# The Permanence of Hypercycles

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**Abstract**

This project focuses on one of the theories on how life started and developed: the hypercycles. Such a process will be modelled with some of the tools from population dynamics. The paper firstly introduces the concept of replicator dynamics and of permanence, both of fundamental importance for showing that in the case of more than four types of population none of them would extinguish. Finally, it constructs the hypercycle model, proves its permanence, and analyses the limit of its time averages of densities of population.

## 1 Introduction

Population dynamics aims at modelling biological environments, taking into consideration the interspecies and intraspecies interactions: their competition levels, the asset of goods available, the likelihood of catastrophes, and many other variables. Of particular interest is how to model prebiotic life, and how life originated. One of the most promising theories is based on hypercycles: every species catalyses the reproduction of a different one, in a cyclic way.

In order to build such a model there will firstly be a short introduction on the replicator dynamics and the concept of permanence. Some useful conditions to check the permanency of a system are going to be stated and proved. In the final section a more rigorous definition of hypercycle will be given, together with a proof of its permanence, and an analysis of the time average of its populations. Every statement and proof closely follows the work of Josef Hofbauer and Karl Sigmund in *Evolutionary Games and Population Dynamics* [1], unless otherwise stated.

## 2 Replicator Dynamics

The dynamics of a population can be often described by using a differential equation. Divide a population into $n$ different types, or species, $E_1, \dots, E_n$, with respective relative frequencies $x_1, \dots, x_n$. Now define the functions $f_1, \dots, f_n$ as the respective fitness functions; they depend on all the frequencies of all the types of the population, namely the vector $\mathbf{x}$. Assume that the population is big enough so that one generation blends into the other continuously, hence it can be assumed that $\mathbf{x}(t)$ evolves as a differentiable function of $t$. Define $\frac{\dot{x_i}}{x_i}$ as the measure of the evolutionary success of the species $E_i$, and according to Darwinism, it can be expressed as the difference between the fitness of the $i^{th}$ type and the average fitness of the whole population, $\bar{f}(\mathbf{x}) = \sum_i x_i f_i(\mathbf{x})$. Hence

$$\frac{\dot{x_i}}{x_i} = \text{fitness of } E_i - \text{average fitness}$$

which yields the *replicator equation*

$$\dot{x_i} = x_i(f_i(\mathbf{x}) - \bar{f}(\mathbf{x})) \qquad i = 1, 2, \dots, n. \tag{2.1}$$

Since relative frequencies are considered, it is useful to define $S_n$, or *simplex*: the subspace of all vectors $\mathbf{x} \in \mathbb{R}^n$ such that if $x_i$ is the $i^{th}$-component of the vector then $x_i \geq 0$ for all $i = 1, 2, \dots, n$ and such that $\sum_{i=1}^n x_i = 1$. The interior of the simplex will be indicated as int $S_n$ and its boundary as $\partial S_n$.

**Proposition 2.1.** *$S_n$ is invariant under* (2.1)*, i.e. if $\boldsymbol{x} \in S_n$ then $\boldsymbol{x}(t) \in S_n$ for all $t \in \mathbb{R}$.*

*Proof.* Define $S = x_1 + x_2 + \dots + x_n$, then by differentiation properties it follows that

$$\begin{aligned}
\dot{S} = \sum_{i=1}^n \dot{x_i} &= \sum_{i=1}^n x_i(f_i(\mathbf{x}) - \bar{f}(\mathbf{x})) \qquad \text{by (2.1)} \\
&= \sum_{i=1}^n x_i f_i(\mathbf{x}) - \sum_{i=1}^n x_i \bar{f}(\mathbf{x}) \\
&= \bar{f}(\mathbf{x}) - \bar{f}(\mathbf{x})S \\
&= (1 - S)\bar{f}(\mathbf{x})
\end{aligned}$$

Hence $S(t) \equiv 1$ is a solution. This immediately implies that if the solution of (2.1) starts on the plane $\sum_i x_i = 1$, then it stays there for all $t \in \mathbb{R}$. Furthermore, if the orbit starts on the boundary of $S_n$, the solution has to stay on it for all time. That is, if $x_i(0) = 0$ for some $i$ then $x_i(t) = 0$ for all $t$, this fact following immediately from equation (2.1). Therefore $S_n$ is invariant under (2.1) □

By Prop. 2.1 the domain of (2.1) can be restricted to $S_n$ – this is going to be the state space considered for the rest of the paper. As premised before, this equation has many applications and uses. For example it can be related with Mendelian machinery of inheritance [Part 4: [1]], or it can be used to model hypercylcles as in Section 4. For the scope of this project the attention will be focused to the case where all the $f_i$ are linear. Since the vector spaces considered will always be finite those functions can be represented as $n \times n$ matrix $A$, called the *pay-off matrix*, and such that $(A\mathbf{x})_i = f_i(\mathbf{x})$. Thus, (2.1) can be rewritten as

$$\dot{x_i} = x_i((A\mathbf{x})_i - \mathbf{x} \cdot A\mathbf{x}) \qquad i = 1, 2, \ldots, n. \tag{2.2}$$

From now on this equation will be considered instead of (2.1), unless otherwise stated. The $ij^{th}$-entry of $A$ will be denoted by $a_{ij}$.

A *rest point* $\mathbf{x} \in S_n$ is such that $\mathbf{x}(t) \equiv \mathbf{x}$ for all $t \in \mathbb{R}$. In this case any rest point in $S_n$ satisfies:

$$(A\mathbf{x})_1 = \cdots = (A\mathbf{x})_n \tag{2.3}$$
$$x_1 = \cdots = x_n \tag{2.4}$$
$$x_i \geq 0 \qquad i = 1, \ldots, n. \tag{2.5}$$

In general there is one, or no solutions to such conditions. In some degenerate cases it might form a linear manifold in $S_n$ [p.86: [1]].

One of the most astonishing properties of the replicator system (2.2) is related to the limit of the time average of the orbit.

**Proposition 2.2.** *Suppose that* (2.2) *admits an interior rest point* $\boldsymbol{p} \in S_n$*, and* $\omega(\boldsymbol{x}(t)) \subseteq$ *int* $S_n$*, then*

$$\lim_{t\to\infty} \frac{1}{T} \int_0^T x_i(t)dt = p_i \qquad \textit{for } i = 1, 2, \ldots, n. \tag{2.6}$$

*Proof.* This proof was inspired by [1, 4]. Let $\mathbf{x}(t)$ be an orbit of (2.2), which satisfies the conditions of the proposition. Since its $\omega$-limit set is in int $S_n$, the orbit has to be bounded away from $\partial S_n$. Hence there exist $\delta_i > 0$ such that $x_i(t) > \delta_i$ , for $t > 0$, and $i = 1, 2, \ldots, n$. Set $\delta = \min_i \delta_i$. Now consider (2.2), and for any $i$

$$\dot{\log(x_i)} = \frac{\dot{x_i}}{x_i} = (A\mathbf{x})_i - \mathbf{x} \cdot A\mathbf{x}.$$

Let $T > 0$

$$\begin{aligned}
\frac{1}{T}\int_0^T \log(\dot{x}_i(t))dt &= \frac{1}{T}\int_0^T (A\mathbf{x}(t))_i - \mathbf{x}(t) \cdot A\mathbf{x}(t)dt \\
\frac{\log(x_i(T)) - \log(x_i(0))}{T} &= \frac{1}{T}\int_0^T \sum_{j=1}^n (a_{ij}x_j(t)) - \mathbf{x}(t) \cdot A\mathbf{x}(t)dt \\
&= \frac{1}{T}\left[\sum_{j=1}^n a_{ij}\int_0^T x_j(t)dt - \int_0^T \mathbf{x}(t) \cdot A\mathbf{x}(t)dt\right] \\
&= \sum_{j=1}^n a_{ij}\frac{\int_0^T x_j(t)dt}{T} - \frac{\int_0^T \mathbf{x}(t) \cdot A\mathbf{x}(t)dt}{T}.
\end{aligned}$$

Define $z_j(T) := \frac{\int_0^T x_j(t)dt}{T}$. From the fact that the flow is bounded away from $\partial S_n$ immediately follows that $\delta < z_j(T) \leq 1$, for all $j = 1, 2, \ldots, n$ and any $T > 0$. Now let $\{T_k\}_{k\leq 1}$ be a sequence tending to $+\infty$ as $k \to +\infty$. Hence

$\{z_j(T_k)\}_{k<1}$ is a bounded sequence, and therefore it admits a convergent subsequence. Slightly abusing notation, we will refer to the converging subsequence as $\{z_j(T_k)\}_{k\leq 1}$. Call $\bar{z}_j$ the limit, i.e.

$$z_j(T_k) \to \bar{z}_j \qquad \text{as } k \to \infty$$

for $j = 1, 2, \ldots, n$. Clearly $\log(x_i(T_k)) - \log(x_i(0))$ is bounded as well and therefore $\frac{\log(x_i(T_k))-\log(x_i(0))}{T_k} \to 0$ as $k \to \infty$. So conclude that if $k \to \infty$

$$\sum_{j=1}^{n} a_{ij}\bar{z}_j = \lim_{T_k\to\infty} \frac{\int_0^{T_k} \mathbf{x}(t)\cdot A\mathbf{x}(t)dt}{T_k}.$$

Since the right hand side is a constant irrespectively of $i$, the limit exists, is finite, and moreover

$$(A\bar{\mathbf{z}})_1 = (A\bar{\mathbf{z}})_2 = \cdots = (A\bar{\mathbf{z}})_n = \lim_{T_k\to\infty} \frac{\int_0^{T_k} \mathbf{x}(t)\cdot A\mathbf{x}(t)dt}{T_k}.$$

The components of the vector $\bar{\mathbf{z}}$ are all positive, and

$$\begin{aligned}
\sum_{j=1}^{n} \bar{z}_j &= \sum_{j=1}^{n} \lim_{T_k\to\infty} \frac{\int_0^{T_k} x_j(t)dt}{T_k} \\
&= \lim_{T_k\to\infty} \sum_{j=1}^{n} \frac{\int_0^{T_k} x_j(t)dt}{T_k} \\
&= \lim_{T_k\to\infty} \frac{\int_0^{T_k} \sum_{j=1}^{n} x_j(t)dt}{T_k} \\
&= \lim_{T_k\to\infty} \frac{T_k}{T_k} = 1
\end{aligned}$$

This, together with the conditions proved before, shows that $\bar{\mathbf{z}} \in \text{int } S_n$, and it can therefore be uniquely identified with the rest point $\mathbf{p} \in S_n$. Hence

$$\bar{z}_j = \lim_{T\to+\infty} \frac{1}{T} \int_0^T x_j(t)dt = p_j$$

$\square$

Therefore even if the the orbit of a replicator dynamic does not tend to any rest point, as long as it remains in int $S_n$, its time average tends to the rest point, component-wise.

# 3 Permanence

The equations previously introduced find applications in various and distinguished disciplines such as biology and ecology theory. In these fields one of the most fascinating problems is analysing the long-time survival of different populations in various habitats. Even if this question sounds easy and straightforward, the amount of variables to consider is important, and therefore, creating a universal fitting mathematical model turned out to be a nearly impossible challenge. Singular cases are usually considered, under various assumptions. Clearly some of the techniques developed have a wider spectrum of applications like Lyapunov's functions, for example used by Volterra when studying his famous system of ODEs, or the linearisation process usually invoked when interested in the stability of a rest point, which is possible thanks to the Hartman-Grobman Theorem [3]. All these methods rely on the outdated idea that every system has a unique, potentially asymptotically, stable rest point (W. B. Arthur, 1954, [p.7: [3]]). Even considering local stability, on the other hand, does not solve the problem: the basin of attraction can go from a small neighbourhood of the point to the whole interior of the state space. From the sixties onwards, thanks to the intuition of pioneers like R. C. Lewontin and J. Maynard-Smith, the importance of systems where multiple equilibria might coexist, or which exhibit wild oscillations of densities of types of populations has been noticed in many different fields ranging form physical sciences to economy, and biology. Hence the need of introducing alternative concepts of stability, for example where any asymptotic behaviour of orbits is allowed as long as the orbit does not get too close to the boundary of the system, or, in other words, if the boundary is somehow repellent. From this peculiar idea the concept of *permanence* was born.

**Definition 3.0.1** (Permanence)**.** *A system is said to be permanent if there exists $\delta > 0$ so that for each $\boldsymbol{x}$ in the interior of $S_n$ there exists $T > 0$ so that $x_i(t) > \delta$ for all $t \geq T$ and $i = 1, \ldots, n$. Or equivalently, there exists $\delta > 0$ such that for $x_i(0) > 0$ for $i = 1, \ldots, n$ implies*

$$\liminf_{t \to +\infty} x_i(t) > \delta \qquad i = 1, \ldots, n$$

It is important to note that $\delta$ is independent from the initial conditions imposed on the orbit. This definition can be interpreted as no species, in a permanent system where enough time has passed, will extinguish if the perturbations are small (less than $\delta$) and rare. Additionally if a type exists in a very small amount at the beginning, it tends to develop until a sizeable amount of it is present.

Checking if a system is permanent directly via the definition is usually hard and complicated, hence the need to have some conditions for checking if permanence holds.

**Theorem 3.1.** *Consider a dynamical system on $S_n$ which leaves the boundary invariant. Let $P : S_n \to \mathbb{R}$ be a differentiable function vanishing on $\partial S_n$ and strictly positive in int $S_n$. If there exists a continuous function $\Psi$ on $S_n$ such that the following two conditions hold:*

$$\Psi(\boldsymbol{x}) = \frac{\dot{P}(\boldsymbol{x})}{P(\boldsymbol{x})} \qquad \text{for } \boldsymbol{x} \in \text{int } S_n \tag{3.1}$$

$$\int_0^T \Psi(\boldsymbol{x}(t))dt > 0 \qquad \text{for some } T > 0,\ \boldsymbol{x} \in \partial S_n \tag{3.2}$$

*then the dynamical system is permanent.*

*Proof.* This proof closely follows the proof of the same statement in [1, 2], with some minor changes.

Choose $T > 0$ in (3.2) as a locally constant function on $\partial S_n$, namely $T(\mathbf{x})$. Therefore $\partial S_n$ can be covered by the open covering induced by $T(\mathbf{x})$, but since $\partial S_n$ is compact, there exists a finite subcovering of the set and hence the function attains its minimum $\tau$, which is clearly positive.

Now for $h > 0$ define the set

$$U_h = \left\{ \mathbf{x} \in S_n : \exists\ T > \tau \text{ such that } \frac{1}{T}\int_0^T \Psi(\mathbf{x}(t))dt > h \right\}$$

and then, for $\mathbf{x} \in U_h$, the function

$$T_h(\mathbf{x}) = \inf \left\{ T > \tau : \frac{1}{T}\int_0^T \Psi(\mathbf{x}(t))dt > h \right\}$$

Notice $\{U_h\}_{h>0}$ is a family of nested sets. Denote with $d(\cdot,\cdot)$ the usual Euclidean metric on $\mathbb{R}^n$.

Claim: For any $\mathbf{x} \in U_h$ and $\alpha > 0$ there exists a $\delta > 0$ such that if $\mathbf{y} \in S_n$ and $d(\mathbf{x},\mathbf{y}) < \delta$, then $\mathbf{y} \in U_h$ and $T_h(\mathbf{y}) \leq T_h(\mathbf{x}) + \alpha$, i.e. $U_h$ is open and $T_h(\mathbf{x})$ is upper semicontinuous on $U_h$.

Proof of claim: Fix $\alpha > 0$, then there exists $T \in [\tau, T_h(\mathbf{x}) + \alpha)$ such that

$$\epsilon := \frac{1}{T}\int_0^T \Psi(\mathbf{x}(t))dt - h > 0$$

Since $\Psi(\mathbf{x})$ is continuous on $S_n$, which is a compact set, then it is also uniformly continuous. Hence there exists $\delta_1 > 0$ such that for all $\mathbf{a}, \mathbf{b} \in S_n$, such that $d(\mathbf{a},\mathbf{b}) < \delta_1$, then

$$|\Psi(\mathbf{a}) - \Psi(\mathbf{b})| < \epsilon.$$

By the continuous dependence of the solution of a differential equation from its initial conditions there exists $\delta > 0$ such that for $\mathbf{x}, \mathbf{y} \in S_n$, and $d(\mathbf{x},\mathbf{y}) < \delta$, then

$$d(\mathbf{x}(t), \mathbf{y}(t)) < \delta_1 \qquad \text{for all } t \in [0, T]\,.$$

Thus, let $\mathbf{x} \in U_h \subset S_n$ and $\mathbf{y} \in S_n$ with $d(\mathbf{x},\mathbf{y}) < \delta$, hence

$$\left| \frac{1}{T}\int_0^T \Psi(\mathbf{x}(t))dt - \frac{1}{T}\int_0^T \Psi(\mathbf{y}(t))dt \right| \leq \frac{1}{T}\int_0^T |\Psi(\mathbf{x}(t)) - \Psi(\mathbf{y}(t))|dt < \epsilon$$

Therefore, directly conclude

$$\frac{1}{T}\int_0^T \Psi(\mathbf{y}(t)) > \frac{1}{T}\int_0^T \Psi(\mathbf{x}(t)) - \epsilon = h$$

which implies that $\mathbf{y} \in U_h$, and $T_h(\mathbf{y}) \leq T < T_h(\mathbf{x}) + \alpha$. ■

Now by (3.2) for each $x \in \partial S_n$, there exists $h > 0$ such that $x \in U_h$. Hence $\{ U_h : h > 0 \}$ is a nested open covering, and by the compactness of $\partial S_n$ we have at least one $h > 0$ such that $\partial S_n \subseteq U_h$. From now on $h$ is fixed in such a way that the simplex is covered by $U_h$.

Since $U_h$ is open, then $S_n \backslash U_h$ is a closed subset of a compact space, hence it is compact as well. On this set the function $P$ attains its minimum. Choose $p > 0$ smaller than the minimum. Now define

$$I(p) = \{ \mathbf{x} \in S_n : 0 < P(\mathbf{x}) \leq p \} \subseteq U_h$$

Claim: If $\mathbf{x} \in I(p)$ then there exists $t > 0$ such that $\mathbf{x}(t) \notin I(p)$
Proof of claim: Suppose, for a contradiction, that the claim is false. Then it is possible to infer that $\mathbf{x}(t) \in U_h$, for all $t > 0$. Therefore, for any $t > 0$, there exists $T \geq \tau$ such that

$$\frac{1}{T}\int_t^{T+t} \Psi(\mathbf{x}(s))ds > h$$

But since we are in int $S_n$ then by (3.1) it follows that $\Psi = \log\dot{(}P)$ and

$$h < \frac{1}{T}\int_t^{T+t} \Psi(\mathbf{x}(s))ds = \frac{1}{T}\int_t^{T+t} \log\dot{(}P)(\mathbf{x}(s))ds = \frac{1}{T}[\log P(\mathbf{x}(T+t)) - \log P(\mathbf{x}(t))]$$

hence

$$P(\mathbf{x}(T+t)) > P(\mathbf{x}(t))e^{hT} \geq P(\mathbf{x}(t))e^{h\tau}.$$

One could then create a positive increasing sequence $\{t_n\}_{n\geq 0}$ with

$$P(\mathbf{x}(t_{n+1})) > P(\mathbf{x}(t_n))e^{h\tau}.$$

This immediately implies that $P(\mathbf{x}(t_n))$ tends to $+\infty$ as $n \to +\infty$, contradicting the boundedness of $P$, deriving from being a continuous function defined on a compact set. ■

Intuitively the closure of $I(p)$ is $\bar{I}(p) = I(p) \cup \partial S_n$. The final claim to prove is the following.
Claim: There exists $q \in (0, p)$ such that if $\mathbf{x}(0) \notin \bar{I}(p)$, then $\mathbf{x}(t) \notin I(q)$, for all $t \geq 0$.
Proof of claim: By the first claim $T_h(\mathbf{x})$ is upper semicontinuous, and hence it has a maximum on the compact set $\bar{I}(p)$, call it $\bar{T}$. Define

$$t_0 = \min\{ t > 0 : \mathbf{x}(t) \in \bar{I}(p) \}$$

i.e. the time when the orbit enters for the first time $\bar{I}(p)$. Let $\mathbf{y} := \mathbf{x}(t_0)$, and hence $P(\mathbf{y}) = p$. Let $m$ be the minimum of $\Psi$ on $S_n$. If $m \geq 0$ everything follows, since it implies that $P$ is never decreasing. Hence assume $m < 0$, and set $q = pe^{m\bar{T}}$. Then for $t \in (0, \bar{T})$

$$\frac{1}{t}\int_0^t \Psi(\mathbf{y}(s))ds \geq m$$

and, following the same idea used in the proof of the second claim,

$$P(\mathbf{y}(t)) \geq P(\mathbf{y})e^{mt} > pe^{m\bar{T}} = q.$$

The solution does not reach $I(q)$ in a time between 0 and $\bar{T}$. But $\mathbf{y} \in I(p)$, so there exists $T \in [\tau, \bar{T})$ such that

$$P(\mathbf{y}(T)) \geq pe^{h\tau} \geq p.$$

Conclude that at the time $T + t$ the orbit $\mathbf{x}(t)$ has left $I(p)$, without having reached $I(q)$. The repetition of this argument shows that the orbit can never reach $I(q)$ at any time. ■

Therefore the orbit is eventually bounded away from the boundary of the simplex. □

The function $P$ used in this theorem can be thought as an *average Lyapunov function*, which measures the distance of $\mathbf{x}$ from $\partial S_n$, and with its time average acting as a Lyapunov function. It is quite straightforward to see that if $\Psi$ is positive then (3.2) is immediately implied, and in particular since $\dot{P} > 0$ for any $\mathbf{x} \in \text{int } S_n$, near the boundary the orbit would be repelled. In this case $P$ behaves like a Lyapunov function. In any other case it is important to use the weaker definition of an average Lyapunov function.

Now that we have establish a criteria for determining if a system is permanent, the aim is to look into an example.

# 4 Hypercycles

Biology has a particular interest in finding out how life firstly originated. The hypotheses are various, and and this project will be focusing on hypercycles. Introduced by Eigen and Schuster in *The Hypercycle - A principle of natural self-organization* [5], hypercycles are a model where one species catalyses the reproduction of the next, until the circle is closed (see Figure 1). This model arises from how fragments of RNA were replicating in the primordial soup. One of the strengths of the model is that, if enough time passes, the species will not extinguish, unless an exterior perturbation kills one particular type, i.e. the system is permanent. Even more surprising is the behaviour of the time averages, which will be analysed in Theorem (4.3).

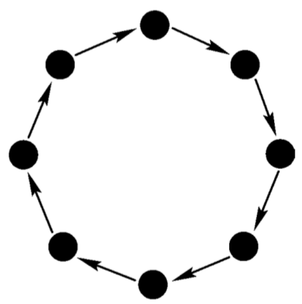

Figure 1: Hypercycle for 8 species [7]

Hypercycles behaviour can be modelled by the replicator equation (2.1). Let $k_i$ be the replication factor between the species $i$ and $i+1$ for $i = 1, 2, \ldots, n$, and where the index $i$ has to be taken mod $n$, i.e. $x_0 = x_n$. The following matrix is then obtained:

$$A = \begin{pmatrix} 0 & 0 & 0 & \ldots & 0 & k_1 \\ k_2 & 0 & 0 & \ldots & 0 & 0 \\ 0 & k_3 & 0 & \ldots & 0 & 0 \\ & & & \vdots & & \\ 0 & 0 & 0 & \ldots & k_n & 0 \end{pmatrix}$$

which yields the *hypercycle equation*

$$\dot{x}_i = x_i \left( k_i x_{i-1} - \sum_{j=1}^{n} k_j x_j x_{j-1} \right). \tag{4.1}$$

Notice that we can assume, without loss of generality, that all the $k_i$ are positive, otherwise the cycle would eventually break. The $x_i$ are the relative frequencies of RNA molecules catalysing each other's replication. The equation (4.1) has a unique interior rest point given by

$$k_1 x_n = k_2 x_1 = \cdots = k_n x_{n-1} \tag{4.2}$$

$$x_1 + x_2 + \cdots + x_n = 1 \tag{4.3}$$

The stability of this point can be easily studied if the coordinates are changed. Set

$$y_i = \frac{k_{i+1} x_i}{\sum_{j=1}^{n} k_{j+1} x_j}.$$

This is a transformation of $S_n$ onto itself. Apply it to (4.1) to obtain

$$\dot{y}_i = y_i \left( y_{i-1} - \sum_{j=1}^{n} y_j y_{j-1} \right) \left( \sum_{s=1}^{n} k_{s+1}^{-1} y_s \right)^{-1}. \tag{4.4}$$

Now notice that the rightmost term is strictly positive. One of the properties of autonomous differential equations is that if two system differ by a positive factor then they share similar orbits. [p. 32: [1]]. Therefore it is possible to exclude the last factor in (4.4) without changing the general behaviour of the orbit. So it is obtained

$$\dot{x}_i = x_i \left( x_{i-1} - \sum_{j=1}^{n} x_j x_{j-1} \right). \tag{4.5}$$

This equation and (4.1) share the same dynamical behaviour, but now the matrix $A$ has been rescaled as

$$A' = \begin{pmatrix} 0 & 0 & 0 & \dots & 0 & 1 \\ 1 & 0 & 0 & \dots & 0 & 0 \\ 0 & 1 & 0 & \dots & 0 & 0 \\ & & & \vdots & & \\ 0 & 0 & 0 & \dots & 1 & 0 \end{pmatrix},$$

a permutation matrix. Now condition (4.2) can be rewritten as

$$x_1 = x_2 = \cdots = x_n \tag{4.6}$$

and together with (4.3) is possible to see that $\mathbf{p} = \frac{1}{n}\mathbf{1}$ in int $S_n$, where $\mathbf{1}$ is an $n \times 1$ column vector whose entries are all 1.

The Jacobian of (4.5) at $\mathbf{p}$:

$$J = \begin{pmatrix} -2\,/\,n^2 & -2\,/\,n^2 & -2\,/\,n^2 & \dots & -2\,/\,n^2 & 1\,/\,n - 2\,/\,n^2 \\ 1\,/\,n - 2\,/\,n^2 & -2\,/\,n^2 & -2\,/\,n^2 & \dots & -2\,/\,n^2 & -2\,/\,n^2 \\ -2\,/\,n^2 & 1\,/\,n - 2\,/\,n^2 & -2\,/\,n^2 & \dots & -2\,/\,n^2 & -2\,/\,n^2 \\ & & & \vdots & & \\ -2\,/\,n^2 & -2\,/\,n^2 & -2\,/\,n^2 & \dots & 1\,/\,n - 2\,/\,n^2 & -2\,/\,n^2 \end{pmatrix}.$$

This is clearly a circulant matrix, and therefore its eigenvalues are

$$\gamma_j = \sum_{k=0}^{n-1} \left( -\frac{2}{n^2} \right) \lambda^{jk} + \frac{1}{n} \lambda^{(n-1)j} = \frac{\lambda^{-j}}{n} \qquad \text{with } \lambda = e^{\frac{2\pi i}{n}}$$

for $j = 1, 2, \dots, n-1$, and $\gamma_0 = \frac{1}{n}$. The eigenvector associated with $\gamma_0$ is $\mathbf{1}$, and therefore normal to $S_n$. It has no relevance to us, since the state space considered is restricted to the simplex. If $n = 2$ the other eigenvalue is $\gamma_1 = \frac{e^{2\pi i}}{2}$, whose real part is $-\frac{1}{2}$. Therefore the rest point is stable. Now suppose that $n = 3$, hence

$$\gamma_j = \frac{1}{3} e^{-\frac{2j\pi i}{3}}, \qquad \text{for } j = 1, 2$$

whose real part is $-\frac{1}{6}$, for $j = 1, 2$. In this case the rest point is stable. This reasoning can not be applied in the case where $n = 4$, since two of the eigenvalues belong to the imaginary axis. Nonetheless, by using a Lyapunov function, it is still possible to assess the stability of the rest point.

Let

$$P(\mathbf{x}) = x_1 x_2 \dots x_n$$

be a Lyapunov function. $P$ vanishes on the boundary of the simplex, and it is positive in its interior. Note that

$$\begin{aligned} \dot{\log P}(\mathbf{x}) &= \sum_{i=1}^{n} \frac{\dot{x}_i}{x_i} \\ &= 1 - n\sum_{j=1}^{n} x_j x_{j-1} \end{aligned}$$

Let $n = 2, 3$. The derivative is everywhere negative, and it is equal to zero at $\mathbf{p}$. This is in line with what was previously proved via eigenvalues. Now set $n = 4$ so that

$$\dot{\log P}(\mathbf{x}) = 1 - 4(x_1 + x_3)(x_2 + x_4) \geq 0$$

since $(x_1 + x_3) + (x_2 + x_4) = 1$ then the only zero in that function is when $(x_1 + x_3) = (x_2 + x_3) = \frac{1}{2}$. Now consider the set $M = \left\{\mathbf{x} \in S_4 : x_1 + x_3 = x_2 + x_4 = \frac{1}{2}\right\}$. Here clearly $\mathbf{p} \in M$, and it is the only element in the invariant set of $M$. Therefore $\mathbf{p}$ is stable even in the case where $n = 4$. For $n \geq 5$ the rest point is unstable, since the eigenvalues have real positive parts. At first one might suppose that the orbit would eventually converge to the boundary, but that is not the case, since the system turns out to be permanent.

**Proposition 4.1.** *The hypercycle system* (4.1) *is permanent.*

*Proof.* This proof considers the most general hypercycle system and uses the same notation as in Theorem (3.1). It closely follows the work of Hofabuer [1]. The Lyapunov function considered above is an excellent candidate for our choice of $P$. Set

$$P(\mathbf{x}) = \prod_{j=1}^{n} x_j.$$

Note that its derivative can be rewritten in terms of $P$, i.e $\dot{P}(\mathbf{x}) = P(\mathbf{x})\Psi(\mathbf{x})$. So in this case define

$$\bar{f}(\mathbf{x}) = \sum_{j=1}^{n} k_j x_j x_{j-1}$$

and, therefore, it follows that

$$\Psi(\mathbf{x}) = \sum_{i=1}^{n} k_i x_{i-1} - n\bar{f}(\mathbf{x}).$$

Condition (3.1) from Theorem (3.1) clearly holds in int $S_n$.
<u>Claim:</u> For all $\mathbf{x} \in \partial S_n$, there exists $T > 0$ such that $\frac{1}{T}\int_0^T \Psi(\mathbf{x}(t))dt > 0$, i.e. condition (3.2) from Theorem (3.1).
<u>Proof of claim:</u> The condition in the claim can be rewritten as

$$\frac{1}{T}\int_0^T \sum_{i=1}^{n} k_i x_{i-1} - n\bar{f}(\mathbf{x}(t))dt > 0$$

for some time $T > 0$, or equivalently

$$\frac{1}{T}\int_0^T \bar{f}(\mathbf{x}(t))dt < \frac{1}{nT}\int_0^T \sum_{i=1}^{n} k_i x_{i-1} dt. \tag{4.7}$$

Now set $k = \min_i k_i > 0$, so that $\sum_{i=1}^{n} k_i \geq k$. Hence, the right hand side of (4.7) is never smaller than $\frac{k}{n}$. Therefore, the new claim is to show that there exists no $\mathbf{x} \in \partial S_n$ such that

$$\frac{1}{T}\int_0^T \bar{f}(\mathbf{x}(t))dt \geq \frac{k}{n}. \tag{4.8}$$

Proceed by contradiction. Assume there exists such a $\mathbf{x} \in \partial S_n$, so that (4.8) holds. In order to show the contradiction, it will be proved by induction that if (4.7) holds then

$$\lim_{t\to+\infty} x_i(t) = 0 \qquad \text{for all } i = 1, 2, \ldots, n \tag{4.9}$$

Since $x \in \partial S_n$ there exists at least one vector component $x_{i_0} \equiv 0$, because if an orbit hits the boundary it can not leave it. This is going to be the base case for the induction. The inductive hypothesis states that if $x_i(t) \to 0$ as $t \to +\infty$, then so does $x_{i+1}$. Since $\mathbf{0} \notin S_n$ we can suppose, without loss of generality, that there exists $x_{i+1}(t) > 0$ for some time $t$. Hence

$$\log(\dot{x}_{i+1}) = \frac{\dot{x}_{i+1}}{x_{i+1}} = k_{i+1}x_i - \bar{f}(\mathbf{x}),$$

and by integrating this expression from 0 to $T$, and dividing it by $T$

$$\begin{aligned}
\frac{\log(x_{i+1}(T)) - \log(x_{i+1}(0))}{T} &= \frac{1}{T}\int_0^T \log(\dot{x}_{i+1}(t))dt \\
&= \frac{1}{T}\int_0^T k_{i+1}x_i(t)dt - \frac{1}{T}\int_0^T \bar{f}(\mathbf{x}(t))dt \\
&\leq \frac{1}{T}\int_0^T k_{i+1}x_i(t)dt - \frac{k}{n}.
\end{aligned}$$

Since $x_i(t) \to 0$ as $t \to +\infty$ the first term of the right hand side can be bounded for $T$ sufficiently large:

$$\frac{1}{T}\int_0^T k_{i+1}x_i(t)dt < \frac{k}{2n}.$$

This implies that

$$\log(x_{i+1}(T)) - \log(x_{i+1}(0)) < -\frac{kT}{2n},$$

which yields

$$x_{i+1}(T) < x_{i+1}(0)e^{-\frac{kT}{2n}}.$$

Therefore it is possible to conclude that $x_{i+1} \to 0$ as $t \to +\infty$ and, moreover, (4.9) holds by induction. This contradicts the fact that $\sum_{i=1}^{n} x_i(t) = 1$, for all times $t$. Therefore the contradiction is reached. Finally for all $\mathbf{x} \in \partial S_n$, there exists $T > 0$ such that

$$\frac{1}{T}\int_0^T \bar{f}(\mathbf{x}(t))dt < \frac{k}{n} \leq \frac{1}{nT}\int_0^T \sum_{i=1}^{n} k_i x_{i-1}$$

The claim is proved. ■

Hence the function $P(\mathbf{x})$ satisfies both conditions (3.1) and (3.2), so the hypercycle system (4.1) is permanent by theorem (3.1). □

This proof can be used to show that even if the constants $k_i$ are replaced in (4.1) by positive functions the system is still permanent [p. 145: [1]]. Since the more general equation (2.1) is permanent, it immediately follows that (4.5) is permanent as well, i.e. the hypercycle system where all $k_i = 1$ is permanent.

Because of the permanence, the orbit of (2.1) is eventually bounded away from the boundary of $S_n$. Since there exists as well an interior rest point, theorem (2.2) applies, and it is possible to conclude that given $\hat{\mathbf{x}} \in S_n$ the rest point of (4.1),

$$\lim_{T\to\infty} \frac{1}{T}\int_0^T \mathbf{x}(t)dt = \hat{\mathbf{x}}.$$

Permanence is quite a strong condition and therefore it allows this result to be extended by using the following theorem.

**Theorem 4.2.** *If the system $\dot{x}_i = x_i f_i(\boldsymbol{x})$ on $\mathbb{R}^n_+$ is permanent, in the sense that there exists a compact set $K$ in the interior of the state space such that all the orbits of the interior end up in $K$, then the degree of the vector field is $(-1)^n$ with respect to any bounded set U, such that $U \subseteq$ int $\mathbb{R}^n_+$, containing all interior $\omega$-limits. In particular, there exists a rest point in int $\mathbb{R}^n_+$*

The proof of this theorem is beyond the scope of this project but it can be found at page 158 in Hofbauer, J., Sigmund, K. [1]. What is of interest for this project is the existence of at least one rest point in every permanent system of a certain kind. Combining this result with Proposition (2.2) and its variation for the Lotka-Volterra equation [pp. 44-45: [1]], the following result follows.

**Theorem 4.3.** *If $\dot{x}_i = x_i((A\boldsymbol{x})_i - \boldsymbol{x}\cdot A\boldsymbol{x})$ for $\boldsymbol{x} \in S_n$ (replicator dynamics equation) or $\dot{x}_i = x_i((r_i + (A\boldsymbol{x})_i))$ for $\boldsymbol{x} \in \mathbb{R}^n_+$, and $r_i \in \mathbb{R}$ for all $i = 1, 2, \dots, n$ (Lotka-Volterra equation) is permanent, then there exists a unique interior rest point $\hat{\boldsymbol{x}}$, and for each $\boldsymbol{x}$ in the interior of the state space*

$$\lim_{T\to+\infty} \frac{1}{T}\int_0^T \boldsymbol{x}(t)dt = \hat{\boldsymbol{x}}.$$

*Proof.* By Theorem (4.2) there exists at least one rest point in the interior of the state space. Suppose there exists two such rest points $\mathbf{x}_1$ and $\mathbf{x}_2$, both belonging to the interior of the state space. It follows from Section 2 that if the replicator dynamics equation is considered

$$A\mathbf{x}_1 = c_1\mathbf{1}$$
$$A\mathbf{x}_2 = c_2\mathbf{1},$$

where $c_1$, and $c_2$ are some real constants, and $\mathbf{1}$ is the $n\times 1$ column vector whose entries are all 1. Any point on the line passing through $\mathbf{x}_1$ and $\mathbf{x}_2$ can be written as

$$\mathbf{m} = \lambda\mathbf{x}_1 + (1-\lambda)\mathbf{x}_2,$$

for $\lambda \in \mathbb{R}$. Therefore $\mathbf{m}$ is a rest point as well, in fact

$$\begin{aligned}(A\mathbf{m})_i - \mathbf{m} \cdot A\mathbf{m} &= (A(\lambda \mathbf{x}_1 + (1-\lambda)\mathbf{x}_2))_i - (\lambda \mathbf{x}_1 + (1-\lambda)\mathbf{x}_2) \cdot A(\lambda \mathbf{x}_1 + (1-\lambda)\mathbf{x}_2) \\ &= \lambda c_1 + (1-\lambda)c_2 - (\lambda \mathbf{x}_1 + (1-\lambda)\mathbf{x}_2) \cdot (\lambda c_1 \mathbf{1} + (1-\lambda)c_2 \mathbf{1}) \\ &= \lambda c_1 + (1-\lambda)c_2 - \lambda^2 c_1 - (1-\lambda)^2 c_2 - \lambda(1-\lambda)c_2 - \lambda(1-\lambda)c_1 \\ &= \lambda(c_1 - \lambda c_1 - c_1 + \lambda c_1) + (1-\lambda)(c_2 - c_2 + \lambda c_2 - \lambda c_2) \\ &= 0.\end{aligned}$$

The line joining $\mathbf{x}_1$ and $\mathbf{x}_2$ is made of rest points, and it will eventually intersect the boundary of the state space. Since the system is permanent, the boundary is repelling, and therefore there can not be rest points arbitrarily close to it. By contradiction there can not be more than one rest point in the interior of the system. An analogous computation proves this fact for the Lotka-Volterra equation. Again, by permanence, if $\mathbf{x}$ is in the interior of the state space, so is $\omega(\mathbf{x})$. Proposition (2.2) hence follows, for the replicator equation. In the case where the system is modelled by the Lotka-Volterra equation one can follow the same procedure as in the proof of Proposition (2.2) to show the convergence. □

# 5 Conclusion

Thanks to these results it is possible to conclude that the hypercycles, even when composed by more than four species, reach a certain stability. This stability has not to be interpreted in the classical sense, but in the permanence sense, i.e. given enough time for the system to start developing, it is possible to reach the stage where no species are threatened with extinction. This clearly would have been fundamental in the early stages of pre-biotic life, since it would have granted enough time for the fragments of RNA to develop all the mutations needed to constitute life.

What is really astonishing is the behaviour of the densities of the various types of population: even though it was virtually impossible for all the species to reach a perfect density equilibrium, i.e. for the system to reach its rest point, once their time averages are considered one can clearly see that a certain regularity arises here as well. Not only does the limit of these averages exists, but it tends to the equilibrium density that each species would have at the rest point of the system. Therefore, even in systems where stability does not seem to exists at first, it is possible to achieve a certain regularity in an unexpected way.

# References

[1] Hofbauer, J., Sigmund, K. *Evolutionary Games and Population Dynamics.* Cambridge: Cambridge University Press; 1998.

[2] Hofbauer, J. A general cooperation theorem for hypercycles. *Monatshefte für Mathematik.* 1981; 91(3): 233-240 Available from: https://doi.org/10.1007/BF01301790.

[3] Hutson, V., Schmitt, K. Permanence and the Dynamics of Biological Systems. *Mathematical Biosciences.* 1992; 111(1): 1-71 Available from: https://doi.org/10.1016/0025-5564(92)90078-B.

[4] Schuster, P., Hofbauer, J., Wolff, R. Selfregulation of behaviour in animal societies, I. Symmetric contests. *Biological Cybernetics* 1981; 40(1) Available from: https://doi.org/10.1007/BF00326675.

[5] Eigen, M., Schuster, P. The Hypercycle - A principle of natural self-organization. Part B: The abstract hypercycle. *Naturwissenschaften* 1978; 65(7): 7-41 Available at: https://doi.org/10.1007/BF00420631.

[6] Van Strien S. *Games and Dynamics: Lecture Notes* [Lecture notes] Imperial College, London. Autumn 2015.

[7] Ay N., Erb I. On a Notion of Linear Replicator Equations. *Journal of Dynamics and Differential Equations* 2005; 17(2): 427-451 DOI: https://doi.org/10.1007/s10884-005-4574-3