



GHOSTS IN THE ORIGINS OF LIFE?

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The so-called bottleneck or *ghost* can appear after a saddle-node bifurcation, leaving a region in phase space by which the flow is attracted although no fixed points are present. Such ghosts, displayed by some dynamical systems, actually cause a delay of the flow. In this paper, we analyze a saddle-node ghost found in a biological model for the two-member hypercycle dynamics. The model predicts a scaling law of the dynamic delay caused by the ghost near the threshold: $\tau \sim \phi^{-1/2}$, consistent with previous results in physical systems. Possible biological meanings for such a dynamical phenomenon are outlined.

Keywords: Hypercycles; saddle-node bifurcation; ghosts; delayed transitions.

1. Introduction

It is well known that a saddle-node bifurcation is the basic mechanism for the creation and destruction of fixed points [Strogatz, 2000]. Such collision of fixed points can give rise to the so-called *ghost* or bottleneck. The ghost sucks trajectories, delaying the flow in phase space, before allowing them passage to the other side. It is also known that the time τ spent in the bottleneck generically increases as:

$$\tau \sim (\mu - \mu_c)^\beta \quad (1)$$

generally with $\beta = -1/2$, μ_c being the value at which the saddle-node bifurcation occurs [Strogatz, 2000]. Dynamic delays and such a scaling law have been discussed in the context of condensed matter physics, where the switching of charge-density waves has been explored [Strogatz & Westervelt, 1989]. In this context, and specifically for one of the models analyzed, the stable node corresponding

to a pinned state with a large polarization coalesced with a saddle-node, giving place to the delay. Such phenomenon, labeled delayed transition, has been characterized and discussed in other dynamical systems, from ferroelectrics [Chandra, 1989] to semiconductor lasers [Hwang & Dymont, 1973; Konnerth & Lanza, 1964; Ripper, 1972]. Strogatz and Westervelt [1989] elegantly attributed such delayed transition to the presence of a ghost. Here, we examine the same phenomenon within the context of early scenarios of living organization. Specifically, we consider the so-called hypercycle model. The hypercycle [Eigen & Schuster, 1979] describes a dynamical system of self-replicating macromolecules which act as catalysists in replication reactions of other species or even catalyze their own replication (see Fig. 1). If $\mathbf{x} = \{x_i\}$ is the set of concentrations of N macromolecules I_i , with $\sum_i x_i = 1$ (i.e. the flows are restricted to a simplex), the simplest hypercycle model is described by a set of

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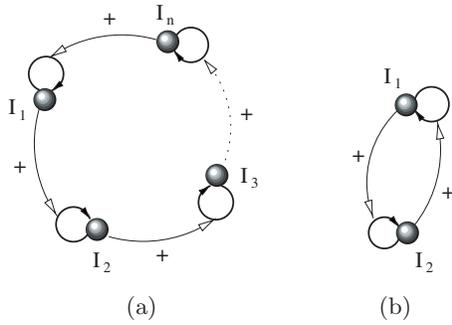


Fig. 1. Catalytic hypercycles: (a) general hypercycle of n species; (b) the two-member hypercycle. Chemical transformation (i.e. self-replication) is represented with thick arrows and catalytic help with thin arrows.

equations:

$$\frac{dx_i}{dt} = \Gamma_i(\mathbf{x}) - \Phi x_i \quad (2)$$

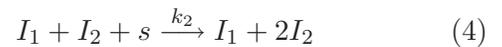
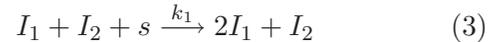
where $\Gamma_i = k_i x_i + k'_i x_i x_j$ ($j = i - 1 + N\delta_{i1}$; $i = 1, \dots, N$). Here Φ is some dilution flux or decay and k_i, k'_i catalytic constants. Such cyclically coupled set of information carriers was proposed as a possible molecular organization scenario of prebiotic replicators, opening a promising framework to understand the origins of life on Earth. The hypercyclic organization allows unlinked informational carriers i.e. replicators, to overcome the informational crisis of error-prone replicators. Such informational constraint is given by the so-called error catastrophe [Eigen & Schuster, 1979; Swetina & Schuster, 1982]. It is well known that the capacity of maintaining the informational content for error-prone replicators is limited by the fidelity of copy, a critical mutation rate exists beyond which information cannot be maintained by natural selection. Hence, replicators have a sharp limit to the information they can carry, given by $\nu_c \approx \mu^{-1}$, where ν is the length of the genome. Dynamics of hypercycles have been extensively characterized [Eigen & Schuster, 1979; Nuño *et al.*, 1993a, 1993b; Rowe, 1997; Stadler & Stadler, 2002], and the presence of bifurcations in such systems have also been outlined [Nuño *et al.*, 1993a; 1993b]. For instance, Nuño *et al.* [1993b] analyzed an hypercycle formed by error-prone self-replicative species, finding a saddle-node bifurcation scenario achieved by tuning the quality factor Q .

In the present paper we extend the analysis of the ghost found by the authors in a mean-field model for the two-member hypercycle [see Fig. 1(b)] dynamics [Solé & Sardanyés, 2005]. Specifically, we focus on the role of the parameters of such a model

in relation to the saddle-node bifurcation as well as in relation to the ‘‘apparition’’ of the ghost. The scaling law previously mentioned is also explored, and the biological relevance for such a dynamical ghost is outlined.

2. Two-Member Hypercycle Model

The two-member hypercycle is one of the simplest hypercycles, formed by two molecular species catalytically coupled [see Fig. 1(b)]. Kinetically, the model can be schematically described by the following set of reactions:



where k_i ($i = 1, 2$) and ε_i ($i = 1, 2$) are the reaction and the decay rates of both hypercyclic species, respectively. Reactions (3) and (4) represent the kinetically assisted replication of both replicators (we assume that replicators use molecular building blocks (labeled s) to generate the new molecules). Reaction (5) represents the hydrolysis of replicators into its mononucleotide components s . Reactions (3)–(5) are modeled by the next set of ordinary differential equations:

$$\frac{dx_i}{dt} = kx_i x_j (1 - x_i - x_j) - \varepsilon x_i \quad (6)$$

with $i, j = 1, 2$; $i \neq j$. Here we consider the symmetric hypercycle i.e. $k_1 = k_2$ and $\varepsilon_1 = \varepsilon_2$. Equation (6) has three fixed points: the extinction state with ($x_1^* = x_2^* = 0$), a stable node ($x_+^{*(1)}, x_+^{*(2)}$) and a saddle-node ($x_-^{*(1)}, x_-^{*(2)}$), with

$$x_{\pm}^{*(1)} = x_{\pm}^{*(2)} = \frac{1}{4} \left[1 \pm \sqrt{1 - \frac{8\varepsilon}{k}} \right] \quad (7)$$

Such a dynamical system has a bifurcation point at $\varepsilon_c \approx k/8$: if $\varepsilon < \varepsilon_c$, the three fixed points live in phase space, but when this critical condition is overcome, a saddle-node bifurcation occurs, being the trivial point $(0, 0)$ the only attractor in phase space. Such a bifurcation leaves a ghost in phase space. In order to analyze the ghost and to explore its properties, we solve numerically Eq. (6) using the standard fourth-order Runge–Kutta method (with a constant time stepsize $\delta_t = 10^{-3}$).

Phase space (x_1, x_2) are represented in Fig. 2 for different decay rates ε . As previously mentioned, below ε_c three fixed points are found in phase space.

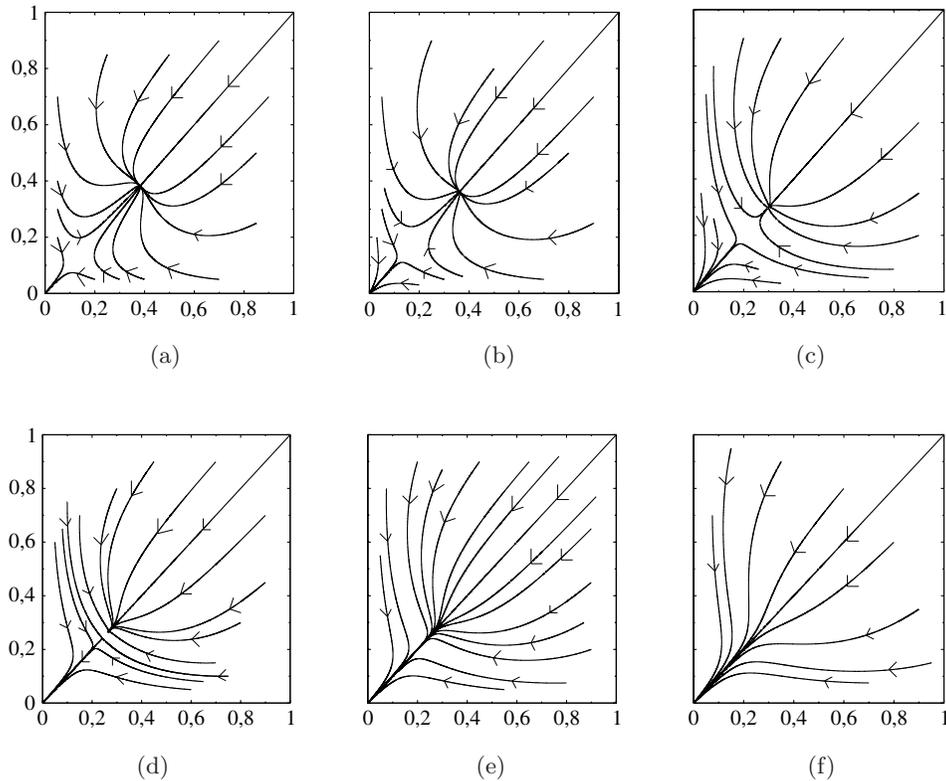


Fig. 2. Flows in phase space for the two-member hypercycle model Eq. (6). Here x -axis and y -axis represent I_1 and I_2 concentrations, respectively. All phase portraits are built with $k = 1$, so the bifurcation point is $\varepsilon_c \approx 0.125$. For $\varepsilon < \varepsilon_c$ ((a) with $\varepsilon = 0.09$, (b) $\varepsilon = 0.1$, (c) $\varepsilon = 0.12$, (d) $\varepsilon = 0.125$) there are three equilibria: the extinction attractor, the coexistence stable node and the saddle-node. For $\varepsilon > \varepsilon_c$ ((e) with $\varepsilon = 0.13$ and (f) $\varepsilon = 0.15$) the coexistence node and the saddle-node have coalesced, leaving a remnant “bottleneck” or ghost into which trajectories are funneled. Such ghosts cause a slow passage of trajectories delaying them before reaching the $(0, 0)$ point.

The increase in the order parameter ε , causes the trip of the stable node and the saddle-node, and both fixed points approach each other. When ε_c is crossed both fixed points coalesce. The flow then always moves towards the trivial attractor, where both hypercycle members extinguish. Such collision leaves a ghost in phase plane [Solé & Sardanyés, 2005]. In Figs. 2(a)–2(c) the three fixed points are present because $\varepsilon < \varepsilon_c$. Also in Fig. 2, from (a) to (c) we increase the decay rate ε , approaching to ε_c . It is shown that the stable node and the saddle-node approach each other. In Fig. 2(d) we are extremely near the bifurcation point, achieved in Figs. 2(e) and 2(f). In these last two figures the flow is attracted by a region of phase space i.e. the ghost, thus a delay in such flow is found before both members reach the trivial attractor $(0, 0)$.

An interesting property of the displacement of the stable node and the saddle-node involves whether the motion of the fixed points is constant. Here, we can consider that the fixed points

$(x_{\pm}^{*(1)}, x_{\pm}^{*(2)})$ move in one dimension because $x_{\pm}^{*(1)} = x_{\pm}^{*(2)}$. Thus we can follow the displacement of the stable node only considering one coordinate of the phase plane. In Fig. 3 we analyze the motion of the stable node on $x_+^{*(1)}$, labeled as x^* . To do that, we represent, for increasing ε values, the steady concentration of $x_+^{*(1)}$. As shown, such motion is not constant, increasing when the saddle-node bifurcation is about to occur. After the bifurcation, the steady concentration value is $x^* = 0$ because the destruction of the stable node implies the extinction scenario.

As previously mentioned, a general scaling law for the time spent in the bottleneck (i.e. delay, labeled τ) has been described in previous models [Strogatz, 2000; Strogatz & Westervelt, 1989]. Such delay generically scales as $(\mu - \mu_c)^\beta$ where μ_c is the value at which the saddle-node bifurcation occurs with μ as the order parameter. This universal law is found near the transition. In our system

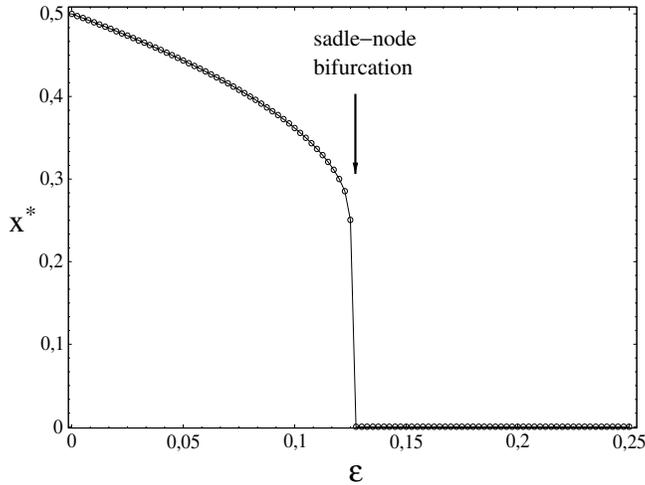


Fig. 3. Evolution of the stable node at increasing ε values with $k = 1$. For such parameter the critical decay rate is $\varepsilon_c \approx 0.125$. As the stable node $(x_+^{*(1)}, x_+^{*(2)})$ moves on a line i.e. $x_+^{*(1)} = x_+^{*(2)}$, the motion of such fixed point is only represented by considering one dimension of the phase plane, here $x_+^{*(1)}$, labeled as x^* . Such motion is not constant, increasing when the saddle-node bifurcation is about to occur.

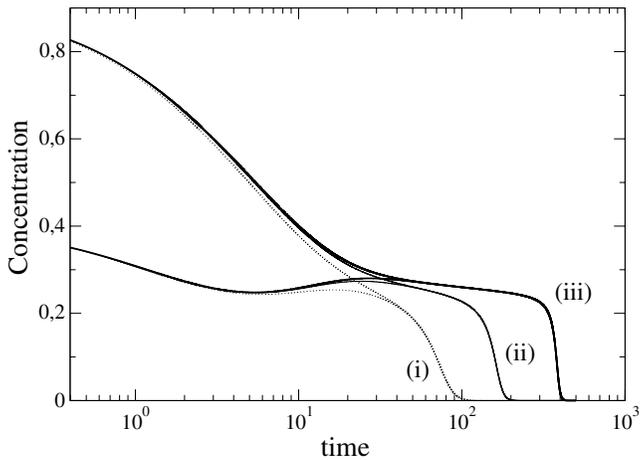


Fig. 4. Delayed collapse of the two-members of the hypercycle (here log-linear plot). Three scenarios are considered: (i) $\varepsilon_1 = 0.135$, (ii) $\varepsilon_2 = 0.1275$ and (iii) $\varepsilon_3 = 0.1255$, all of them with $k = 1$. In each scenario, we represent both members of the hypercycle (as initial conditions $x_1 = 0.9$ and $x_2 = 0.4$). From (i) to (iii) we approach, from above, to the bifurcation point $\varepsilon_c \approx k/8$. Such approach implies an increase in the time needed for both hypercyclic species to become extinguished.

we define such delay τ as the time needed for both hypercycle members to achieve extinction. The first approach to analyze the delay τ in the two-member hypercycle dynamics caused by the ghost is developed representing the time evolution of both species with decay rates above the bifurcation point.

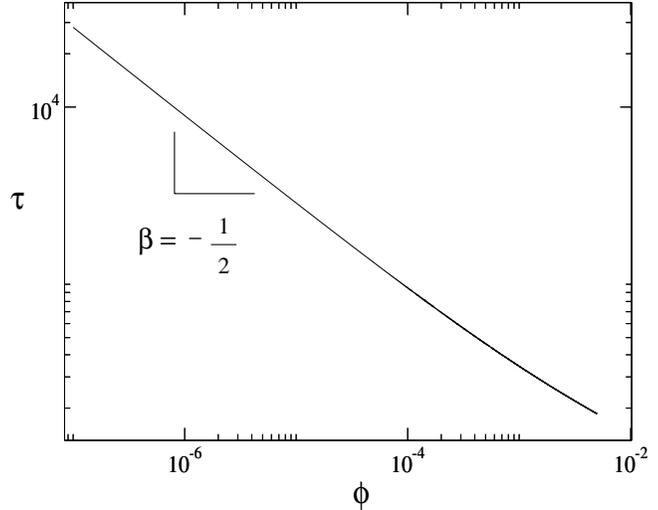


Fig. 5. Dependence of delay τ on ϕ (here log-log plot) with $\phi \equiv (\varepsilon - \varepsilon_c)$ for the mean-field two-member hypercycle model. Curve obtained by numerical integration of Eq. (6) (using a stepsize $\delta_t = 0.01$) with $k = 1$. For small ϕ the curve has a slope of $-1/2$.

In Fig. 4 we show the concentration of both replicators as a function of time with $k = 1$ using (i) $\varepsilon_1 = 0.135$; (ii) $\varepsilon_2 = 0.1275$; and (iii) $\varepsilon_3 = 0.1255$. It is shown that the delay τ increases when ε approaches, from above, to the bifurcation point. The presence of such scaling law is also found in this biological model. Figure 5 shows that very close to the threshold the delay scales as $\phi = (\varepsilon - \varepsilon_c)^\beta$ with $\beta = -1/2$. Hence, the power-law distribution follows $\tau \sim \phi^{-1/2}$ as $\phi \rightarrow 0$. This confirms the universal pattern suggested by previous studies [Strogatz, 2000; Strogatz & Westervelt, 1989].

3. Discussion

In this paper we have analyzed a ghost recently found in a model for the two-member hypercycle dynamics. Such ghost appears after a saddle-node bifurcation (see Fig. 2). It is shown that the motion of the stable node due to the order parameter of the model (i.e. the decay rate ε) is not constant, accelerating near the bifurcation point (see Fig. 3). Such ghost causes a delay in the flow before the hypercycle members get extinguished (see Fig. 4). It is also shown that the delay associated to the presence of the ghost scales with $\phi^{-1/2}$ as $\phi \rightarrow 0$ (see Fig. 5), with $\phi \equiv \varepsilon - \varepsilon_c$, is in agreement with the scaling law obtained for other systems with delayed transitions [Strogatz, 2000; Strogatz & Westervelt, 1989].

The presence of such delay in this hypercycle might have interesting biological implications,

that could be interpreted in the context of the origins of life. Such a delay causes both species to remain in the system for a longer time before being extinguished. We suggest that this “resistance” to extinction could be given by the nature of the growth of the hypercyclic replicators. Replicators catalytically coupled unfold hyperbolic growth [Eigen & Schuster, 1979; Szathmáry & Maynard Smith, 1997]. Such explosive growth, which is highly nonlinear, is reduced, in our model, by a linear decay i.e. the hydrolysis reaction. Our result suggests that the balance between catalytically assisted growth and decay might cause this dynamical delay. In order to give a biological meaning to such ghost we must go beyond the mathematical result interpreting such delayed behavior more realistically. In this context, [Nuño *et al.*, 1993b] stated that weak variations of either temperature or pH may lead to important changes in the values of the parameters of an hypercyclic system [Nuño *et al.*, 1993b]. Assuming that hydrolysis rates could change in time due to the variation of some of these environmental parameters, the extinction scenario driven by high decay rates could move backwards if such decay rate decreased due to external fluctuations. In such cases, the system could return to the scenario where coexistence is possible, so the coalesced fixed points could appear again if the order parameter changes. If both replicators spend more time before extinguishing (because of the ghost), the probability to avoid extinction and return to the stable coexistence scenario increases. Such a delaying capacity may signal an evolutive advantage in a fluctuating environment, being positively selected by natural selection.

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