Coexistence stability in a four-member hypercycle with error tail through center manifold analysis

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COEXISTENCE STABILITY IN A FOUR-MEMBER HYPERCYCLE WITH ERROR TAIL THROUGH CENTER MANIFOLD ANALYSIS

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ABSTRACT. Establishing the conditions allowing for the stable coexistence in hypercycles has been a subject of intensive research in the past decades. Deterministic, time-continuous models have indicated that, under appropriate parameter values, hypercycles are bistable systems, having two asymptotically stable attractors governing coexistence and extinction of all hypercycle members. The nature of the coexistence attractor is largely determined by the size of the hypercycle. For instance, for 2-member hypercycles the coexistence attractor is a stable node. For larger dimensions more complex dynamics appear. Numerical results on so-called elementary hypercycles with $n = 3$ and $n = 4$ species revealed, respectively, coexistence via strongly- and weakly-damped oscillations. Stability conditions for these cases have been provided by linear stability and Lyapunov functions. Typically, linear stability analysis of 4-member hypercycles indicates two purely imaginary eigenvalues and two negative real eigenvalues. For this case, stability can not be fully characterized linearizing near the fixed point. In this letter we determine the stability of a non-elementary 4-member hypercycle which considers exponential and hyperbolic replication terms under mutation giving place to an error tail. Since Lyapunov functions are not available for this case, we use the center manifold theory to rigorously show that the system has a stable coexistence fixed point. Our results also show that this fixed point can not undergo a Hopf bifurcation, as supported by numerical simulations previously reported.

1. INTRODUCTION

The stability of hypercycles is a very important subject of research within the origin-of-life framework. Hypercycles are catalytic sets of macromolecules that can catalyze their own replication or the replication of other species of the network, which usually has cyclic architecture [5]. Catalytic sets have been a subject of study in different fields. For instance, hypercycles have been largely investigated in the framework of prebiotic evolution [2, 5, 11, 18], suggested of being

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responsible for one the major transitions in evolution: the transition from quasispecies to hypercycles as a possible way to surpass the information crisis at early stages of biological evolution [4, 5, 18]. Hypercycle equations have been also used to study the dynamics of other complex systems. For instance, ecological dynamical systems [8, 13, 18, 19].

The conditions allowing the asymptotic persistence of hypercycles have been investigated during the past decades. The nature of the coexistence attractor for small hypercycles is well known. For instance, when $n = 2$, the coexistence attractor is a stable node [5, 12, 14, 15] since linearization near these equilibria revealed two negative eigenvalues. For larger hypercycles the nature of the coexistence attractor slightly changes. Specifically, the stability for the so-called elementary hypercycle in [5] has been determined by using Lyapunov functions. Together with these results, further numerical simulations have revealed that hypercycles with $n = 3$ and $n = 4$ have, respectively, a coexistence attractor which is achieved via fastly- and weakly-damped oscillations [5, 16]. For the $n = 4$ dimension, linear stability analysis shows two imaginary eigenvalues with zero real part and two negative eigenvalues. This particular condition does not allow to characterize the stability of this putative attractor. As mentioned, in the elementary hypercycle studied in Ref. [5] the stability for $n = 4$ was determined using a Lyapunov function. For the system explored in this letter, which considers the hypercycle with the error tail, it is not clear at all how to find a Lyapunov function. However, a rigorous stability analysis can be performed using the center manifold theory.

In this letter we perform this analysis showing that the dynamics restricted to the center manifold corresponding to the two imaginary eigenvalues is a stable (degenerate) focus of order two, which implies that this equilibrium point is certainly an attractor. Our study also shows that the stable fixed point can not undergo a Hopf bifurcation, thus no periodic orbits can born from this equilibrium point.

2. MATHEMATICAL MODEL

The hypercycle model we analyze describes the time evolution of the relative concentration of n molecular species with the so-called error tail [2, 17]. If we denote by $\{I_1, \ldots, I_n\}$ the hypercycle species and I_e the species forming the error tail, the differential equations describing their concentrations $x = (x_1, \ldots, x_n)$ and x_e are

$$(1) \qquad \dot{x}_i = x_i(A_i Q + K_i x_{i-1} Q - \hat{\Phi}(x, x_e)),$$

for $i = 1, \ldots, n$, and

$$\dot{x}_e = x_e(A_e - \Phi(x, x_e)) + (1 - Q)\sum_{i=1}^{n} x_i(A_i + K_i x_{i-1}),$$

where $x_0 \equiv x_n$, $K_i, A_i > 0$, $1 \le i \le n$, $A_e > 0$, $Q \in (0,1)$ and

$$\hat{\Phi}(x, x_e) = \sum_{i=1}^{n} x_i(A_i + K_i x_{i-1}) + A_e x_e.$$

System (1) describes a hypercycle model of dimension n with both Malthusian and heterocatalytic (nonlinear) reproduction together with mutation. Both constants A_i and K_i denote the Malthusian and heterocatalytic replication rates, respectively. The parameter Q is the replication quality factor or copying fidelity. Finally, $\hat{\Phi}(x, x_e)$ is the dilution flow that keeps the total population constant; it also introduces competition between all the replicators forming the hypercycle and the error tail.

The hyperplane $H = \{(x, x_e) \in \mathbb{R}^{n+1} | \sum_{i=1}^{n} x_i + x_e = 1\}$ is invariant by the flow. Accordingly, we will restrict our study to the solutions in H. Moreover, we can forget about the error tail and omit the term x_e because it is given by $x_e = 1 - \sum_{i=1}^{n} x_i$. Thus we are let to consider the differential equation

$$(2) \qquad \dot{x}_i = f_i(x) = x_i(A_i Q + K_i x_{i-1} Q - \Phi(x)),$$

$1 \le i \le n$, where $\Phi(x) = \sum_{i=1}^{n} x_i(A_i + K_i x_{i-1}) + A_e(1 - \sum_{i=1}^{n} x_i)$ and $x = (x_1, \ldots, x_n)$.

We will restrict to the biological meaningful region, namely the set

$$S = \left\{ (x_1, \ldots, x_n) \mid 0 \le x_i \le 1, \sum_{i=1}^{n} x_i \le 1 \right\},$$

which is positively invariant by the evolution of the hypercyclel. That is, the flow will never come out from S and it will exist for any positive time. Additionally, we will assume that $K_i = 1$ to simplify the model.

3. The symmetric hypercycle

We will take $A_i = A_e = a$, $\forall i \in \{1, \ldots, n\}$, for some $a > 0$. We refer to this case as the symmetric hypercycle, which assumes that all hypercycle elements are selectively neutral. The following proposition gives the equilibrium points in any dimension. The proof is an elementary computation which can be found in [10].

Proposition 1. *For the values of (a, Q) such that $Q^2/(1 - Q) \geq 4na$, Eq. (2) has three fixed points in S: $x_0 = \vec{0}$, and x_+^*, x_-^*, whose coordinates are*

$$x_{\pm, i}^* = \frac{Q \pm \sqrt{Q^2 - 4na(1 - Q)}}{2n},$$

for all $i \in \{1, \ldots, n\}$. When $Q^2/(1 - Q) < 4na$, the only fixed point of Eq. (2) in S is the origin.

The coordinates of the non trivial equilibrium points are actually the two solutions of $nx_i^2 - Qx_i + a(1 - Q) = 0$. Notice that for $Q = Q_{SS} := 2\left(\sqrt{na(1 + na)} - na\right)$ a saddle-node bifurcation occurs and the two equilibria x_+^* and x_-^* appear for $Q > Q_{SS}$.
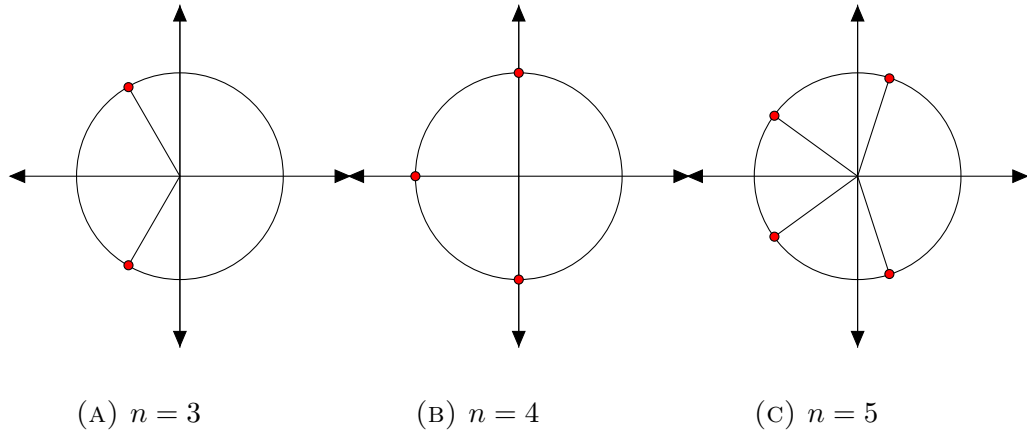

(A) $n = 3$ (B) $n = 4$ (C) $n = 5$

FIGURE 1. Eigenvalues λ_j^+ for $0 < j < n$ on the circle of radius $k = Q\,x_{+,1}^*$ in $\mathbb{C}$. The case $n = 4$, analyzed in this letter, displays two eigenvalues with negative real part and a couple of complex eigenvalues with zero real part (λ_0^+ is not displayed).

3.1. **Stability of the equilibrium points.** In this section we will classify the character of the fixed points. We first note that the right-hand side of (2) for the symmetric case can be written as

$$f_i(x) = x_i F_i(x), \qquad i \in \{1, \ldots, n\},$$

where $F_i(x) = a(Q - 1) + Qx_{i-1} - \sum_{j=1}^n x_j x_{j-1}$.

Since

$$\frac{\partial f_i}{\partial x_j}(x) = \delta_{ij} F_i(x) + x_i \frac{\partial F_i}{\partial x_j}(x),$$

where δ_{ij} is the Kronecker delta function and

$$\frac{\partial F_i}{\partial x_j}(x) = \begin{cases} Q - x_{j+1} - x_{j-1}, & j = i - 1, \\ -x_{j+1} - x_{j-1}, & j \neq i - 1, \end{cases}$$

it turns out that the components of the Jacobian of f are

$$(3) \qquad \frac{\partial f_i}{\partial x_j}(x) = \begin{cases} x_i(Q - x_{j+1} - x_{j-1}), & j = i - 1, \\ x_i(-x_{j+1} - x_{j-1}), & j \notin \{i - 1, i\}, \\ F_i(x) + x_i(-x_{i+1} - x_{i-1}), & j = i. \end{cases}$$

Substitution of $x_i = 0$, for all $i = 1, \ldots, n$, into (3) leads to $\mathrm{D}f(\vec{0}) = \mathrm{diag}(a(Q-1), \ldots, a(Q-1))$. Therefore the eigenvalues of $\mathrm{D}f(\vec{0})$ are all equal to $a(Q-1) < 0$ so $x^* = \vec{0}$ is an attracting fixed point independently of the parameter values (a, Q), $a > 0$, $Q \in (0, 1)$. In the same way we will analyze the stability of the fixed points x_+^* and x_-^* given in Proposition 1. Using again equation (3), together with the fact that all the components are equal, we obtain the following expression for the entries of the Jacobian matrix

$$\frac{\partial f_i}{\partial x_j}(x_\pm^*) = \begin{cases} x_{\pm,1}^*(Q - 2x_{\pm,1}^*), & j = i - 1, \\ -2(x_{\pm,1}^*)^2, & j \notin \{i - 1, i\}, \\ F_i(x_{\pm,1}^*) - 2(x_{\pm,1}^*)^2, & j = i. \end{cases}$$

Notice that $F(x_{\pm,1}^*) = a(Q-1) + Qx_{\pm,1}^* - n(x_{\pm,1}^*)^2 = 0$, because the coordinates $x_{\pm,1}^*$ are exactly the solutions of $nx_i^2 - Qx_i + a(1-Q) = 0$. Therefore if we denote $b_\pm := -2(x_{\pm,1}^*)^2$ and $d_\pm := x_{\pm,1}^*(Q - 2x_{\pm,1}^*)$,

$$\mathrm{D}f(x_\pm^*) = \begin{pmatrix} b_\pm & b_\pm & \ldots & b_\pm & d_\pm \\ d_\pm & \ddots & \ddots & \ddots & b_\pm \\ b_\pm & \ddots & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & b_\pm \\ b_\pm & \ldots & b_\pm & d_\pm & b_\pm \end{pmatrix},$$

which is a circulant matrix. There are explicit formulas to get the eigenvalues and the eigenvectors for circulant matrices, see e.g., [7]. In our case, these formulas give

$$\lambda_j^\pm = \sum_{k=0}^{n-2} -2(x_{\pm,1}^*)^2 \exp\left(2\pi i\, jk/n\right)$$

$$(4) \qquad\qquad + x_{\pm,1}^*(Q - 2x_{\pm,1}^*) \exp\left(2\pi i\, j(n-1)/n\right),$$

where $i^2 = -1$ and $j \in \{0, \ldots, n-1\}$. If $j \neq 0$, using that the sum of the geometric progression $\sum_{k=0}^{n-1} \exp\left(2\pi i \, jk/n\right)$ is zero, we can simplify (4) to obtain:

$$\lambda_j^\pm = x_{\pm,1}^* Q \exp\left(2\pi i \, j(n-1)/n\right), \quad j \in \{1, \ldots, n-1\}.$$

For $j = 0$ we get:

$$\lambda_0^\pm = x_{\pm,1}^*(Q - 2x_{\pm,1}^*) - 2(n-1)(x_{\pm,1}^*)^2$$

$$= Qx_{\pm,1}^* - 2n(x_{\pm,1}^*)^2 = -Qx_{\pm,1}^* + 2a(1 - Q),$$

using that $a(Q-1) + Qx_{\pm,1}^* - n(x_{\pm,1}^*)^2 = 0$.

Observe that for x_-^* we have that $\lambda_0^- > 0$, and so x_-^* is unstable independently of the character of other eigenvalues. On the other hand, since $\lambda_0^+ = x_{+,1}^*(Q - 2nx_{+,1}^*)$ and $x_{+,1}^* > Q/(2n) > 0$, then $\lambda_0^+ < 0$. Thus, to determine the stability character of x_+^* we need to study the sign of the real part of λ_j^+ for $0 < j \leq n$. As it is illustrated in Figure 1, we have that for $n \leq 3$ all these eigenvalues have negative real part and for $n \geq 5$ we will always have eigenvalues with positive real part. Therefore for $n \leq 3$ the equilibrium point x_+^* is an attractor and for $n \geq 5$ it is unstable. It remains the discussion in the case $n = 4$, for which x_+^* is non hyperbolic.

3.2. Stability of x_+^* when $n = 4$.

In order to simplify the notation, we introduce the parameters $k := Q\, x_{+,1}^*$ and $c := k - 2a(1 - Q)$. Notice that both k and c are positive. Then, for $n = 4$, the eigenvalues of $\mathrm{D}f(x_\pm^*)$ read as

$$\lambda_0^+ = -c, \qquad\qquad \lambda_1^+ = ke^{2\pi i \frac{3}{4}} = -ik,$$

$$\lambda_2^+ = ke^{2\pi i \frac{3}{2}} = -k, \qquad \lambda_3^+ = ke^{2\pi i \frac{9}{4}} = ik,$$

and their corresponding eigenvectors are:

$$v_0 = (1, 1, 1, 1)^\top, \qquad\qquad v_1 = (1, i, -1, -i)^\top,$$

$$v_2 = (1, -1, 1, -1)^\top, \qquad\qquad v_3 = (1, -i, -1, i)^\top.$$

The invariant subspace generated by v_1 and v_3 (thought as a vector space over $\mathbb{C}$) is also generated by $w_1 := \frac{1}{2}(v_1 + v_3)$, $w_2 := \frac{i}{2}(v_3 - v_1)$ and moreover,

$$\mathrm{D}f(x_\pm^*)w_1 = -\frac{i}{2}kv_1 + \frac{i}{2}kv_3 = kw_2,$$

$$\mathrm{D}f(x_\pm^*)w_2 = -\frac{1}{2}kv_1 - \frac{1}{2}kv_3 = -kw_1.$$

This linear study is not sufficient to draw conclusions about the stability of the equilibrium $x_{+,1}^*$. At this point, we know that two eigenvalues are negative and the other two have zero real part. Moreover, in this situation, the point x_+^* has

a center manifold which is tangent to the linear space generated by v_1 and v_3. If we are able to prove that the equilibrium point of the system restricted to the center manifold is asymptotically stable, then by Theorem 2 in [3, Ch. 1] we will prove that the equilibrium of the four dimensional system (2) is asymptotically stable. Let us then compute the center manifold and study the restriction of (2) on it.

To reduce the vector field to the central manifold it is convenient to perform a translation of the point x_+^*, say $z = x - x_+^*$ to the origin followed by a linear change $z = C\,y$, where C is the matrix whose columns are the vectors w_1, w_2, v_2 and v_0, that is,

$$C = \begin{pmatrix} 1 & 0 & 1 & 1 \\ 0 & 1 & -1 & 1 \\ -1 & 0 & 1 & 1 \\ 0 & -1 & -1 & 1 \end{pmatrix},$$

In the new set of variables $y = (y_1, y_2, y_3, y_4)$, the vector field is expressed as

$$(5) \qquad \dot{y} = C^{-1} f\left(C\,y + x_+^*\right) =: G(y),$$

which is topologically conjugate to (2) since translations and invertible linear maps are diffeomorphisms.

Performing the whole calculation and using the fact that $a(Q-1) + Qx_{+,1}^* - 4(x_{+,1}^*)^2 = 0$, we can express $G(y) = G_1(y) + G_2(y) + G_3(y)$, where the subindex stands for the degree of the polynomial in y and

$$G_1(y) = \begin{pmatrix} -k\,y_2 \\ k\,y_1 \\ -k\,y_3 \\ -c\,y_4 \end{pmatrix}, \qquad G_3(y) = 4(y_3^2 - y_4^2)\begin{pmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \end{pmatrix},$$

$$G_2(y) = \begin{pmatrix} Q(y_1(y_4 - y_3) - y_2(y_3 + y_4)) - 8x_{+,1}^* y_1 y_4 \\ Q(y_1(y_4 - y_3) + y_2(y_3 + y_4)) - 8x_{+,1}^* y_2 y_4 \\ -(Qy_1 y_2 + 8x_{+,1}^* y_3 y_4) \\ (-Q + 4x_+^*)y_3^2 + (Q - 12x_{+,1}^*)y_4^2 \end{pmatrix}.$$

Notice that now the linear part of the system corresponds to the expected one.

3.3. **Reduction to the center manifold.** The resulting system (5) is polynomial of degree 3 and therefore a C^∞ function. Thus by the center manifold theorem [3] we know that $\vec{0}$ has a center manifold $W^c = \mathrm{graph}(h)$ tangent to the vector space generated by the eigenvectors corresponding to the eigenvalues with zero real part, that is, the plane generated by y_1 and y_2. The center manifold is

locally parameterized by a C^r function h with r as large as we want. We rewrite (5) in the form

$$
(6) \qquad \begin{cases} \dot{\xi} &= A\,\xi + u(\xi,\eta), \\ \dot{\eta} &= B\,\eta + v(\xi,\eta), \end{cases}
$$

with $\xi = (y_1, y_2)$, $\eta = (y_3, y_4)$,

$$
A = \begin{pmatrix} 0 & -k \\ k & 0 \end{pmatrix} \quad \text{and} \quad B = \begin{pmatrix} -k & 0 \\ 0 & -c \end{pmatrix},
$$

and $u(\xi,\eta)$ and $v(\xi,\eta)$ represent the nonlinear terms of the system.

In this notation, W^c is represented by $\eta = h(\xi)$. Then, the condition of graph(h) being invariant by (6) is $\dot{\eta} = Dh(\xi)\dot{\xi}$, that is,

$$
B\,\eta + v(\xi,\eta) = Dh(\xi)\,(A\,\xi + u(\xi,\eta)) .
$$

Substituting $\eta = h(\xi)$ into this equation gives

$$
(7) \qquad B\,h(\xi) + v(\xi,h(\xi)) = Dh(\xi)\,(A\,\xi + u(\xi,h(\xi))) .
$$

From now on, we rename variables y_1 and y_2 by x and y, respectively, so that $\xi = (x,y)$. For our purposes it is enough to know the quadratic terms of the function h; accordingly, we write

$$
(8) \qquad h(x,y) = \begin{pmatrix} a_{20}x^2 + a_{11}xy + a_{02}y^2 \\ b_{20}x^2 + b_{11}xy + b_{02}y^2 \end{pmatrix} + \mathcal{O}(3).
$$

Substituting (8) into (7), we have

$$
\begin{pmatrix} -ka_{20}x^2 - ka_{02}y^2 - (ka_{11} + Q)\,xy \\ -c(b_{20}x^2 + b_{02}y^2 + b_{11}xy) \end{pmatrix} = k \begin{pmatrix} a_{11}x^2 - a_{11}y^2 + 2(a_{02} - a_{20})xy \\ b_{11}x^2 - b_{11}y^2 + 2(b_{02} - b_{20})xy \end{pmatrix},
$$

from which we obtain

$$
a_{11} = -\frac{Q}{5k}, \quad a_{20} = \frac{Q}{5k}, \quad a_{02} = -\frac{Q}{5k},
$$
$$
b_{11} = 0, \qquad b_{20} = 0, \qquad b_{02} = 0.
$$

Thus, our function h will be

$$
h(x,y) = \begin{pmatrix} \dfrac{Q}{5k}(x^2 - xy - y^2) \\[2mm] 0 \end{pmatrix} + \mathcal{O}(3).
$$

Now, we can write the system restricted to the center manifold, $A \begin{pmatrix} x \\ y \end{pmatrix} + u(x, y, h(x, y))$, which reads as

$$(9) \quad \begin{cases} \dot{x} = -ky - \dfrac{Q^2}{5k}(x^3 - 2xy^2 - y^3) + \mathcal{O}(4), \\[2mm] \dot{y} = kx - \dfrac{Q^2}{5k}(x^3 - 2x^2y + y^3) + \mathcal{O}(4). \end{cases}$$

A first attempt to determine the stability of $\vec{0}$ is to change to polar coordinates (r, θ). The derivative of r is:

$$\dot{r} = r^3 \frac{Q^2}{5k} \left[\sin^3 \theta \, (\cos \theta - \sin \theta) - \cos^3 \theta \, (\cos \theta + \sin \theta) + 4 \cos^2 \theta \sin^2 \theta \right].$$

We note that the sign of $\dot{r}$ depends on θ, see Figure 2(upper), so it does not provide a conclusive information concerning stability. However, the flow of the vector field of system (9), see Figure 2(lower), shows evidence that the equilibrium point is stable.

In order to prove the stability, we will look for the normal form of the system at the origin, see [9, Ch. 3.3]. For this purpose it is convenient to write system (9) in complex variables, $z = x + i\,y$ and $\overline{z} = x - i\,y$:

$$(10) \quad \dot{z} = ikz - (1 + 3\,i)\frac{Q^2}{20\,k}\, z^2 \overline{z} - (3 + i)\frac{Q^2}{20\,k}\, \overline{z}^3 + \mathcal{O}(4),$$

and the equation for $\overline{z}$, which is the complex conjugate of the one for z. In these variables, the linear part is diagonal. An additional advantage of working in these variables is that we only need to transform one equation because the other remains its conjugate. Since the eigenvalues are $\pm ik$, the resonant terms for the equation (10) are $z^{n+1}\overline{z}^n$, with $n \geq 1$. The explicit calculations give that the normal form of (10) is

$$(11) \quad \dot{z} = ikz - \frac{Q^2 \, (1 + 3\,i)}{20k} z^2 \overline{z} + \mathcal{O}(5).$$

Alternatively, we can apply Theorem A in [6] to system (10), see [1, Ch. IX.2] for a more classical reference, to conclude that $\vec{0}$ is an attracting equilibrium point. However, for this case we can proceed directly writing (11) in polar coordinates by means of the change $z = r\,e^{i\theta}$, which leads to

$$\begin{cases} \dot{r} &= -\dfrac{Q^2}{20\,k}r^3 + \mathcal{O}(5), \\[2mm] \dot{\theta} &= k - \dfrac{3\,Q^2}{20\,k}r^2 + \mathcal{O}(4). \end{cases}$$
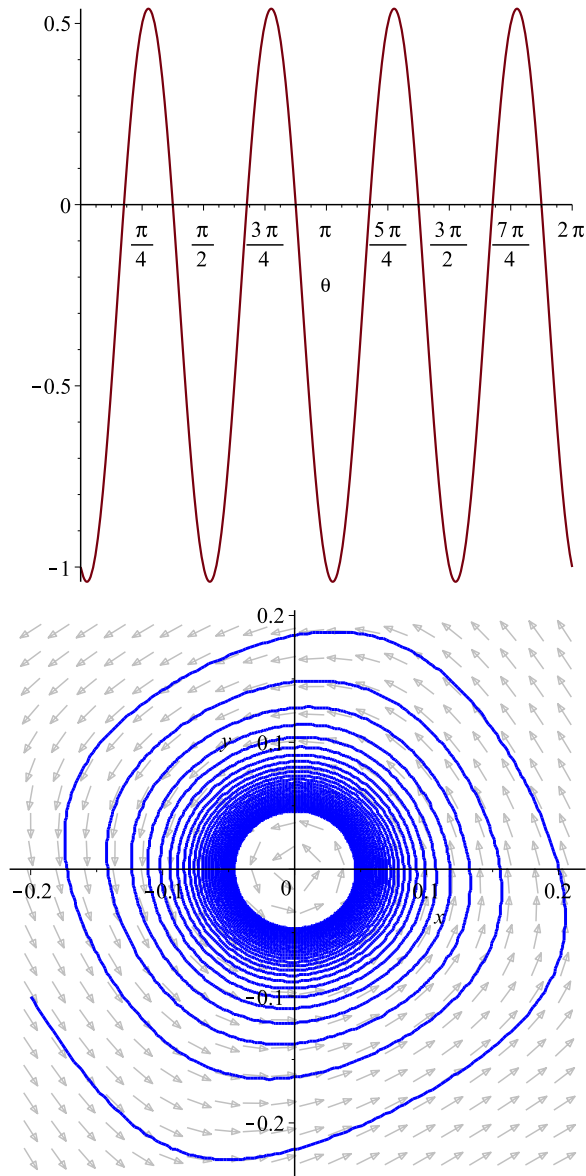
FIGURE 2. Radial derivative and phase portrait for system (9).
(Upper) Plot of $\dot{r}/r^3$ with respect to θ. (Lower) Flow for Eqs. (9)
around $\vec{0}$ for $a = 0.5$, $Q = 0.95$. Grey arrows indicate the vector
field.

Notice that near the origin $\dot{r} < 0$ and $\dot{\theta} > 0$, so it is clear that the origin is
asymptotically stable, and so it is for system (9) (recall that the stability of the
fixed points is preserved under locally topological conjugacies). Finally, as we
pointed out at the end of Section 3.1, using Theorem 2 in [3, Ch. 1] we reach the

conclusion that the fixed point x_+^* in the original fourth dimensional system (2) is an attractor.

The fact thar $\dot{r} < 0$ for all values of the (considered) parameters prevents the birth of a periodic orbit from $\vec{0}$ (which corresponds to x_+^* in the present variables), which implies that no Hopf bifurcation can take place.

4. Discussion

In this letter we have conducted a stability analysis using the center manifold theory for hypercycles with $n = 4$ species and an error tail formed by mutant replicators. Previous works provided numerical evidences that the coexistence in hypercycles was governed by a stable fixed point [5, 16]. Numerical simulations indicated that such a fixed point can be achieved with different damped oscillatory modes (i.e., fastly damped oscillations for $n = 3$ and weakly-damped oscillations for $n = 4$) [5]. Moreover, for the so called elementary hypercycle in [5] Lyapunov functions are known for these fixed points when $n = 3$ and $n = 4$ so they are asymptoticaly stable. Despite these previous results, and for other types of hypercycles beyond the elementary ones, linear stability analysis around the coexistence attractor for $n = 4$ gives two purely imaginary eigenvalues and two other negative eigenvalues. Since Lyapunov functions for these cases are not available, no direct conclusions about the stability of this fixed point can be attained.

As mentioned above, we here explore the stability in the coexistence for a hypercycle with four species in a slightly different model from the one analyzed in [5]. In particular, it introduces another layer of complexity by considering that replicators can synthesize neutral mutants, which ultimately act as parasites, since they do not reciprocate the catalytic support to the replicators forming the catalytic cycle. To determine the stability for this case we have performed a reduction to the center manifold, showing that this fixed point is locally asymptotically stable, in agreement with numerical results conducted for this type of hypercycle [2].

Our approach also indicates that a Hopf bifurcation giving place to a periodic orbit underlying coexistence dynamics is not possible. In this sense, our approach reinforces the results suggesting that the minimal hypercycle size for which periodic orbits can exist is $n > 4$ species [5, 11]. Our analytical results thus complement previous studies on the stability of hypercycles with the so-called error tail [2, 17].

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