ON THE LINEARITY OF REPLICATOR EQUATIONS

NIHAT AY[†*+] AND IONAS ERB[×*]

[†]*SANTA FE INSTITUTE*
1399 HYDE PARK ROAD
SANTA FE, NM 87501 USA

[×]*INTERDISCIPLINARY CENTRE FOR BIOINFORMATICS*
UNIVERSITY OF LEIPZIG
KREUZSTR. 7B
04103 LEIPZIG, GERMANY

[*]*MAX-PLANCK INSTITUTE FOR MATHEMATICS IN THE SCIENCES*
INSELSTR. 22–26
04103 LEIPZIG, GERMANY

[+]*MATHEMATICAL INSTITUTE*
FRIEDRICH-ALEXANDER-UNIVERSITY ERLANGEN-NUREMBERG
BISMARCKSTR. 1
91054 ERLANGEN, GERMANY

Abstract. We show that replicator equations follow naturally from the exponential affine structure of the simplex known from information geometry. It is then natural to call replicator equations linear if their fitness function is affine. For such linear replicator equations an explicit solution can be found. The approach is also demonstrated for the example of Eigen's hypercycle, where some new analytic results are obtained using the explicit solution.

1. Introduction

In mathematical biology, replicator equations play a fundamental role in describing evolutionary game dynamics and population dynamics (see [HS]). These equations are given for the dynamics $t \mapsto \boldsymbol{x}(t)$ on the standard simplex in $\mathbb{R}^n$, where the extremal points correspond to the individual pure strategies or species labelled by $i = 1, 2, \ldots, n$:

$$\dot{x}_i \;=\; x_i \left(f_i(\boldsymbol{x}) - \sum_{j=1}^{n} x_j f_j(\boldsymbol{x}) \right). \tag{1}$$

Date: October 2003, *Emails*: (nay, ierb)@mis.mpg.de.
Key words and phrases. Replicator equation, exponential affine structure, hypercycle system.

For each i, the function f_i describes the *fitness* of i, and x_i measures its relative frequency. In many applications, mainly linear fitness functions are studied. These functions are given by a matrix $A = (a_{i,j})_{1 \leq i,j \leq n}$:

$$f_i(\boldsymbol{x}) \;=\; \sum_{j=1}^{n} a_{i,j}\, x_j. \tag{2}$$

Although this ansatz is intended to give the easiest description, the resulting replicator equation (1) is quadratic, and only in some specified situations complete solutions are known. In this article, we introduce the notion of linearity that is new in the context of replicator dynamics but naturally appears in information geometry (see [AN]). The present approach allows to analyse linear replicator equations with a variety of interesting properties. In particular, the solution curves for such equations can be written down explicitly.
The basic idea has already been pursued in the literature [J, SG]: A logarithmic ansatz instead of (2) leads to a system that is linear in new variables. Let us briefly illustrate this by an easy example. We consider the matrix

$$A = \begin{pmatrix} 0 & -2 & 2 \\ 1 & 1 & -2 \\ -1 & 1 & 0 \end{pmatrix}$$

and, as mentioned, instead of the ansatz (2) we now make the following corresponding logarithmic replicator ansatz

$$\dot{x}_1 \;=\; x_1(-2\ln x_2 + 2\ln x_3 - c) \tag{3}$$

$$\dot{x}_2 \;=\; x_2(\ln x_1 + \ln x_2 - 2\ln x_3 - c) \tag{4}$$

$$\dot{x}_3 \;=\; x_3(-\ln x_1 + \ln x_2 - c), \tag{5}$$

with

$$c \;=\; x_1(-2\ln x_2 + 2\ln x_3) + x_2(\ln x_1 + \ln x_2 - 2\ln x_3) + x_3(-\ln x_1 + \ln x_2).$$

In order to solve this system of differential equations, we define T_3 to be the subspace of $\mathbb{R}^3$ consisting of all vectors whose coordinates sum up to zero and consider the diffeomerphism $T_3 \to S_3$ that maps the coordinates v_1,v_2, and v_3 of a vector in T_3 to the point in the simplex with the coordinates

$$x_i \;=\; \frac{e^{v_i}}{e^{v_1} + e^{v_2} + e^{v_3}}, \qquad i = 1, 2, 3.$$

A straightforward calculation shows that, pulling the vector field that corresponds to the equations (3), (4), and (5) back, we get a vector field on T_3 that corresponds to the following system of linear differential equations:

$$\dot{v}_1 \;=\; -2v_2 + 2v_3, \tag{6}$$

$$\dot{v}_2 \;=\; v_1 + v_2 - 2v_3, \tag{7}$$

$$\dot{v}_3 \;=\; -v_1 + v_2, \tag{8}$$

This system is easy to solve. In figure 1 the phase portrait for such a system is shown. Both the dynamics in the variables $\boldsymbol{v}$ and $\boldsymbol{x}$ are plotted.

This paper is organized as follows: In section 2, the abstract mathematical framework is presented. It is shown how the affine structure of the simplex is defined, in what respect replicator equations can be considered linear ODE's and what their solutions are. In section 3 we consider Eigen's catalytic hypercycle. The knowledge of a complete solution allows for a linear dynamical-systems approach. This leads to simple observations regarding the behaviour of the system in different dimensions.

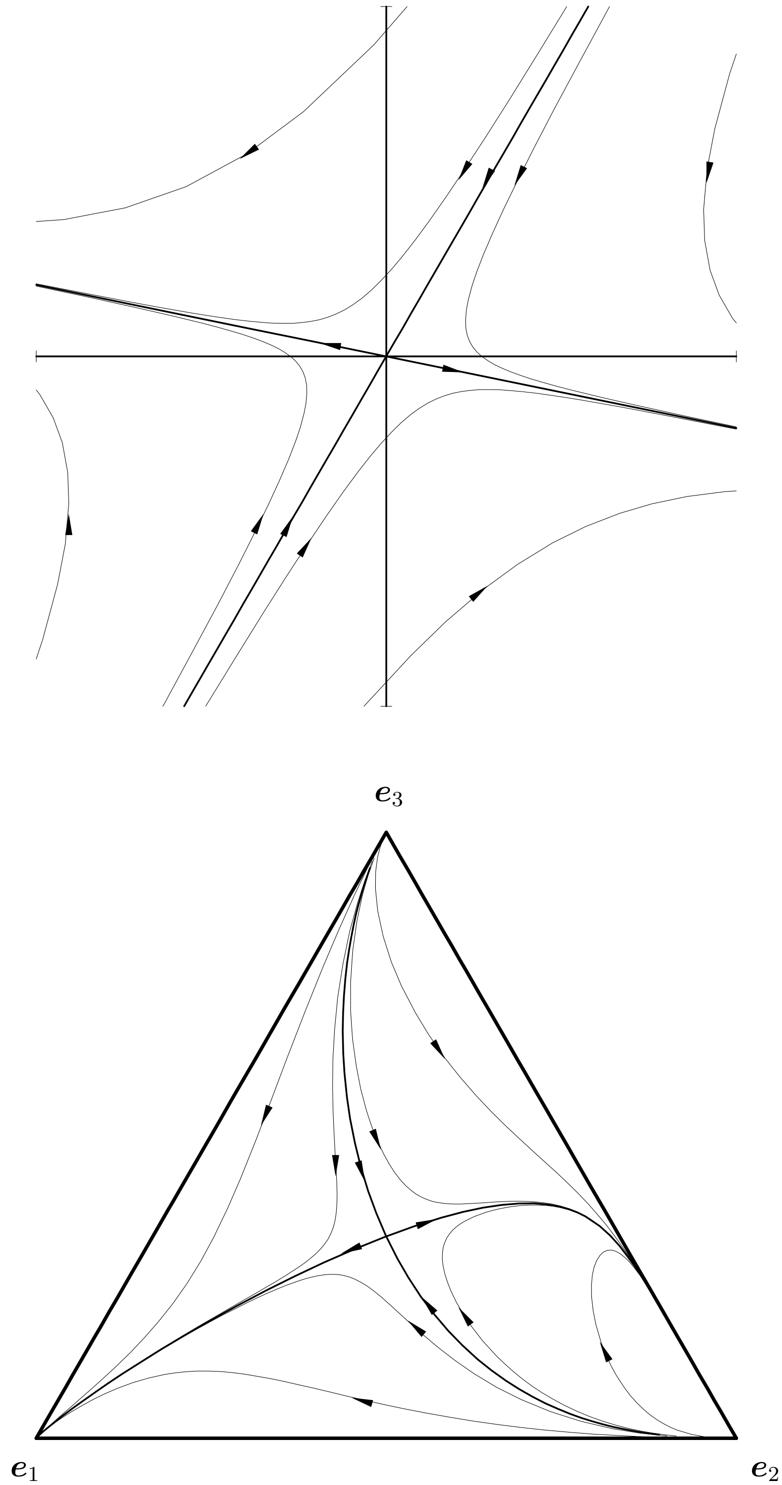

FIGURE 1. Example of dynamics on T_3 and S_3

2. How replicator equations follow from an affine structure

2.1. **The logarithmic linearity.** We consider the elements of $\mathbb{R}^n$ as columns, and the map $\dagger : (x_1, \dots, x_n) \mapsto (x_1, \dots, x_n)^\dagger$ transposes rows into columns. The canonical basis of $\mathbb{R}^n$ is written as $\boldsymbol{e}_i$, $i = 1, \dots, n$. Consider the open simplex $S_n \subset \mathbb{R}^n$,

$$S_n \ := \ \left\{ \boldsymbol{x} = (x_1, \dots, x_n)^\dagger \in \mathbb{R}^n \ : \ x_i > 0 \text{ for all } i, \ \sum_{i=1}^n x_i = 1 \right\},$$

and its tangent space

$$T_n \ := \ \left\{ \boldsymbol{v} = (v_1, \dots, v_n)^\dagger \in \mathbb{R}^n \ : \ \sum_{i=1}^n v_i = 0 \right\}.$$

The exponential map $\exp : S_n \times T_n \to S_n$,

$$(\boldsymbol{x}, \boldsymbol{v}) = ((x_1, \dots, x_n)^\dagger, (v_1, \dots, v_n)^\dagger) \ \mapsto \ \exp(\boldsymbol{x}, \boldsymbol{v}) \ := \ \sum_{i=1}^n \frac{x_i \cdot e^{v_i}}{\sum_{j=1}^n x_j \cdot e^{v_j}} \, \boldsymbol{e}_i,$$

defines an affine structure on S_n. We will also use the restrictions

$$\exp_{\boldsymbol{x}} \ := \ \exp|_{\{\boldsymbol{x}\} \times T_n}, \qquad \boldsymbol{x} \in S_n.$$

For each two points $\boldsymbol{x}$ and $\boldsymbol{y}$, the difference vector that translates $\boldsymbol{x}$ into $\boldsymbol{y}$ is given by

$$\operatorname{vec}(\boldsymbol{x}, \boldsymbol{y}) \ = \ \exp_{\boldsymbol{x}}^{-1}(\boldsymbol{y}) \ = \ \sum_{i=1}^n \left(\ln \frac{y_i}{x_i} \ - \ \frac{1}{n} \sum_{j=1}^n \ln \frac{y_j}{x_j} \right) \boldsymbol{e}_i.$$

Definition 2.1. A map $f : S_n \to \mathbb{R}^n$ is called *affine*, if there is a linear map $f_0 : T_n \to \mathbb{R}^n$

$$f\big(\exp_{\boldsymbol{x}}(\boldsymbol{v})\big) \ = \ f(\boldsymbol{x}) + f_0(\boldsymbol{v}) \qquad\qquad \text{for all } \boldsymbol{x} \in S_n, \, \boldsymbol{v} \in T_n.$$

Here, f_0 is uniquely determined. The set of all affine maps $S_n \to \mathbb{R}^n$ is denoted by $\operatorname{Aff}(S_n, \mathbb{R}^n)$.

Let $\boldsymbol{c}$ denote the point $(\frac{1}{n}, \dots, \frac{1}{n})^\dagger \in S_n$, and let $\operatorname{Lin}(T_n, \mathbb{R}^n)$ denote the set of linear maps $T_n \to \mathbb{R}^n$. There is a one-to-one correspondence between $\operatorname{Aff}(S_n, \mathbb{R}^n)$ and $\mathbb{R}^n \times \operatorname{Lin}(T_n, \mathbb{R}^n)$. For each pair $(\boldsymbol{a}, f_0) \in \mathbb{R}^n \times \operatorname{Lin}(T_n, \mathbb{R}^n)$ we assign the affine map

$$(\boldsymbol{a}, f_0) \ \mapsto \ f := \boldsymbol{a} + f_0\big(\operatorname{vec}(\boldsymbol{c}, \cdot)\big).$$

Extending the linear part f_0 to an endomorphism on $\mathbb{R}^n$ allows to give a matrix representation of f:

$$f \ = \ \boldsymbol{a} + A \operatorname{vec}(\boldsymbol{c}, \cdot), \qquad A \in \mathcal{M}(n, \mathbb{R}). \tag{9}$$

Here, $\mathcal{M}(n,\mathbb{R})$ denotes the set of $(n\times n)$-matrices with real entries. In order to describe this representation more precisely, we consider the inclusion map $\iota : T_n \longrightarrow \mathbb{R}^n$. Its pseudo inverse with respect to the canonical scalar product is given by the orthogonal projection $\pi : \mathbb{R}^n \longrightarrow T_n$ onto T_n. Denoting the set of endomorphisms on $\mathbb{R}^n$ by $\mathrm{End}(\mathbb{R}^n)$, these maps induce

$$\iota^* : \ \mathrm{End}(\mathbb{R}^n) \ \to \ \mathrm{Lin}(T_n,\mathbb{R}^n), \qquad g \mapsto \iota^*(g) := g\circ\iota = g|_{T_n},$$

$$\pi^* : \ \mathrm{Lin}(T_n,\mathbb{R}^n) \ \to \ \mathrm{End}(\mathbb{R}^n), \qquad g \mapsto \pi^*(g) := g\circ\pi.$$

Using the representation ρ of endomorphisms on $\mathbb{R}^n$ by matrices with respect to the canonical basis, we have the following diagram:

$$\mathcal{M}(n,\mathbb{R}) \ \stackrel{\rho}{\longrightarrow} \ \mathrm{End}(\mathbb{R}^n) \ \underset{\stackrel{\longleftarrow}{\pi^*}}{\stackrel{\iota^*}{\longrightarrow}} \ \mathrm{Lin}(T_n,\mathbb{R}^n)$$

Proposition 2.2.
(1) *The kernel of the map $\iota^*\circ\rho$ is given by*

$$\mathcal{V}(T_n) \ = \ \left\{ \begin{pmatrix} b_1 & \cdots & b_1 \\ \vdots & \ddots & \vdots \\ b_n & \cdots & b_n \end{pmatrix} \ : \ b_1,\ldots,b_n \in \mathbb{R} \right\}.$$

Therefore, if a matrix A solves the equation (9), then $A+\mathcal{V}(T_n)$ represents the whole solution set.
(2) *The map $\rho^{-1}\circ\pi^*$ represents the canonical representation of linear maps $T_n \to \mathbb{R}^n$. Its image is given by*

$$\mathcal{V}(T_n^{\perp}) \ = \ \left\{ A = (a_{i,j})_{1\le i,j\le n} \in \mathcal{M}(n,\mathbb{R}) \ : \ \textstyle\sum_{j=1}^n a_{i,j} = 0 \textit{ for all } i \right\}.$$

(3) *We have the orthogonal decomposition*

$$\mathcal{M}(n,\mathbb{R}) \ = \ \mathcal{V}(T_n^{\perp}) \oplus \mathcal{V}(T_n),$$

and the projection onto $\mathcal{V}(T_n^{\perp})$ along $\mathcal{V}(T_n)$ is given by

$$\begin{pmatrix} a_{1,1} & \cdots & a_{1,n} \\ \vdots & \ddots & \vdots \\ a_{n,1} & \cdots & a_{n,n} \end{pmatrix} \ \mapsto \ \begin{pmatrix} a_{1,1} - \frac{1}{n}\sum_{j=1}^n a_{1,j} & \cdots & a_{1,n} - \frac{1}{n}\sum_{j=1}^n a_{1,j} \\ \vdots & \ddots & \vdots \\ a_{n,1} - \frac{1}{n}\sum_{j=1}^n a_{n,j} & \cdots & a_{n,n} - \frac{1}{n}\sum_{j=1}^n a_{n,j} \end{pmatrix}.$$

2.2. **The logarithmic derivative and replicator equations.** In this article, a curve $t \mapsto \boldsymbol{x}(t)$ in S_n is called $(*)$-differentiable in t_0 if the limit of

$$\frac{1}{t-t_0}\,\mathrm{vec}(\boldsymbol{x}(t_0), \boldsymbol{x}(t))$$

exists for $t \to t_0$. In that case, the limit $\frac{d^*\boldsymbol{x}}{dt}(t_0)$ is called the $(*)$-derivative of $t \to \boldsymbol{x}(t)$ in t_0. For the derivative that is induced by the additive affine structure of $\mathbb{R}^n$ we use the usual notations $\frac{d\boldsymbol{x}}{dt}(t_0)$ or $\dot{\boldsymbol{x}}(t_0)$. We have the following relation between these two notions of differentiation:

Proposition 2.3. *A curve $t \mapsto \boldsymbol{x}(t)$ in S_n is $(*)$-differentiable if and only if it is differentiable. Furthermore, the following relation holds:*

$$\frac{d^*\boldsymbol{x}}{dt} \;=\; \sum_{i=1}^{n}\left(\frac{1}{x_i}\frac{dx_i}{dt} \;-\; \frac{1}{n}\sum_{j=1}^{n}\frac{1}{x_j}\frac{dx_j}{dt}\right)\boldsymbol{e}_i. \tag{10}$$

Consider a vector field $f : S_n \to T_n$, which assigns to each point $\boldsymbol{x}$ of the simplex S_n a vector of the tangent space T_n. We are interested in solution curves $t \mapsto \boldsymbol{x}(t)$ of the ordinary differential equation

$$\frac{d^*\boldsymbol{x}}{dt} \;=\; f\circ\boldsymbol{x}. \tag{11}$$

Proposition 2.3 implies the following statement:

Proposition 2.4. *Let $f : S_n \to T_n$ be a differentiable vector field. Then a differentiable curve $t \mapsto \boldsymbol{x}(t)$ is a solution of the equation (11) if and only if $t \to \boldsymbol{v}(t) := \exp_{\boldsymbol{c}}^{-1}\big(\boldsymbol{x}(t)\big)$ solves the equation*

$$\dot{\boldsymbol{v}} \;=\; f\circ\exp_{\boldsymbol{c}}\circ\,\boldsymbol{v}.$$

Definition 2.5. Given a map $f : S_n \to \mathbb{R}^n$, $\boldsymbol{x} \mapsto f(\boldsymbol{x}) = (f_1(\boldsymbol{x}), \ldots, f_n(\boldsymbol{x}))^\dagger$, the equation

$$\dot{x}_i \;=\; x_i\left(f_i(\boldsymbol{x}) \;-\; \sum_{j=1}^{n} x_j f_j(\boldsymbol{x})\right), \qquad i = 1, \ldots, n, \tag{12}$$

is called *replicator equation*. The replicator equation (12) is called *linear* if f is affine in the sense of definition 2.1.

The following theorem establishes a relation between the equation (11) and the corresponding replicator equation.

Theorem 2.6. *Let $f : S_n \to T_n$ be a differentiable map. A differentiable curve $t \mapsto \boldsymbol{x}(t) = (x_1(t), \ldots, x_n(t))^\dagger$ in S_n is a solution of the equation (11) if and only if it solves the corresponding replicator equation (12).*

Theorem 2.6 allows to interpret replicator equations as ordinary differential equations with respect to the $(*)$-affine structure. But this correspondence is not one-to-one. Obviously, the replicator equation (12) does not change if we replace f by $f + g$, where g is a map $S_n \to T_n^\perp$. We choose the natural representative of f

$$f^c : \;\; S_n \;\to\; T_n, \qquad \boldsymbol{x} \;\mapsto\; f^c(\boldsymbol{x}) := \sum_{i=1}^{n} \left(f_i(\boldsymbol{x}) - \frac{1}{n} \sum_{j=1}^{n} f_j(\boldsymbol{x}) \right) \boldsymbol{e_i}.$$

Then, according to Theorem 2.6, the replicator equation (12), which is induced by a map f with values in $\mathbb{R}^n$, is equivalent to

$$\frac{d^* \boldsymbol{x}}{dt} \;=\; f^c \circ \boldsymbol{x}.$$

In the following, we consider linear replicator equations. In that case $f \in \mathrm{Aff}(S_n, \mathbb{R}^n)$, and f has a unique representation

$$f \;=\; \boldsymbol{a} + f_0\big(\mathrm{vec}(\boldsymbol{c}, \cdot)\big),$$

where $\boldsymbol{a} \in \mathbb{R}^n$ and $f_0 \in \mathrm{Lin}(T_n, \mathbb{R}^n)$. One easily sees

$$f^c \;=\; \pi(\boldsymbol{a}) + (\pi \circ f_0)\big(\mathrm{vec}(\boldsymbol{c}, \cdot)\big).$$

If we start with a matrix representation of the linear part of f,

$$f_0(\boldsymbol{v}) \;=\; A\,\boldsymbol{v} \qquad \text{for all } \boldsymbol{v} \in T_n,$$

$$A \;=\; \begin{pmatrix} a_{1,1} & \cdots & a_{1,n} \\ \vdots & \ddots & \vdots \\ a_{n,1} & \cdots & a_{n,n} \end{pmatrix},$$

then $(\pi \circ f_0)(\boldsymbol{v}) = A^c \boldsymbol{v}$, where A^c is given by

$$A^c \;:=\; \begin{pmatrix} a_{1,1} - \frac{1}{n}\sum_{i=1}^n a_{i,1} & \cdots & a_{1,n} - \frac{1}{n}\sum_{i=1}^n a_{i,n} \\ \vdots & \ddots & \vdots \\ a_{n,1} - \frac{1}{n}\sum_{i=1}^n a_{i,1} & \cdots & a_{n,n} - \frac{1}{n}\sum_{i=1}^n a_{i,n} \end{pmatrix}.$$

Thus, in addition to the freedom of choice stated in Proposition 2.2 (1), we have further possibilities in describing the same dynamics, namely due to the replacement of A by A^c.

The following theorem summarizes our results on our notion of linear replicator equations:

Theorem 2.7. *Let $\boldsymbol{a} \in \mathbb{R}^n$ and $A \in \mathcal{M}(n, \mathbb{R})$, and consider the affine map*

$$f: \; S_n \;\to\; \mathbb{R}^n, \qquad \boldsymbol{x} \;\mapsto\; f(\boldsymbol{x}) := \boldsymbol{a} + A\,\mathrm{vec}(\boldsymbol{c}, \boldsymbol{x}).$$

Then the corresponding linear replicator equation is given by

(13)

$$\dot{x}_i \;=\; x_i \left(a_i + \sum_{j=1}^{n} a_{i,j} \ln \frac{x_j}{(x_1 \cdots x_n)^{\frac{1}{n}}} \;-\; \sum_{k=1}^{n} x_k \left(a_k + \sum_{j=1}^{n} a_{k,j} \ln \frac{x_j}{(x_1 \cdots x_n)^{\frac{1}{n}}} \right) \right).$$

A differentiable curve $t \mapsto \boldsymbol{x}(t) = (x_1(t), \ldots, x_n(t))^\dagger$ in S_n is a solution of the equation (13) if and only if $t \to \boldsymbol{v}(t) := \exp_{\boldsymbol{c}}^{-1}\big(\boldsymbol{x}(t)\big)$ solves the equation

$$\dot{\boldsymbol{v}} \;=\; \pi(\boldsymbol{a}) + A^c\, \boldsymbol{v}.$$

For the initial condition $\boldsymbol{v}(0) = \boldsymbol{v}_0 \in T_n$, we get the following solution for the replicator equation (13):

$$\boldsymbol{x}(t) \;=\; \exp_{\boldsymbol{c}}\big(\boldsymbol{v}(t)\big),$$

$$\boldsymbol{v}(t) \;=\; e^{tA^c} \boldsymbol{v}_0 + \int_0^t e^{(t-\tau)A^c}\, \pi(\boldsymbol{a})\, d\tau. \tag{14}$$

Thus to solve the replicator equation, we only have to find the solution $\boldsymbol{v}(t)$ for the linear system. We identify A^c with a complex matrix that has entries with vanishing imaginary part. Particularly easy to solve are systems where we can find a basis of $\mathbb{C}^n$ that puts the matrix A^c in diagonal form, i.e. where we can find linearly independent eigenvectors. If $\lambda_k = \alpha_k + i\beta_k$ is a complex eigenvalue to eigenvector $\boldsymbol{v}^k = \boldsymbol{u}^k + i\boldsymbol{w}^k$, so is $\bar{\lambda}_k = \alpha_k - i\beta_k$ to eigenvector $\bar{\boldsymbol{v}}^k = \boldsymbol{u}^k - i\boldsymbol{w}^k$ (since A^c has real entries). Notice that by definition A^c has the eigenvector $\mathbf{1}$ to eigenvalue 0. We have the following implications of Theorem 2.7 for homogeneous systems where A^c can be diagonalized:

Corollary 2.8. *Let $\boldsymbol{a} = \mathbf{0}$ and let A^c be such that it can be diagonalized in $\mathbb{C}^n$. We denote eigenvectors of A^c by $\mathbf{1}, \boldsymbol{v}^1, \ldots, \boldsymbol{v}^{n-1}$, their eigenvalues by 0, λ_1, $\ldots$, λ_{n-1}. Then there exist C_k following from the initial condition $\boldsymbol{v}^k(0)$ such that the (real) solution on T_n is given by*

$$\boldsymbol{v}(t) = \sum_{k=1}^{n-1} \boldsymbol{v}^k(t).$$

In case of a real eigenvalue λ_k,

$$\boldsymbol{v}^k(t) = C_k e^{\lambda_k t} \boldsymbol{v}^k.$$

In case of an eigenvalue $\lambda_k = \alpha_k + i\beta_k$ *with* $\beta_k \neq 0$ *to eigenvector* $\boldsymbol{v}^k = \boldsymbol{u}^k + i\boldsymbol{w}^k$,

$$\boldsymbol{v}^k(t) = C_k e^{\alpha_k t} \left(\cos(\beta_k t)\boldsymbol{u}^k + \sin(\beta_k t)\boldsymbol{w}^k\right).$$

Theorem 2.7 and its Corollary 2.8 make the intuitive idea that is sketched in the introduction more precise. In a complete classification of the generic cases for linear (and homogeneous) systems in the two-dimensional simplex, the corollary covers all cases except the one with one-dimensional eigenspace. The classification (analogous to the one in [Br]) is shown in figure 2. By generic we mean that eigenvectors do not have equal components and thus their coordinate lines end in corners of the simplex. For a description of the dynamics for the original ansatz (2) see [St].

$\lambda_1 < \lambda_2 < 0$

left: coordinate lines ending in different corners

right: coordinate lines ending in the same corners

$\lambda_1 < 0 < \lambda_2$

left: coordinate lines ending in different corners

right: coordinate lines ending in the same corners

$\lambda_1 = \lambda_2 \neq 0$

left: 2-dim eigenspace

right: 1-dim eigenspace

$\lambda_{1,2} = \alpha \pm i\beta$

left: $\alpha \neq 0$

right: $\alpha = 0$

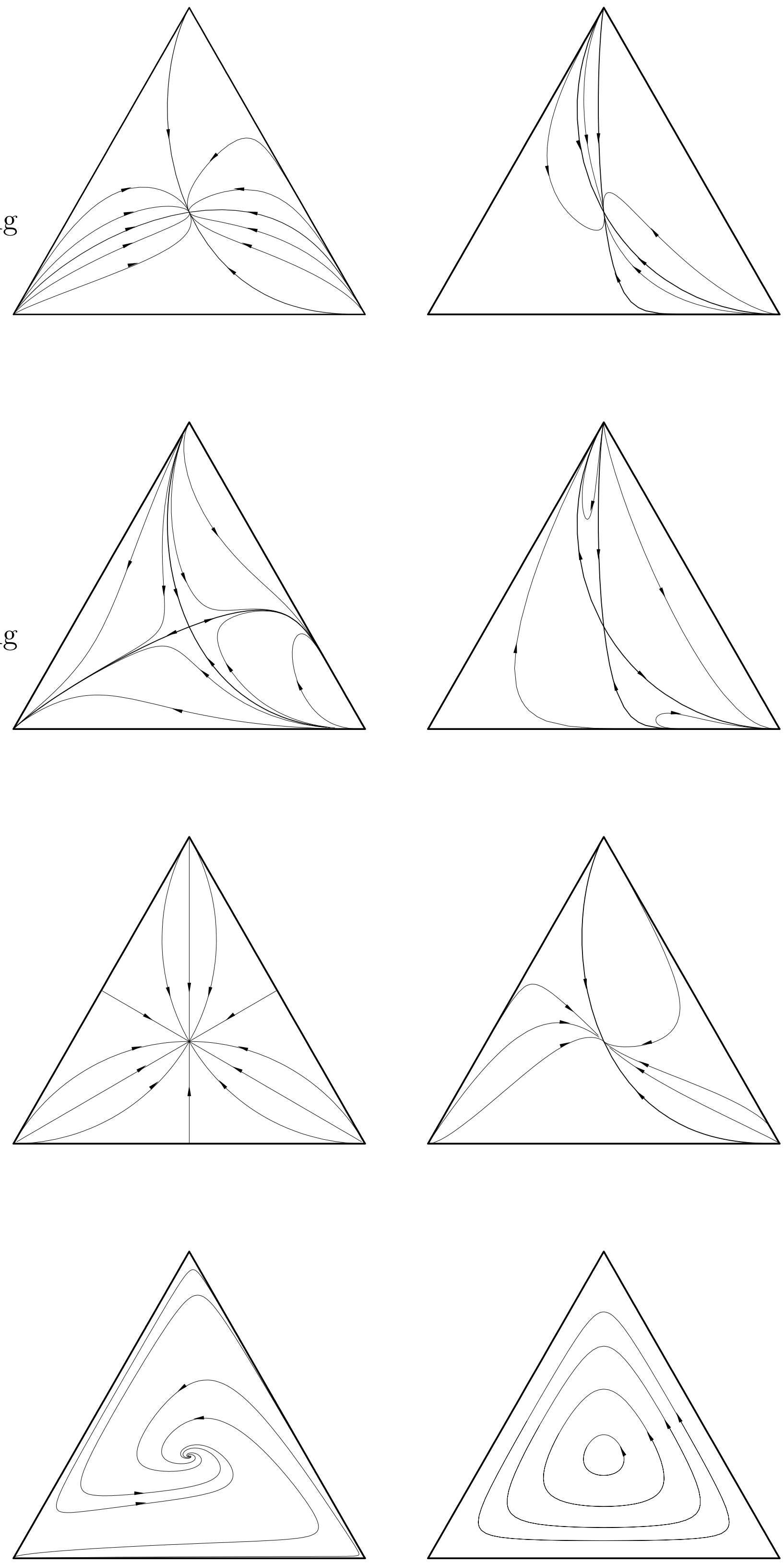

FIGURE 2. Generic phase portraits for S_3

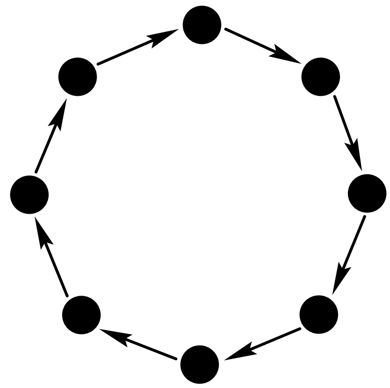

FIGURE 3. A hypercycle of eight species

3. HYPERCYCLE EQUATIONS

In the following we will present some results for a model example that follow immediately from our approach. They are only intended to demonstrate the way analytic results can be obtained and are certainly not all one can do (see also [J, Ar]). For a more general approach to the hypercycle see [HMS].

3.1. **Our approach to the hypercycle.**

Eigen's self-reproductive catalytic hypercycle [Ei] is a system of n species where each catalyses the existence of the consecutive species until the cycle is closed. Figure 3 shows the graph of this kind of interaction for eight species. The matrix representation of the hypercycle is given by

$$A = \begin{pmatrix} 0 & 0 & 0 & \cdots & 0 & 1 \\ 1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 1 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 1 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 1 & 0 \end{pmatrix}$$

In [HS], this matrix leads to the following replicator equation:

$$\dot{x}_i \;=\; x_i \left(x_{i-1} - \sum_{k=1}^{n} x_k \, x_{k-1} \right), \tag{15}$$

where the indices are counted mod n: $x_0 := x_n$. Although the qualitative aspects of this dynamical system are well understood (see [HS]), it is generally not possible to provide an explicit formula for the corresponding solution curves. Using (13) in our Theorem 2.7, the matrix A and $\boldsymbol{a} := \mathbf{0}$ lead to the following alternative replicator equation:

$$\dot{x}_i \;=\; x_i\left(\ln x_{i-1} - \sum_{k=1}^{n} x_k \ln x_{k-1}\right). \tag{16}$$

A similar solvable model is already being used in [J]. In the following, we will show that the qualitative aspects of this ansatz remain close to the original model (15). Based on the fact that our equations are explicitly solvable, we will provide further analytical results. These are obtained using the centred version of A, the matrix A^c. We obtain it by replacing the 0 entries of A by $-1/n$ and the 1 entries by $(n-1)/n$. Eigenvalues and eigenvectors of matrices with a cyclic permutation of the rows are easily obtained [HS]:

Lemma. *An $n\times n$ matrix whose entries in the first row are $c_0,\dots c_{n-1}$ and whose following rows are cyclically permuted by a shift to the right has eigenvalues and eigenvectors given by*

$$\lambda_k = \sum_{j=0}^{n-1} c_j\gamma^{kj}, \quad \boldsymbol{v}^k = (1,\gamma^k,\gamma^{2k},\dots\gamma^{(n-1)k})^\dagger, \quad k=0,\dots n-1, \tag{17}$$

where the shorthand $\gamma := e^{i2\pi/n}$ is used.

Eigenvalues and eigenvectors of A^c (see equation (23) in the appendix) together with Corollary 2.8 now lead to a complete solution of (16):

Proposition 3.1. *We set $\varphi_k := \frac{2\pi}{n}k$, $\alpha_k := \cos\varphi_k$ and $\beta_k := \sin\varphi_k$, where $k=1,\dots,n-1$. The explicit solution for the hypercycle model (16) is then given by $\boldsymbol{x}(t) \;=\; \exp_{\boldsymbol{c}}(\boldsymbol{v}(t))$, where*

$$\boldsymbol{v}(t) \;=\; \sum_{i=1}^{n}\sum_{k=1}^{\lfloor\frac{n}{2}\rfloor} e^{\alpha_k t}\big(C_k\sin(\beta_k t+\varphi_k(i-1)) + C_{n-k}\cos(\beta_k t+\varphi_k(i-1))\big)\boldsymbol{e}_i.$$

Here, the C_k are real numbers following from the initial-condition vector $\boldsymbol{v}(0)$ on T_n, and $\lfloor r\rfloor$ stands for the largest integer smaller than or equal to a given real number r.

Let us now consider some special cases in lower dimensions.
n=2: T_2 is spanned by the eigenvector $(1,-1)^\dagger$ belonging to the eigenvalue -1. This will be called the stable eigenspace in Proposition 3.2 below. The solution on the simplex S_2 is $\boldsymbol{x}(t)=\exp(\boldsymbol{v}(t))$. Using Proposition 3.1, for $\boldsymbol{v}(t)$ we find

$$\boldsymbol{v}(t) = C_1 e^{-t}\begin{pmatrix}1\\-1\end{pmatrix}. \tag{18}$$

Letting t go to infinity, we reach $(0,0)^\dagger$, which is mapped by $\exp_{\boldsymbol{c}}$ to $(1/2, 1/2)^\dagger$, the centre of the simplex. This is the stable restpoint of the dynamics.
n=3: T_3 is spanned by two eigenvectors belonging to eigenvalues with negative real part (stable eigenspace). The solution on T_3 is

$$\boldsymbol{v}(t) = e^{-t/2} \begin{pmatrix} C_1 \sin \frac{\sqrt{3}}{2}t + C_2 \cos \frac{\sqrt{3}}{2}t \\ C_1 \sin\left(\frac{\sqrt{3}}{2}t + \frac{2\pi}{3}\right) + C_2 \cos\left(\frac{\sqrt{3}}{2}t + \frac{2\pi}{3}\right) \\ C_1 \sin\left(\frac{\sqrt{3}}{2}t + \frac{4\pi}{3}\right) + C_2 \cos\left(\frac{\sqrt{3}}{2}t + \frac{4\pi}{3}\right) \end{pmatrix}. \tag{19}$$

Because of the exponentially decreasing prefactor, $\boldsymbol{v}(t)$ will again go to $\mathbf{0}$ as $t \to \infty$. Solution curves are spirals towards the origin. On the simplex S_3, the centre is again a stable rest point (see figure 4).

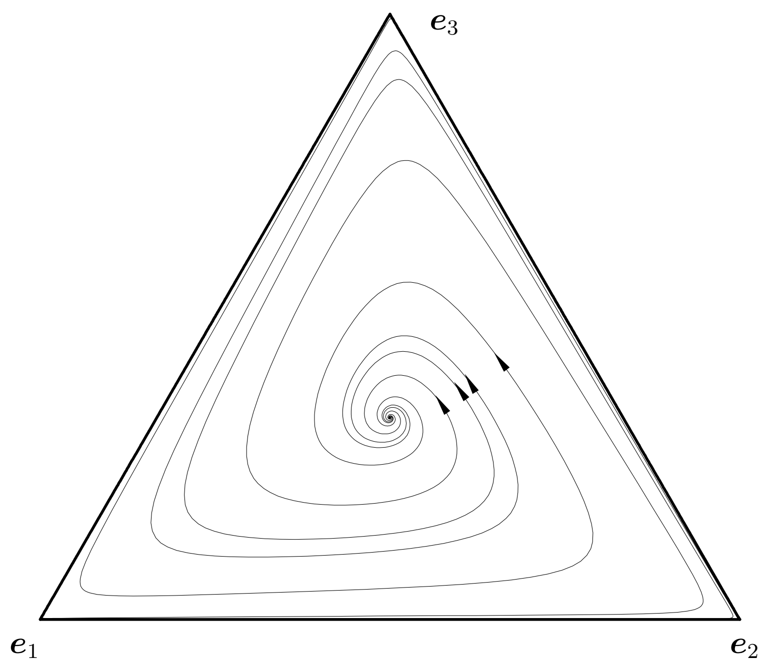

FIGURE 4. The hypercycle dynamics on S_3

Whether the spiraling is clockwise or anticlockwise is determined by the direction of the hypercycle: $(A^c)^\dagger$ models the hypercycle in opposite direction. The transformed matrix has the same eigenvectors but with λ_1 and λ_2 swapped.
n=4: T_4 is spanned by an eigenvector belonging to eigenvalue -1 (stable eigenspace) and two eigenvectors belonging to eigenvalues with vanishing real part. These two span the centre eigenspace defined in Proposition 3.1 below. The solution on

T_4 is

$$\boldsymbol{v}(t) = \begin{pmatrix} C_1 \sin t + C_3 \cos t + C_2 e^{-t} \\ C_1 \cos t - C_3 \sin t - C_2 e^{-t} \\ -C_1 \sin t - C_3 \cos t + C_2 e^{-t} \\ -C_1 \cos t + C_3 \sin t - C_2 e^{-t} \end{pmatrix}. \tag{20}$$

One can see that certain sums of components, namely $v_1(t)+v_3(t)$ and $v_2(t)+v_4(t)$, tend to zero for $t \to \infty$. This asymptotic behaviour translates via the exponential map to $x_1(t)x_3(t) = x_2(t)x_4(t)$ for $\boldsymbol{x}(t)$. Points fulfilling this condition form a saddle surface in the simplex (which is called Wright manifold in a different context [HS]). The asymptotic behaviour of the solutions is described by closed curves on this surface (see figure 5).

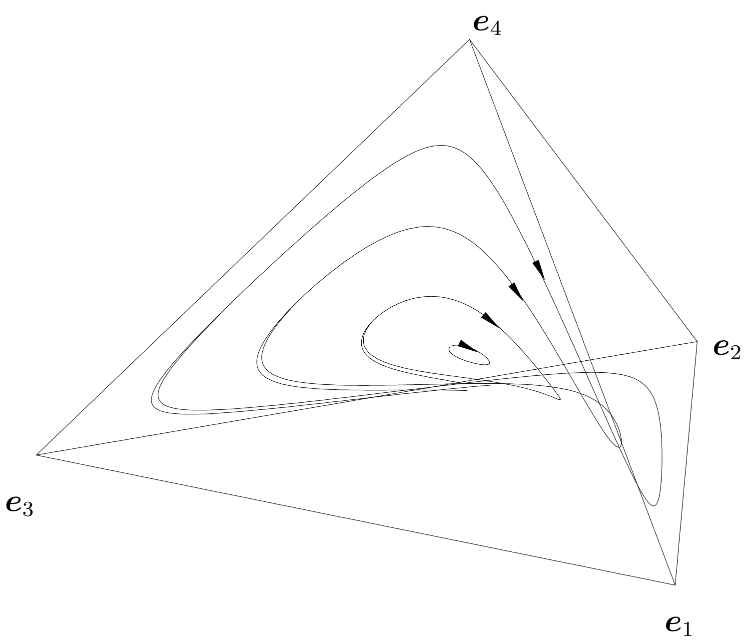

FIGURE 5. Hypercycle dynamics on S_4 for large t

For $n \geq 5$, there are always eigenvalues with strictly positive real parts, i.e. there exists an unstable eigenspace and the system in some sense loses stability.

Proposition 3.2. *Let E^u, E^s, E^c denote the unstable, stable and centre eigenspace, i.e. the subspaces of T_n which are spanned by the eigenvectors $\boldsymbol{v}^k$ belonging to* *eigenvalues with strictly positive, strictly negative and vanishing real part α_k respectively. $\boldsymbol{v}^k$ and α_k are given by (23). The dimensions of the eigenspaces are*

$$\dim(E^u) = \begin{cases} 2(\frac{n}{4} - 1) & \text{if } n/4 \in \mathbb{N}, \\ 2\lfloor \frac{n}{4} \rfloor & \text{othws.} \end{cases}$$

$$\dim(E^c) = \begin{cases} 2 & \text{if } n/4 \in \mathbb{N}, \\ 0 & \text{othws.} \end{cases}$$

$$\dim(E^s) = n - 1 - 2\lfloor \frac{n}{4} \rfloor.$$

This leads to an immediate corollary where a precise statement about the stability of the hypercycle is made. We have the following standard definitions: A rest point is *stable* if for any of its neighbourhoods U there are neighbourhoods W such that $\boldsymbol{x} \in W$ implies $\boldsymbol{x}(t) \in U$ for all $t \geq 0$. We speak of *asymptotic* stability if in addition $\boldsymbol{x}(t)$ converges to the rest point for all $\boldsymbol{x} \in W$. If *all* orbits in the state space converge to the rest point, we speak of *global* stability.

Corollary 3.3. *For $n \leq 4$, the centre $\boldsymbol{c}$ of S_n is a stable restpoint. For $n = 2, 3$, $\boldsymbol{c}$ is even globally stable. For $n \geq 5$, $\boldsymbol{c}$ is unstable.*

This result is very similar to the one obtained for the original ansatz (15) in [HS], where the rest point also is unstable for $n \geq 5$ but is globally stable up to $n = 4$. Intuitively it is clear that for $n \geq 5$ for many initial conditions the dynamics will spiral away from the centre and will get closer and closer to the boundary of S_n. Following the direction of the cycle, each concentration will successively approach 1 while the others vanish. We will give a result in Proposition 3.5. Since there is always a stable eigenspace, we can also choose initial conditions such that $\boldsymbol{x}(t)$ converges to the barycentre of the simplex, i.e. all concentrations stay constant for long enough times. For n dividable by four we have a centre eigenspace, so in addition to the cases mentioned, there will be periodic orbits where at no time a concentration approaches zero or one (see figure 6):

Corollary 3.4. *For n such that $n/4 \in \mathbb{N}$ there are periodic orbits where for all times the concentrations of the species stay outside neighbourhoods of zero and one. On the centre eigenspace $E^c \subset T_n$ these orbits are circles of radius $\sqrt{\frac{n}{2}(C^2_{\frac{n}{4}} + C^2_{\frac{3n}{4}})}$.*

Proposition 3.5. *We define the ω-limit set of $\boldsymbol{x}$ as*

$$\omega_+(\boldsymbol{x}) := \{\boldsymbol{y} \in S_n | \text{ there exists } t_m \nearrow \infty \text{ such that } \boldsymbol{x}(t_m) \to \boldsymbol{y} \text{ for } m \to \infty\}.$$

Then for $n \geq 5$, there are $\boldsymbol{x}$ for which the corners of the simplex belong to $\omega_+(\boldsymbol{x})$.

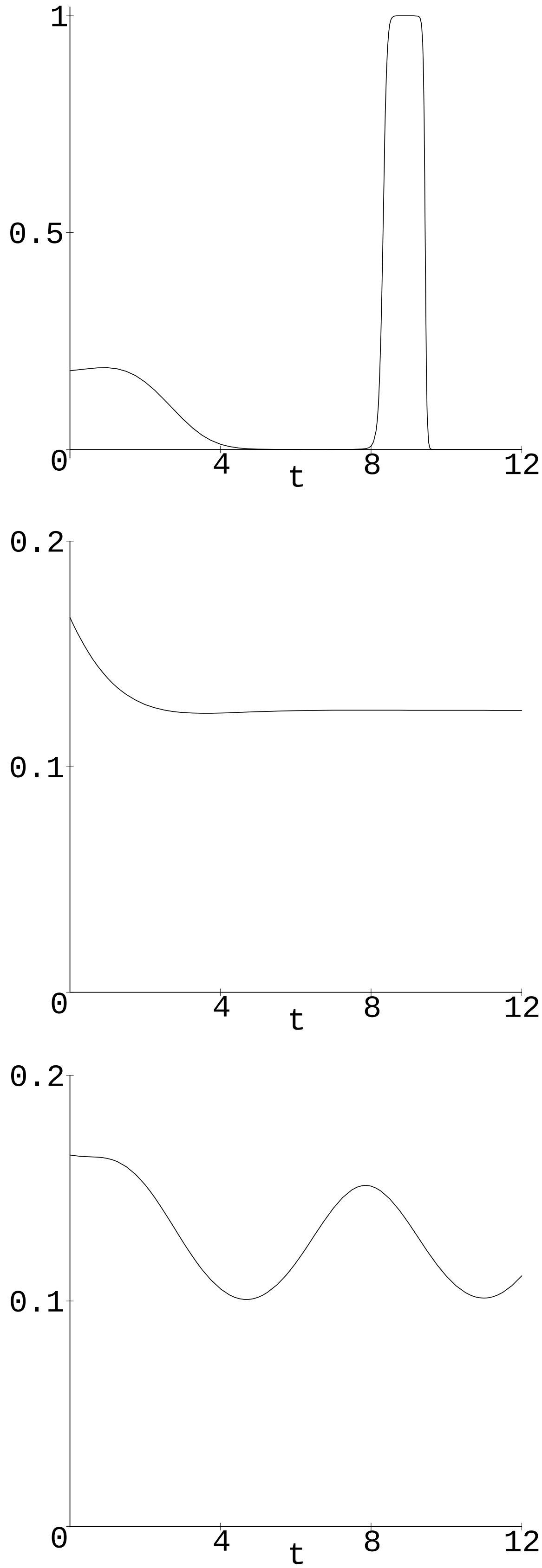

FIGURE 6. n=8: one component of $\boldsymbol{x}(t)$ for different initial conditions

3.2. **Generalisation of the model.** Let us now consider a model where one species not only catalyses the following one but the following m species. In the rows of the matrix A the 0's to the left of the single 1 entry are replaced by further 1's. The form of the solution of this system is not altered. While for $m = 1$ the eigenvalues were just equal to the last component of their eigenvectors, here the eigenvalues are the sum of the last m components:

Proposition 3.6. *The solution of the generalized hypercycle model where each species catalyses the m following ones is of the same form as given in Proposition 3.1, where α_k and β_k are to be replaced by*

$$\alpha_k(m) = \sum_{l=1}^{m} \cos(\varphi_k l), \quad \beta_k(m) = \sum_{l=1}^{m} \sin(\varphi_k l).$$

From this it is clear that we know again the stable, unstable and centre eigenspaces for all m and n. For some cases it is easy to find explicit expressions for their dimensions. In the following propositions we give results for $m = 2$ and for m close to n. The stability of the system increases with m:

m	least n for existence of E^u
1	5
2	7
n-3	13
n-2	-

Proposition 3.7. *For $m = 2$, the dimensions of the eigenspaces are given by*

$$\dim(E^u) = \begin{cases} 2(\frac{n}{6} - 1) & \textit{if } n/6 \in \mathbb{N}, \\ 2\lfloor \frac{n}{6} \rfloor & \textit{othws.} \end{cases}$$

$$\dim(E^c) = \begin{cases} 3 & \textit{if } n/6 \in \mathbb{N}, \\ 1 & \textit{if } n/6 \notin \mathbb{N},\ n/2 \in \mathbb{N}, \\ 0 & \textit{othws.} \end{cases}$$

$$\dim(E^s) = n - 1 - \begin{cases} (2\frac{n}{6} + 1) & \textit{if } n/2 \in \mathbb{N}, \\ 2\lfloor \frac{n}{6} \rfloor & \textit{othws.} \end{cases}$$

.

Clearly, similar corollaries as Corollary 3.3 and 3.4 follow. Here, we have an additional phenomenon in that $\boldsymbol{v}^{\frac{n}{2}}$, whose components are alternating 1's and -1's, belongs to the centre eigenspace now. If we choose initial conditions on its coordinate line, the system will stay there forever, the concentrations do not change. For $m = n-2$, the only centre eigenspace possible consists of this coordinate line.

Proposition 3.8. *For the generalized hypercycle model for m close to n there are the following expressions for the dimensions of the eigenspaces:*
For $m = n-1$ all eigenvalues are -1, so there is only a stable eigenspace of dimension $n-1$.
For $m = n-2$, the centre eigenspace is spanned by $\boldsymbol{v}^{\frac{n}{2}}$ (if n is even). Thus the dimension of the centre eigenspace is 1 whenever n is even and 0 otherwise. There is no unstable eigenspace, so the dimension of the stable eigenspace is $n-2$ for n even and $n-1$ for n odd.
For $m = n-3$ the dimensions of the eigenspaces are

$$\dim(E^u) = \begin{cases} 2(\frac{n}{12}-1) & \textit{if } n/12 \in \mathbb{N}, \\ 2\lfloor\frac{n}{12}\rfloor & \textit{othws.} \end{cases}$$

$$\dim(E^c) = \begin{cases} 4 & \textit{if } n/12 \in \mathbb{N}, \\ 2 & \textit{if } n/4 \notin \mathbb{N},\ n/3 \in \mathbb{N} \textit{ or } n/3 \notin \mathbb{N},\ n/4 \in \mathbb{N}, \\ 0 & \textit{othws.} \end{cases}$$

$$\dim(E^s) = n-1-\begin{cases} \left(2\lfloor\frac{n}{12}\rfloor+2\right) & \textit{if at least one of } n/3, n/4 \in \mathbb{N}, \\ 2\lfloor\frac{n}{12}\rfloor & \textit{othws.} \end{cases}$$

4. Proofs

Proof of Proposition 2.2.
(1) It is easy to see that a matrix $A \in \mathcal{M}(n, \mathbb{R})$ satisfies

$$(\iota^* \circ \rho)(A)(\boldsymbol{v}) \;=\; A\boldsymbol{v} \;=\; \boldsymbol{0} \qquad \text{for all } \boldsymbol{v} \in T_n$$

if and only if $A \in \mathcal{V}(T_n)$.
(2) Let A be an image element of $\rho^{-1} \circ \pi^*$. Thus, there exists a map $g \in \mathrm{Lin}(T_n, \mathbb{R}^n)$ with

$$A \;=\; (\rho^{-1} \circ \pi^*)(g) \;=\; \rho^{-1}(\pi^*(g)) \;=\; \rho^{-1}(g \circ \pi). \tag{21}$$

If we choose $\boldsymbol{v} \in T^\perp$, that is $\boldsymbol{v} = (a, \ldots, a)^\dagger$ for some $a \in \mathbb{R}$, then (21) implies

$$A\boldsymbol{v} \;=\; \rho^{-1}(g \circ \pi)\boldsymbol{v} \;=\; (g \circ \pi)(\boldsymbol{v}) \;=\; g(\pi(\boldsymbol{v})) \;=\; g(\boldsymbol{0}) \;=\; \boldsymbol{0}.$$

This implies $A \in \mathcal{V}(T_n^\perp)$. It remains to prove that each element A of $\mathcal{V}(T_n^\perp)$ is an image element of $\rho^{-1} \circ \pi^*$: We choose $g : T_n \to \mathbb{R}^n$, $\boldsymbol{v} \mapsto g(\boldsymbol{v}) := A\boldsymbol{v}$. For each $\boldsymbol{v} \in T_n$, and for each $\boldsymbol{w} \in T_n^\perp$, this implies

$$\begin{aligned}
(\rho^{-1} \circ \pi^*)(g)(\boldsymbol{v} + \boldsymbol{w}) \;&=\; \rho^{-1}(g \circ \pi)(\boldsymbol{v} + \boldsymbol{w}) \;=\; \rho^{-1}(g(\boldsymbol{v})) \\
&=\; \rho^{-1}(A\boldsymbol{v}) \;=\; A\boldsymbol{v} \;=\; A(\boldsymbol{v} + \boldsymbol{w}).
\end{aligned}$$

(3) Let $A = (a_{i,j})_{i,j} \in \mathcal{V}(T_n^\perp)$, and $B = (b_{i,j})_{i,j} = (b_i)_{i,j} \in \mathcal{V}(T_n)$. Then

$$\langle A, B \rangle \;=\; \sum_{i,j} a_{i,j}\, b_{i,j} \;=\; \sum_{i,j} a_{i,j}\, b_i \;=\; \sum_i b_i \sum_j a_{i,j} \;=\; 0.$$

Therefore, $\mathcal{V}(T_n^\perp)$ and $\mathcal{V}(T_n)$ are orthogonal with respect to the canonical scalar product $\langle \cdot, \cdot \rangle$. The fact that each matrix $(a_{i,j})_{i,j}$ can be written as

$$\left(a_{i,j} - \frac{1}{n} \sum_k a_{i,k} \right)_{i,j} + \left(\frac{1}{n} \sum_k a_{i,k} \right)_{i,j}$$

completes the proof. □

Proof of Proposition 2.3. We fix $\boldsymbol{x}(t_0)$ and consider the map $S_n \to T_n$, $\boldsymbol{x} \mapsto \mathrm{vec}(\boldsymbol{x}(t_0), \boldsymbol{x})$. This is a diffeomorphism in the usual sense. For this reason, the curve $t \mapsto \boldsymbol{x}(t)$ in S_n is differentiable if and only if the composition $t \mapsto \mathrm{vec}(\boldsymbol{x}(t_0), \boldsymbol{x}(t))$ in T_n is differentiable. The latter property is equivalent to the $(*)$-differentiability of the curve in S_n. This proves the first statement of the

Proposition 2.3. We now prove (10):

$$
\begin{aligned}
\frac{d^*\boldsymbol{x}}{dt}(t_0) &= \lim_{\substack{t\to t_0\\ t\neq t_0}} \frac{\operatorname{vec}(\boldsymbol{x}(t_0),\boldsymbol{x}(t))}{t-t_0} \\
&= \lim_{\substack{t\to t_0\\ t\neq t_0}} \sum_{i=1}^{n} \left(\frac{\ln x_i(t)-\ln x_i(t_0)}{t-t_0} - \frac{1}{n}\sum_{k=1}^{n} \frac{\ln x_k(t)-\ln x_k(t_0)}{t-t_0} \right) \boldsymbol{e}_i \\
&= \sum_{i=1}^{n} \left(\frac{d(\ln\circ x_i)}{dt}(t_0) - \frac{1}{n}\sum_{k=1}^{n} \frac{d(\ln\circ x_k)}{dt}(t_0) \right) \boldsymbol{e}_i \\
&= \sum_{i=1}^{n} \left(\frac{1}{x_i(t_0)}\frac{dx_i}{dt}(t_0) - \frac{1}{n}\sum_{k=1}^{n} \frac{1}{x_k(t_0)}\frac{dx_k}{dt}(t_0) \right) \boldsymbol{e}_i.
\end{aligned}
$$

□

Proof of Proposition 2.4. The differential of $\exp_{\boldsymbol{c}}^{-1}$ with respect to the $(*)$-structure is nothing but the identity map on T_n:

$$
d^*\exp_{\boldsymbol{c}}^{-1}(\boldsymbol{x},\boldsymbol{v}) = \boldsymbol{v}. \tag{22}
$$

This implies

$$
\begin{aligned}
\dot{\boldsymbol{v}}(t_0) &= \frac{d(\exp_{\boldsymbol{c}}^{-1}\circ\boldsymbol{x})}{dt}(t_0) \\
&= d^*\exp_{\boldsymbol{c}}^{-1}\left(\boldsymbol{x}(t_0), \frac{d^*\boldsymbol{x}}{dt}(t_0)\right) \\
&\overset{(22)}{=} \frac{d^*\boldsymbol{x}}{dt}(t_0) \\
&= (f\circ\boldsymbol{x})(t_0) \\
&= (f\circ\exp_{\boldsymbol{c}}\circ\exp_{\boldsymbol{c}}^{-1}\circ\boldsymbol{x})(t_0) \\
&= (f\circ\exp_{\boldsymbol{c}})\big(\boldsymbol{v}(t_0)\big).
\end{aligned}
$$

□

Proof of Theorem 2.6. Assume that equation (11) holds. With (10) we get

$$
f_i(\boldsymbol{x}) = \frac{\dot{x}_i}{x_i} - \frac{1}{n}\sum_{j=1}^{n}\frac{\dot{x}_j}{x_j},
$$

which is equivalent to

$$
\dot{x}_i = x_i\left(f_i(\boldsymbol{x}) + \frac{1}{n}\sum_{j=1}^{n}\frac{\dot{x}_j}{x_j}\right).
$$

Using $\dot{\boldsymbol{x}} \in T_n$, this implies

$$\frac{1}{n}\sum_{j=1}^{n}\frac{\dot{x}_j}{x_j} \;=\; -\sum_{j=1}^{n} x_j f_j(\boldsymbol{x}).$$

Therefore (12) holds.
Now assume that (12) is satisfied. We obtain (11) in the following way:

$$\begin{aligned}
\frac{d^*\boldsymbol{x}}{dt} &\overset{(10)}{=} \sum_{i=1}^{n}\left(\frac{\dot{x}_i}{x_i} - \frac{1}{n}\sum_{j=1}^{n}\frac{\dot{x}_j}{x_j}\right)\boldsymbol{e}_i \\
&\overset{(12)}{=} \sum_{i=1}^{n}\left(\left(f_i(\boldsymbol{x}) - \sum_{k=1}^{n} x_k f_k(\boldsymbol{x})\right) - \frac{1}{n}\sum_{j=1}^{n}\left(f_j(\boldsymbol{x}) - \sum_{k=1}^{n} x_k f_k(\boldsymbol{x})\right)\right)\boldsymbol{e}_i \\
&= \sum_{i=1}^{n}\left(f_i(\boldsymbol{x}) - \frac{1}{n}\sum_{j=1}^{n} f_j(\boldsymbol{x})\right)\boldsymbol{e}_i \\
&\overset{f\in T_n}{=} \sum_{i=1}^{n} f_i(\boldsymbol{x})\,\boldsymbol{e}_i \;=\; f(\boldsymbol{x}).
\end{aligned}$$

□

Proof of Theorem 2.7. Although this theorem represents the central statement of our article, it is an immediate consequence of the Proposition 2.4 and a general formula for the solutions of linear differential equations which is well-known in dynamical system theory (see for example [Ro]). □

Proof of Proposition 3.1. The solution on the tangent space T_n is obtained from the eigenvalues λ_k and eigenvectors $\boldsymbol{v}^k$ of A^c according to Theorem 2.7 and Corollary 2.8. We obtain them using the lemma in section 3.1. Leaving out $\lambda_0 = 0$, $\boldsymbol{v}^k = \mathbf{1}$, which are not relevant for the solution (we have no dynamics in the direction perpendicular to T_n), one finds (see (26) for m=1)

(23)
$$\lambda_k = \alpha_k - i\beta_k, \quad v_i^k = \cos(\varphi_k(i-1)) - i\sin(\varphi_k(i-1)), \quad k = 1,\dots n-1, i = 1,\dots,n,$$

where φ_k, α_k and β_k are defined in the proposition. According to Corollary 2.8, for the pairs[1] of complex eigenvalues $\lambda_{k,n-k} = \alpha_k \mp i\beta_k$, the corresponding real solutions are

$$C_{k,n-k}e^{\alpha_k t}\left(\cos(\beta_k t)\boldsymbol{u}^k \pm \sin(\beta_k t)\boldsymbol{w}^k\right), \tag{24}$$

where $\boldsymbol{u}^k$ and $\boldsymbol{w}^k$ are the real and imaginary parts of $\boldsymbol{v}^k$. In case of even n also the single real eigenvalue $\lambda_{\frac{n}{2}} = -1$ occurs. Its solution $C_{\frac{n}{2}}e^{\lambda_{\frac{n}{2}}t}\boldsymbol{v}^{\frac{n}{2}}$ can also be

[1]For such pairs we write $\lambda_{k,l} = \alpha \pm i\beta$ meaning that the sign above belongs to λ_k, the sign below to λ_l.

expressed in the above way. The general solution on T_n can thus be written as

$$\boldsymbol{v}(t) = \sum_{k=1}^{\lfloor \frac{n}{2} \rfloor} e^{\alpha_k t} \left(C_k \left(\sin(\beta_k t)\boldsymbol{u}^k + \cos(\beta_k t)\boldsymbol{w}^k \right) + C_{n-k} \left(\cos(\beta_k t)\boldsymbol{u}^k - \sin(\beta_k t)\boldsymbol{w}^k \right) \right). \tag{25}$$

Finally using $\cos x \cos y - \sin x \sin y = \cos(x+y)$ and $\sin x \cos y + \cos x \sin y = \sin(x+y)$, we obtain the proposition. □

Proof of Proposition 3.2. For $\alpha_k = \cos\varphi_k < 0$ we need $\pi/2 < \varphi_k < 3\pi/2$ i.e. $n/4 < k < 3n/4$. If $\alpha_k = 0$ then $k = n/4, 3n/4$. All the rest of the k's, i.e. $k < n/4$ and $k > 3n/4$ yield $\alpha_k > 0$. Now there is exactly one eigenvector to each eigenvalue. Using $\lambda_{k,n-k} = \alpha_k \mp i\beta_k$, we see that for $\alpha_k > 0$ we have pairs $k, n-k$ and the condition $k < n/4$ is equivalent to $n-k > 3n/4$. The dimension of E^u is thus twice the number of k's being smaller than $n/4$. The dimension of E^c is two whenever $n/4, 3n/4$ are natural numbers. Since $1 \leq k \leq n-1$, the dimension of E^s is $(n-1)-\mathrm{dim}E^u-\mathrm{dim}E^c$. □

Proof of Corollary 3.4. As used in the proof of Proposition 3.1, solutions on E^c are given by

$$\boldsymbol{v}^c(t) = C_{\frac{n}{4}}(\sin t\ \boldsymbol{u}^{\frac{n}{4}} + \cos t\ \boldsymbol{w}^{\frac{n}{4}}) + C_{\frac{3n}{4}}(\cos t\ \boldsymbol{u}^{\frac{n}{4}} - \sin t\ \boldsymbol{w}^{\frac{n}{4}})$$

The components of this expression differ only w.r.t. being even or odd. We thus find

$$\sum_i (v_i^c)^2(t) = \frac{n}{2}(C_{\frac{n}{4}} \sin t + C_{\frac{3n}{4}} \cos t)^2 + \frac{n}{2}(C_{\frac{n}{4}} \cos t - C_{\frac{3n}{4}} \sin t)^2 = \frac{n}{2}(C^2_{\frac{n}{4}} + C^2_{\frac{3n}{4}}).$$

The square root of this is the norm of $\boldsymbol{v}^c(t)$. □

Proof of Proposition 3.5. For the corners we show that for certain time series t_m, $m \in \mathbb{N}$, the dynamics tends to one of the corners as $m \to \infty$. For this, we choose initial conditions to our convenience: Let k be such that $\alpha_k > 0$ (and thus $\beta_k \neq 0$). Let $C_l = 0$ for all $l \neq k$ and let $C_k > 0$. The components of $\boldsymbol{v}(t)$ are then given by

$$v_i(t) = e^{\alpha_k t} C_k \sin\left(\beta_k t + \varphi_k(i-1)\right).$$

We now construct $t_m(k,j) = 1/\beta_k(\pi/2 - \varphi_k(j-1) + 2\pi m)$ for $m \in \mathbb{N}$. Inserting this in the above equation yields

$$v_i(m) = e^{\cot\varphi_k(\pi/2 - \varphi_k(j-1) + 2\pi m)} C_k \sin\left(\frac{\pi}{2} + 2\pi m + \varphi_k(i-j)\right).$$

The sine is one whenever $(i-j)/n \in \mathbb{Z}$, which can only be the case for $i=j$. Thus the j-th component is largest and the sequence of points in S_n

$$\boldsymbol{x}(m) = \sum_{i=1}^{n} \frac{1}{1+\sum_{l\neq i} e^{v_l(m)-v_i(m)}} \boldsymbol{e}_i$$

will tend to $\boldsymbol{e}_j$ as $m \to \infty$ because the exponent in the above equation will tend to $-\infty$ for all $l \neq i$ only in case of $i=j$. □

Proof of Proposition 3.6. Using (17), we find that the eigenvectors do not change and that the eigenvalues are given by

$$\lambda_k(m) = \sum_{j=0}^{n-1-m} \left(-\frac{1}{n}\right) \gamma^{kj} + \sum_{j=n-m}^{n-1} \frac{n-1}{n} \gamma^{kj} = \sum_{j=0}^{n-1} \left(-\frac{1}{n}\right) \gamma^{kj} + \sum_{j=n-m}^{n-1} \gamma^{kj} = \sum_{j=1}^{m} \gamma^{-kj}, \tag{26}$$

where the last equality is obtained using that the first sum on the LHS is zero and $\gamma^{n-k} = \gamma^{-k}$. We have again pairs $\lambda_{k,n-k}(m) = \sum_{j=1}^{m} \cos\varphi_k j \mp i \sum_{j=1}^{m} \sin\varphi_k j$ and for n even, $\lambda_{\frac{n}{2}}(m)$ is 0 or -1 for m even or odd respectively. □

Proof of Proposition 3.7. Since $\alpha_k(2) = \cos\varphi_k + \cos 2\varphi_k = 2\cos(3\varphi_k/2)\cos(\varphi_k/2)$, we only have to check for how many k's the cosines of $3\varphi_k/2$ and $\varphi_k/2$ have different sign to find out the dimension of the stable eigenspace. 1) $0 < \varphi_k/2 < \pi/2$: it follows that $0 < 3\varphi_k/2 < 3\pi/2$, we have different signs if $\pi/2 < 3\varphi_k/2 < 3\pi/2$ i.e. $n/6 < k < n/2$. 2) $\pi/2 < \varphi_k/2 < \pi$: we have $3\pi/2 < 3\varphi_k/2 < 3\pi$, we have different signs if $3\pi/2 < 3\varphi_k/2 < 5\pi/2$ i.e. $n/2 < k < 5n/6$. So taking 1) and 2) together we find that $\alpha_k(2) < 0$ whenever $k \neq n/2$ and $n/6 < k < 5n/6$. Since there are pairs $k, n-k$ giving the same cosine and $k < n/6$ is equivalent to $k > 5n/6$, $\dim E^s = 2|\{k \in \mathbb{N} : k < n/6\}|$. For $\alpha_k(2) = 0$, $3\varphi_k/2 = (1/2+l)\pi$ for $l = 0,1,2$, so $k = n/6,\ n/2,\ 5n/6$. Clearly, the rest of the k's belongs to eigenvalues with positive real parts. □

Proof of Proposition 3.8. The sum over the eigenvector components is 0, and $\lambda_k(m)$ is the sum of the last m components of the respective eigenvector. We can also use the fact that the first component of all eigenvectors is 1, so $\lambda_k(n-1) = -1$ for all k. It also follows that $\lambda_k(n-2) = -1 - v_2^k$, so $\alpha_k(n-2) = -1 - \cos\varphi_k \leq 0$ where the equality can only hold in case of $k = n/2$. Accordingly, for $m = n-3$ we use $\alpha_k(n-3) = -1 - (\cos\varphi_k + \cos 2\varphi_k) = -1 - \alpha_k(2)$. So when is $\alpha_k(2) + 1 \leq 0$? We write $\cos\varphi_k + \cos 2\varphi_k + 1 = \cos\varphi_k + 2\cos^2\varphi_k$. Taking the root of this quadratic equation we get that $\cos\varphi_k$ is 0 or $-1/2$ for $\alpha_k(2) = -1$. Thus $\varphi_k = \pi/2, 2\pi/3, 4\pi/3, 3\pi/2$ giving the k's that span E^c. Since $d/d\varphi_k(\alpha_k(2))$ is negative for $\varphi_k = \pi/2$, by continuity $\alpha_k(2) < -1$ for $\pi/2 < \varphi_k < 2\pi/3$.

Similarly, for $4\pi/3 < \varphi_k < 3\pi/2$ we have $\alpha_k(2) < -1$ since $d/d\varphi_k(\alpha_k(2))$ is negative for $\varphi_k = 4\pi/3$. Now we have again pairs $k, n-k$: $\pi/2 < \varphi_k < 2\pi/3$ is equivalent to $4\pi/3 < \varphi_{n-k} < 3\pi/2$, so $\dim E^u = 2|\{k \in \mathbb{N} : n/4 < k < n/3\}|$. $\square$

Acknowledgements

This work was done mainly at the Max-Planck Institute for Mathematics in the Sciences and the Interdisciplinary Centre for Bioinformatics in Leipzig. N.A. also thanks the Santa Fe Institute where the paper was finished. The authors want to thank Jürgen Jost and Peter Stadler for supporting this project both financially and with valuable discussions and hints.

References

[AN] Amari, Shun-ichi; Nagaoka, Hiroshi. *Methods of Information Geometry*, AMS Translations of Mathematical Monographs **191**, Oxford University Press, Oxford (2000)

[Ar] Arrigoni, Mauro *Modello di iperciclo autonomo per la selezione di molecole biologiche*, Sguardo matematico nellea biologia, Mendrisio - ottobre 1990.

[Ay] Ay, Nihat (2002). *An Information-Geometric Approach to a Theory of Pragmatic Structuring*. Annals of Probability **30** 416-436.

[Br] Bröcker, Theodor: *Analysis in mehreren Variablen*, B.G. Teubner, Stuttgart, 1980.

[Ei] Eigen, M.: *Selforganization of Matter and the Evolution of Biological Macromolecules*, Naturwiss. **58** 465-523 (1971).

[HMS] Hofbauer, J; Mallet-Paret, J.; Smith, H.L.: *Stable periodic solutions for the hypercycle system*, Journal of Dynamics and Differential Equations **3**, 423-436.

[HS] Hofbauer, Josef; Sigmund, Karl. *Evolutionary Games and Population Dynamics*, Cambridge University Press (1998)

[J] Jones, B.L.: *A Solvable Selfreproductive Hypercycle Model for the Selection of Biological Molecules*, J. Math. Biology **4** 187-193 (1977).

[Ro] Robinson, Clark: *Dynamical Systems*, CRC Press, Boca Raton, 1994.

[St] Stadler, Peter: *Dynamics of Small Autocatalytic Reaction Network IV: Inhomogeneous Replicator Equations*, BioSystems **26** 1-19 (1991).

[SG] Steiner, Antonio; Gander, Martin J.: *Le soluzioni delle equazioni preda-predatore*, Il Volterriano **5** 9-28 (1995).

[We] Weibull, Jörgen W.: *Evolutionary Game Theory*, MIT Press, Cambridge, Massachusetts, 1996.