. We assume (w.l.o.g.) throughout that $a_{ii} = 0$ for all $i = 1, \dots, n$.

For $k \in \{1, \dots, n\}$, we denote by E_k the kth corner of Δ_n, i.e., the vector whose kth coordinate is 1 and all the others are 0. All the corners are equilibria. For $l \neq k$, the eigenvalue at E_k in the direction E_l is a_{lk}.

For $i, j \in \{1, \dots, n\}$ with $i \neq j$, we denote by $\mathcal{F}_{ij}$ the edge $\{x \in \Delta_n \mid x_i + x_j = 1\}$. There exists a unique edge equilibrium E_{ij} in $\mathcal{F}_{ij}$ (strictly between E_i and E_j) if and only if $\operatorname{sgn} a_{ij} = \operatorname{sgn} a_{ji} \neq 0$. If E_{ij} exists, its ith and jth coordinates are given by $\frac{a_{ij}}{a_{ij}+a_{ji}}$ and $\frac{a_{ji}}{a_{ij}+a_{ji}}$, respectively. The internal eigenvalue (within the edge $\mathcal{F}_{ij}$) at E_{ij} is given by $-\frac{a_{ij}a_{ji}}{a_{ij}+a_{ji}}$. For $k \neq i, j$, the external eigenvalue at E_{ij} in the direction E_k is given by

$$\Gamma_{ij}^k = \frac{\dot{x}_k}{x_k}\Big|_{x=E_{ij}} = \frac{a_{ki}a_{ij} + a_{kj}a_{ji} - a_{ij}a_{ji}}{a_{ij} + a_{ji}}, \tag{26}$$

see [8, (20.17)].

Let $\widehat{x} \in \Delta_n$ be an equilibrium of the ODE (25) with support $I \subseteq \{1, \dots, n\}$. Then $(A\widehat{x})_i = \widehat{x}^\mathsf{T} A\widehat{x}$ for $i \in I$ and $\widehat{x}_i = 0$ for $i \notin I$. The equilibrium $\widehat{x}$ is said to be *saturated* if $(A\widehat{x})_i \leq \widehat{x}^\mathsf{T} A\widehat{x}$ for all $i \notin I$. Note that $(A\widehat{x})_i - \widehat{x}^\mathsf{T} A\widehat{x}$ is the external eigenvalue at $\widehat{x}$ in the direction i. Therefore, an equilibrium is saturated if and only if all the external eigenvalues are non-positive. In particular, we have the following lemma.

Lemma A.1. *Consider the ODE (25) with $a_{ii} = 0$ for all $i = 1, \dots, n$. Then the following statements hold.*

- *(i) Every interior equilibrium is saturated.*
- *(ii) The corner E_k is saturated if and only if $a_{ik} \le 0$ for all $i \ne k$.*
- *(iii) If there exists a unique edge equilibrium E_{ij} in the edge $\mathcal{F}_{ij}$, it is saturated if and only if $\Gamma_{ij}^k \le 0$ for all $k \ne i, j$.*

For a proof of the following lemma, see [9, Theorem 7.2.1].

Lemma A.2. *If an interior orbit of the ODE (25) converges to an equilibrium $\widehat{x}$ on the boundary of Δ_n, as $t \to \infty$, then $\widehat{x}$ is saturated.*

Appendix B. The replicator dynamics with matrix (8)

Assuming there exists a unique edge equilibrium E_{ij} on the edge $\mathcal{F}_{ij}$ for the ODE (9) with matrix (8), we compute the corresponding external eigenvalues. The formula (26) gives

$$
\begin{aligned}
&\Gamma_{12}^3 = \Gamma_{12}^4 = \Gamma_{34}^1 = \Gamma_{34}^2 = 0,\\
&\Gamma_{13}^k = \frac{1}{(b_1 - b_3) + (a_3 - a_1)} \cdot \begin{cases} (-c_4), & k = 2,\\ (+c_2), & k = 4, \end{cases}\\
&\Gamma_{23}^k = \frac{1}{(b_2 - b_3) + (a_2 - a_3)} \cdot \begin{cases} (-c_4), & k = 1,\\ (+c_1), & k = 4, \end{cases}\\
&\Gamma_{24}^k = \frac{1}{(b_4 - b_2) + (a_2 - a_4)} \cdot \begin{cases} (-c_3), & k = 1,\\ (+c_1), & k = 3, \end{cases}\\
&\Gamma_{14}^k = \frac{1}{(b_4 - b_1) + (a_4 - a_1)} \cdot \begin{cases} (-c_3), & k = 2,\\ (+c_2), & k = 3, \end{cases}
\end{aligned}
$$

where c_1, c_2, c_3, c_4 are given by the equations (10). Assuming $a_4 \le a_2 < a_1 \le a_3$, we have

$$
\begin{aligned}
\operatorname{sgn}\Gamma_{13}^2 &= -\operatorname{sgn} c_4, & \operatorname{sgn}\Gamma_{13}^4 &= +\operatorname{sgn} c_2,\\
\operatorname{sgn}\Gamma_{23}^1 &= +\operatorname{sgn} c_4, & \operatorname{sgn}\Gamma_{23}^4 &= -\operatorname{sgn} c_1,\\
\operatorname{sgn}\Gamma_{24}^1 &= -\operatorname{sgn} c_3, & \operatorname{sgn}\Gamma_{24}^3 &= +\operatorname{sgn} c_1,\\
\operatorname{sgn}\Gamma_{14}^2 &= +\operatorname{sgn} c_3, & \operatorname{sgn}\Gamma_{14}^3 &= -\operatorname{sgn} c_2.
\end{aligned}
\tag{27}
$$

References

[1] B. Boros, J. Hofbauer, S. Müller, On global stability of the Lotka reactions with generalized mass-action kinetics, Acta Appl. Math. 151 (1) (Oct. 2017) 53–80.
[2] B. Boros, J. Hofbauer, S. Müller, G. Regensburger, Planar S-systems: global stability and the center problem, ArXiv e-prints, arXiv:1707.02104, July 2017, Discrete Contin. Dyn. Syst. Ser. A, in press.
[3] B. Boros, J. Hofbauer, S. Müller, G. Regensburger, The center problem for the Lotka reactions with generalized mass-action kinetics, Qual. Theory Dyn. Syst. 17 (2018) 403–410.
[4] P. Brechmann, A.D. Rendall, Dynamics of the Selkov oscillator, ArXiv e-prints, arXiv:1803.10579 [q-bio.SC], Mar. 2018.
[5] G. Butler, P. Waltman, Persistence in dynamical systems, J. Differential Equations 63 (2) (1986) 255–263.
[6] A. Dancsó, H. Farkas, M. Farkas, G. Szabó, Investigations into a class of generalized two-dimensional Lotka–Volterra schemes, Acta Appl. Math. 23 (2) (1991) 103–127.
[7] J. Hofbauer, A general cooperation theorem for hypercycles, Monatsh. Math. 91 (3) (1981) 233–240.
[8] J. Hofbauer, K. Sigmund, The Theory of Evolution and Dynamical Systems: Mathematical Aspects of Selection, Cambridge University Press, 1988.
[9] J. Hofbauer, K. Sigmund, Evolutionary Games and Population Dynamics, Cambridge University Press, 1998.
[10] Y.A. Kuznetsov, Elements of Applied Bifurcation Theory, third edition, Appl. Math. Sci., vol. 112, Springer-Verlag, New York, 2004.
[11] M.A. Savageau, Biochemical systems analysis: I. Some mathematical properties of the rate law for the component enzymatic reactions, J. Theoret. Biol. 25 (1969) 365–369.
[12] E.E. Sel'kov, Self-oscillations in glycolysis, Eur. J. Biochem. 4 (1) (1968) 79–86.
[13] E.C. Zeeman, Population dynamics from game theory, in: Global theory of dynamical systems, in: Lecture Notes in Math., vol. 819, Springer, Berlin, 1980, pp. 471–497.