Noise-induced stabilization of saddle-node ghosts

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Abstract

It is known that saddle-node (s-n) bifurcations leave a saddle remnant (or ghost) in the region of the phase space where the annihilation of the fixed points occurred. The corresponding time delay, \( t_d \), found right after the bifurcation is known to follow the scaling law \( t_d \sim (\epsilon - \epsilon_c)^{-1/2} \), where \( \epsilon \) and \( \epsilon_c \) are the control parameter and its critical value, respectively. While the properties of such delays are well understood for deterministic systems, much less is known about how intrinsic noise influences this phenomenon. As a first step towards analysing this issue, in this article we explore a model with autocatalysis and a two-species hypercycle to analyse the impact of noise on delayed transitions in one- and two-dimensional dynamical systems suffering a s-n bifurcation. The first model is investigated with Gillespie simulations and the diffusion approximation, focusing on the behaviour and properties close to the bifurcation. A Fokker–Planck equation is derived, together with the stochastic potential. We show that the slowing down of the dynamics remains robust to noise. In fact, we prove both analytically and numerically that increasing noise lengthens the delays after bifurcation threshold. Furthermore, the inverse square-root scaling law is not robust to fluctuations. By contrast, scaling properties are identified in the mean extinction times as criticality is approached from above the bifurcation. This noise-induced stabilisation of the delays is also found in the two-dimensional system.

1. Introduction

Local bifurcations involve changes in equilibrium points and are extremely important in multitude of nonlinear systems since they govern transitions between qualitatively different dynamics. Bifurcations involve continuous or discontinuous changes in the order parameter of dynamical systems as the control parameter reaches its critical value, giving place, respectively, to the so-called first- or second-order phase transitions in statistical physics. Bifurcations have been experimentally reported in chemistry [1, 2], physics [3–6], and biology [7, 8]. Bifurcations in biological systems (e.g., ecosystems) have been proposed to govern extinction processes and populations collapse [7, 9–15].

Continuous transitions cause changes between active and quiescent states [16]. These transitions occur in chemical reactions, epidemic spreading, fixation of alleles in population genetics, and propagation of computer viruses [17–21]. Continuous transitions are typically governed by transcritical bifurcations, although other types of bifurcations such as the pitchfork bifurcation can also give place to continuous dynamical changes [22, 23]. Other bifurcations cause catastrophic transitions [10, 11]. For instance, saddle-node (s-n) bifurcations usually involve that the orbits that where attracted by the node that bifurcated jump to a different, distant, attractor, giving place to the abrupt transition. This bifurcation, typically found in catalytic systems [24–26], was first identified experimentally in electronics [4]. Moreover, Dai et al mapped a s-n bifurcation in detail in laboratory experiments with yeast [7]. S-n bifurcations are
also found in multitude of mathematical models incorporating strong nonlinearities e.g., food-chains [27] or host-parasite dynamics [28]. References [29, 30] provide recent reviews on bifurcations (including the s-n) and transients (see below) in ecological systems.

Catastrophic shifts are of extreme importance in nature since they involve a radical change in the steady-state of a system once the bifurcation threshold is crossed [9, 14]. Sudden collapses can occur in socioecological systems [31–33] as well as in ecosystems such as lakes, fisheries, coral reefs, or savannas. All these systems can undergo abrupt collapses due to small changes in environmental conditions [34–40]. Once such collapse occurs, recovery can be extremely problematic [16, 35]. This bifurcation is found in many bistable systems, where two states are locally stable, and, once the bifurcation occurs, one of them becomes globally asymptotically stable and the other one disappears. The remaining fixed point in biological dynamical systems is usually the origin, which, being an absorbing state, involves population’s extinction.

A well-known effect of the s-n bifurcation is that transients typically suffer extremely long delays for values of the control parameter, $\epsilon$, just above the bifurcation $\epsilon \gtrsim \epsilon_c$, where $\epsilon_c$ is its critical value [23]. This effect, known as a delayed transition or ghost [23, 41], occurs due to the presence of a saddle remnant. Upon collision of equilibrium points at the bifurcation value, the modulus of the velocity field in the vicinity of the region of the phase space where the s-n collision has occurred is very small. The closer we are to the critical value, the smaller the velocity field. As a consequence, the dynamics remains influenced within the region of the phase space where the collision took place, hence the name ghost. Delayed transitions have been extensively studied in deterministic systems such as models of charge density waves [41] and electronic circuits [4]. More recently, this phenomenon has been also described in hypercycles [25, 42], autocatalysis [42, 43], and in mathematical models for semi-arid ecosystems [15].

The time that the orbits spend in this ghost region, $t_d$, is known to scale with the quantity $\phi = \epsilon - \epsilon_c$. That is, with the distance of the bifurcation parameter to the bifurcation value. Specifically, $t_d$ follows an inverse square-root scaling law, $t_d \sim \phi^{-1/2}$ [23]. Reference [4] has provided the first experimental evidence of this phenomenon and the corresponding scaling law in an electronic circuit analog to the Duffing’s model.

Most of the analyses devoted to understand the dynamics of s-n ghosts have been preformed using deterministic models [4, 15, 23–25, 41–45]. Few studies (mainly computational) have discussed this phenomenon considering stochasticity [15, 25, 26], but none of them has provided a thorough analysis, specially on the impact of noise in the scaling properties of transients. Key questions still remain unanswered. Is this delaying phenomenon robust to noise? Is the inverse square-root scaling found in stochastic dynamics? As a first step towards ascertaining the effects of noise in the vicinity of the s-n bifurcation, we study, both analytically and numerically, a simple model of biological cooperation given by autocatalysis [24, 26]. This is a kind of biological normal form [46] undergoing a s-n bifurcation. Specifically, we show that the ghost phenomenon is robust to intrinsic noise. Beyond that, we prove that this model exhibits noise-induced stabilization of the s-n ghost. Contrary to intuition, we find that the delay associated with the ghost prolongs itself as the level of noise increases. Stochastic simulations show a different scaling behaviour of the extinction time to bifurcation distance, where the inverse square-root scaling of the deterministic dynamics is not found. Similar results are found in a two-variable dynamical system undergoing a s-n bifurcation, suggesting universality in the identified stochastic scaling.

The paper is organised as follows. In section 2, we introduce a one-dimensional deterministic model suffering a s-n bifurcation. This model, which has been largely investigated in references [24, 42, 43, 47], describes the dynamics of autocatalytic replicators together with exponential decay and competition. Section 2.1 summarises the mean field dynamics and section 2.2 provides a full analysis of the stochastic dynamics by means of the master equation and Gillespie simulations. Due to the low dimension of this system, we also study the Fokker–Plank equation that allows us to compute the effective stochastic potential. Finally, we use these stochastic approaches to determine the delaying capacities of the ghost as well as the scaling features near bifurcation threshold under demographic noise. In section 3 we extend the previous analyses to a two-dimensional system also considering catalytic dynamics, now in the form of hypercycles [25, 26, 48] (circular catalytic networks). Here we also provide a summary of the mean field dynamics and then we study the system with intrinsic noise using Gillespie simulations. The goal of analysing this second model is to see whether the behaviour close to the stochastic s-n bifurcation in the one-dimensional system still holds in the phase plane dynamics.

2. One-dimensional dynamical system

2.1. Mean-field dynamics

In this section we provide a brief summary of the mean field dynamics of a population of replicators that
cooperate (autocatalytically) and undergo exponential degradation. These processes obey the following set of reactions:

\[ s + A + A \xrightarrow{k} 3A, \]
\[ A \xrightarrow{\epsilon} s, \]

\( s \) being some resources needed for reproduction, which are not explicitly considered. In order to account for resource limitations, we include intra-specific competition to reactions \((1)\) and \((2)\) by means of a logistic term (see e.g., [24, 25, 26, 47, 49]), obtaining:

\[
\frac{dx}{dt} = f(x) = kx^2 \left(1 - \frac{x}{\eta}\right) - \epsilon x. \tag{3}
\]

The state variable \(x(t)\) is the population of species \(A\) at time \(t\). Constant \(\eta\) is the carrying capacity and introduces competition between the replicators also bounding the system.

Equation \((3)\) has three equilibrium points: \(x_0^* = 0\) and \(x_{\pm}^* = \eta \left(1 \pm \sqrt{\Delta/k}\right)/2\), with \(\Delta = k(4\epsilon/\eta) - c\). \(x_{\pm}^*\) are real (biologically meaningful) if the discriminant \(\Delta \geq 0\). The \(s-n\) bifurcation occurs when \(\Delta = 0\). Without loss of generality, we can consider the degradation rate, \(\epsilon\), as the control parameter, and the equilibrium \(x_{\pm}^*\) as the order parameter.

The critical (bifurcation) value is \(\epsilon_c = \eta k/4\) (see the bifurcation diagrams in red in figure \(2(a)\)). For \(\epsilon = \epsilon_c\), the fixed points \(x_0^*\) and \(x_{\pm}^*\) collide in a \(s-n\) bifurcation. Before the collision, the system is bistable, meaning that there exist two stable equilibrium values \((x_0^* = 0\) and \(x_{\pm}^*)\), which will be achieved depending on the initial condition. Note that after the collision, the equilibria \(x_{\pm}^* \in \mathbb{C}\) since \(\Delta < 0\). A useful tool to investigate and visualise the dynamics of equation \((3)\) is the potential function:

\[
U(x) = -\int f(x) \, dx = -x^2 \left[kx \left(\frac{1}{3} - \frac{x}{4\eta}\right) - \frac{1}{2} \epsilon\right]. \tag{4}
\]

The potential of figure \(1(a)\) (left panel), computed with \(\epsilon < \epsilon_c\), has two wells corresponding to the stable fixed points \(x_0^* = 0\) and \(x_{\pm}^*\), separated by the repeller \(x^c\). When \(\epsilon \geq \epsilon_c\), the potential develops a long plateau, associated with a very slow relaxation towards the (only) fixed point, \(x^c\), and producing the delayed transition (middle panel in figure \(1(b)\)). When \(\epsilon\) is further increased above the critical value, the plateau disappears and the slow relaxation towards \(x_0^*\) is lost (see right panel in figure \(1(a)\)). Figure \(1(b)\) displays the inverse square-root scaling law numerically obtained from equation \((3)\), plotting the extinction times \(T_\epsilon\) against the function \(\phi = \epsilon - \epsilon_c\). Finally, figure \(1(c)\) displays ghost orbits and the typical bottleneck with a plateau shape from different initial conditions close to the bifurcation value from above.

### 2.2. Stochastic dynamics

In this section we introduce a stochastic model with the aim of analysing the effect of intrinsic noise on the post-bifurcation phenomenon summarised in section 2.1. We start our analysis by formulating the corresponding master equation (ME), which we study both numerically and analytically by means of a diffusion approximation. Specifically, our aim is to ascertain the effects of noise on the delayed transitions arising at the vicinity of the \(s-n\) bifurcation and its impact on the scaling of transients.

#### 2.2.1. Reactions and master equation

We introduce a Markovian stochastic model consisting of three elementary processes: quadratic autocatalysis, binary (cubic) annihilation (for the purpose of including intra-specific competition), and (linear) degradation [50]:

\[
A + A \xrightarrow{k/C} A + A + A, \quad r_1 = +1, \tag{5}
\]
\[
A + A + A \xrightarrow{k/C^2} A + A, \quad r_2 = -1, \tag{6}
\]
\[
A \xrightarrow{\epsilon} \emptyset, \quad r_3 = -1. \tag{7}
\]

Here \(r_i\) are the components of the corresponding stoichiometric vector. The propensities (transition rates) for this system are modelled using the law of mass action:

\[
W_1 = (k/C) n (n - 1),
\]
\[
W_2 = (k/C^2) n (n - 1) (n - 2),
\]
\[
W_3 = \epsilon n,
\]
Figure 1. Deterministic dynamics of equation (3). (a) Potential function, $U(x)$, computed using equation (4). From left to right we set: $\epsilon = 0.05$, $\epsilon = 0.25$, and $\epsilon = 0.35$. The grey region indicates the biologically meaningless value of the population ($x < 0$). (b) Inverse square-root scaling law tied to the saddle remnant. The time the orbits spend in the bottleneck follow a power law of exponent $-\frac{1}{2}$ as $\epsilon$ grows above $\epsilon_c$, here with $\phi = (\epsilon - \epsilon_c)$. (c) Time series (in log-linear scale) for different initial conditions near bifurcation threshold $\epsilon = \epsilon_c + 10^{-8}$. In all the analyses we have used $k = \eta = 1$ thus $\epsilon_c = 0.25$.

where $n$ is the number of particles and $C$ the system’s size. The ME, which dictates the evolution of the probability of having $n$ particles at time $t$, $P(n, t)$, is given by:

$$
\frac{\partial}{\partial t} P(n, t) = \frac{k}{C} \left[ (n-1)(n-2)P(n-1, t) + \frac{1}{C} n(n-1)(n+1)P(n+1, t) \right] 
+ \epsilon (n+1)P(n+1, t) - \left[ \frac{k}{C} n(n-1) + \frac{1}{C} n(n-1)(n-2) \right] P(n, t).
$$

2.2.2. Gillespie simulations

We have performed a stochastic numerical study of reactions (5)–(7) using the Gillespie algorithm [51]. First, we have investigated the effect of increasing the degradation rate, $\epsilon$, for different values of the system’s size, $C$ (see figure 2). Figure 2(a) shows average values of $x = n/C$ at steady state for different system’s sizes: $C = 500$ (left panel); $C = 10^3$ (middle panel); and $C = 10^4$ (right panel). The deterministic bifurcation diagrams are displayed overlapped with red lines. We observe that the stochastic system undergoes the transition at a lower degradation rate value than the one predicted by the mean-field model. Note that we are using $\epsilon$ as the degradation rate for both the deterministic and the stochastic system.

Further computational exploration is reported in figure 3, where we show the variation of the extinction probability, $P_e$, as $\epsilon$ is let to increase. $P_e$ is computed as the number of realisations involving extinction divided by the total number of $10^3$ realisations and using $10^8$ iterations in the Gillespie algorithm. The vertical blue lines indicate the critical stochastic value (hereafter labeled as $\epsilon_s^{(c)}$) obtained for different system’s sizes. Specifically, we plot $P_e$ comparing the value of $\epsilon$ with the deterministic bifurcation value $\epsilon_c$ ($\epsilon = 0.25$, vertical red line in the figures). For analysis purposes, the value of $\epsilon_s^{(c)}$ obtained with the Gillespie simulations will be considered the lowest value of $\epsilon$ where $P_e = 1$. This ensures that all the realisations have gone to extinction and thus we can assume that the $s-n$ bifurcation has already occurred. This threshold will be used in the following sections to study the stochastic bifurcation numerically.
Figure 2. Deterministic versus stochastic bifurcations. (a) Mean population equilibria (±SD) obtained from the Gillespie simulations using (from left to right) $C = 500$, $C = 10^3$, and $C = 10^4$, using $k = 1$ and $x(0) = 0.75 \cdot C$. Each data point is the mean of the normalized (over the system’s size) populations averaged over $10^5$ replicas. The transparent, grey thick line is included to ease the visualization of the stochastic data. Overlapped in red we display the predicted values for the mean field model, setting $k = \eta = 1$. The stable fixed point $x^*$ is indicated with a solid line. The unstable equilibrium $x^*$ is shown with a dashed line. Note that the order parameter suffers a first-order phase transition. The vertical dotted line in red displays the bifurcation value for the deterministic case. (b) Stochastic potential, $U^*(x)$, obtained from equation (12) setting $C = 5000$, with $\epsilon^c(C = 5000) \approx 0.22217$. Here we use (from left to right): $\epsilon = 0.1$, $\epsilon = 0.2222$, and $\epsilon = 0.4$ (for comparison with the deterministic potential see figure 1(a)).

2.2.3. Diffusion approximation and effective potential
In order to make analytical progress, we will now consider the diffusion of the stochastic system given by reactions (5)-(7). The stochastic dynamics of the system can be rewritten as follows:

$$n(t + \Delta t) = n(t) + \sum_{i=1}^{3} r_i Y(\lambda_i),$$

where $\Delta t > 0$ represents a time step, which we will discussed later. $Y(\lambda_i)$ stands for statistically independent Poisson random variables for each reaction with parameter:

$$\lambda_i = \int_{t}^{t+\Delta t} W_i(n(s)) ds, \quad 1 \leq i \leq 3.$$  

Under appropriate conditions and, following the standard procedure (see, for example, references [52, 53]), we can take a diffusion limit to derive a Langevin equation from equation (8). Briefly, the diffusion approximation consists of doing a coarse-graining of the time variable where we take time steps of duration $\Delta t$ so that they can be considered small enough in comparison with the macroscopic characteristic time scales, but large enough compared with the typical waiting times associated with the elementary processes that drive the stochastic dynamics of the system. The latter condition implies that each elementary process fires up many times within the time interval, $\Delta t$, so that their cumulative effect can be addressed by means of the central limit theorem, so that each random variable $Y(\lambda_i)$, which counts how many times process $i$ has occurred, can be approximated by a Gaussian random number. The conditions for such limit to make sense, both mathematically and physically, have been discussed extensively, in particular by Kurtz and coworkers [52] and Gillespie [53]. Following the standard procedure (see, for example, reference [53]), the corresponding Langevin equation is given by:

$$dx(t) = f(x) \, dt + \sqrt{D(x)} \, dB_t,$$

where

$$f(x) = \sum_{i=1}^{3} r_i \omega_i(x) = x(kx(1-x) - \epsilon),$$

and $D(x) = \sum_{i=1}^{3} r_i \omega_i(x)^2$. 

5
The steady state solution of equation (10), can be calculated by a simple quadrature. In particular, taking

\[ D(x) = C^{-1} \sum_{i=1}^{3} r_i^2 \omega_i(x) = C^{-1} x(\epsilon + kx(1 + x)), \]

and where we have considered the re-scaled number of individuals, \( x \equiv n/C \). The re-scaled transition rates, defined as \( W_i(n) = C \omega_i(x) + O(C^0) \), are:

\[ \omega_1(x) = kx^2, \]
\[ \omega_2(x) = kx^3, \]
\[ \omega_3(x) = cx. \]

and \( dB_t \) is a Gaussian white noise with \( \langle dB_t \rangle = 0 \) and \( \langle dB_t^2 \rangle = dt \). Equation (9) leads to the corresponding Fokker–Plank equation (FPE), which dictates the time evolution of the conditional probability density function (PDF), \( P(x, t|x_0, t_0) \):

\[
\frac{\partial}{\partial t} P(x, t|x_0, t_0) = -\frac{\partial}{\partial x} \left[f(x) P(x, t|x_0, t_0)\right] + \frac{1}{2} \frac{\partial^2}{\partial x^2} \left(D(x) P(x, t|x_0, t_0)\right). \tag{10}
\]

The steady state solution of equation (10), can be calculated by a simple quadrature. In particular, taking into account that the FPE can be written as, \( \partial_t P = -\partial_j J_i \), the zero-flux steady-state solution:

\[ J = f(x) P(x) - \frac{1}{2} \frac{\partial}{\partial x} (D(x) P(x)) = 0, \]

is given by:

\[
P(x) = \frac{A}{D(x)} \exp \left(2 \int \frac{f(y)}{D(y)} \, dy\right), \tag{11}
\]

where \( A \) is the normalization constant. The steady state PDF, \( P(x) \), can be rewritten as \( P(x) = Ae^{-U(x)} \), where

\[ U^{(0)}(x) = -2 \int \frac{f(y)}{D(y)} \, dy + \ln |D(x)| \]

is the effective potential, whose closed form expression is given by:

\[
U^{(0)}(x) = -2 C \Psi(x) + \ln |D(x)|, \tag{12}
\]
where $\Psi(x) = -x + \ln[\epsilon + kx(1 + x)] - kg(\Omega)$, and:

$$g(\Omega) = \int_{1}^{\epsilon} \frac{dy}{e + ky + ky^2} = \begin{cases} \frac{1}{\sqrt{\Omega}} \ln \frac{2kx + k - \sqrt{\Omega}}{2kx + k + \sqrt{\Omega}} ; & \text{when } \Omega > 0, \\ -1/\left(kx + \frac{k}{2}\right) ; & \text{when } \Omega = 0, \\ \frac{2}{\sqrt{-\Omega}} \arctan \left(\frac{2kx + k}{\sqrt{-\Omega}}\right) \right) ; & \text{when } \Omega < 0. \end{cases}$$

with $\Omega = k(k - 4\epsilon)$.

The analysis of the effective potential (figure 2(b)) shows that the behaviour of the stochastic system is qualitatively the same as that of its mean-field limit (see figure 1(a)). Specifically, the stochastic systems experience a transition from bimodality (when $\epsilon < \epsilon_c^{(s)}$) to monomodality (when $\epsilon > \epsilon_c^{(s)}$) at a critical value of the decay rate, $\epsilon_c^{(s)}$. Such a critical value varies with system’s size, $C$, as shown in figure 3(b), where we show analytical results, and in figure 3(c), where we show simulation results overlapped with our analytical calculations (see the white dashed line).

2.2.4. Stochastic delayed transitions and scaling behaviour

Further to the transition between bimodality and monomodality, a behaviour akin to the s-n bifurcation in the mean-field limit, we observe that, for values of the control parameter $\epsilon \geq \epsilon_c^{(s)}$, the effective potential exhibits the same plateau behaviour as its deterministic counterpart (figure 1(a)). This property of the effective potential implies that the ghost-like behaviour exhibited by the mean-field model is also present in the stochastic dynamics. In other words, the diffusion approximation shows that the delayed transition in the vicinity of the transition is robust to intrinsic noise.

In order to check the validity of this analytical prediction, we have performed simulations for different values of the system’s size, $C$ (the lower the value of $C$, the larger the associated level of noise). The values of $\epsilon_c^{(s)}$ have been computed as we discussed at the end of section 2.2.2. These bifurcation values are shown for each value of $C$ in the table of figure 4(a). By inspection of single sample paths generated using Gillespie simulations, shown in figure 4(b), we observe that the bottleneck dynamics is also visible in the stochastic model, being much longer at large noise levels (see also [15, 25, 26]).

In order to gain better quantitative understanding of the ghost phenomenon in the stochastic system, we have computed the mean extinction times (here plotting the standard error of the mean (SEM) to ease visualization) for different values of the system’s size, $T_e(C)$ as the quantity $\phi^{(i)} = \epsilon - \epsilon_c^{(s)}$ changes. Interestingly, the delaying capacity of the ghost increases as the system’s size decreases. Since the level of intrinsic noise is inversely proportional to the system’s size, this result implies that noise stabilizes the ghost: the delay that the stochastic system experiences within the vicinity of the transition is prolonged under larger fluctuations. This is a counterintuitive result since one would expect that higher levels of noise should push the stochastic paths through the bottleneck region faster.

The noise-induced stabilisation effect can be studied within the diffusion approximation, by analysing how the shape of the effective potential, $U(x)$, changes as the system’s size is varied. The results are shown in figure 5. Specifically, when $0 < \phi^{(i)} \ll 1$ (i.e. above, but very close to the bimodal-to-monomodal transition), we observe that the length of the plateau exhibited by potential is enlarged as the system’s size (noise) $C$, decreases (increases). This feature is consistent with the noise-induced prolongation of the delay.

Motivated by the scaling behaviour exhibited by the mean-field system regarding its delayed dynamics in the vicinity of a s-n bifurcation, we have sought a scaling behaviour close to the stochastic bimodal-to-monomodal transition. Specifically, we have analysed the changes in the mean extinction times, $T_e(C)$ as the quantity $\phi^{(i)} = \epsilon - \epsilon_c^{(s)}$ slightly increases, which measures the distance to the transition. The results are shown in figure 4(c). In particular, by inspection, we can immediately see that the power-law behaviour characteristic of the mean-field dynamics is missing in the presence of intrinsic noise. However, further in depth exploration of the simulated data, using the methods developed in [54], shows that the extinction time near the transition threshold exhibits scaling behaviour (at smaller values of $\phi^{(i)}$). The collapse of the different curves of figure 4(c), shown in figure 4(d), has been performed using the parametric scaling method described in section 4.2 in reference [54]. For example, to collapse two curves, a re-scaling of the two axes is done with arbitrary exponents, $a$ and $b$. Then, a distance measure (i.e., euclidean) between the logarithm of the re-scaled curves is computed, and the minimization of this distance is performed with the simplex method [55]. For more than two curves, the distances are summed for each pair of curves then also being minimized. It is important to notice that the distance depends only on two parameters given by
Figure 4. (a) Mean stochastic bifurcation values (±SD) averaged over 50 evaluations of $\epsilon^c(C)$ computed with the Gillespie algorithm. (b) Bottleneck followed by 25 stochastic realisations setting $\epsilon=\bar{\epsilon}^c(C)+10^{-4}$ with $C=500$ (upper) and $C=4000$ (lower). (c) Mean extinction times, $\bar{T}_e$ (±SEM), as a function of the distance to bifurcation, $\phi(x)=\epsilon-\bar{\epsilon}^c(C)$, computed using different carrying capacities: $C=500$ (black), $C=1000$ (red), $C=2000$ (green), $C=4000$ (orange), $C=8000$ (blue). The inset display the curves in log-log scale. Mean values have been obtained by averaging the extinction times over $10^3$ realisations. (d) Scaling and collapse of the mean extinction times close to the stochastic bifurcation shown in panel (c). In all these analyses we used $k=1$ and $x(0)=0.75\cdot C$.

Figure 5. Effective potentials computed from equation (12) for the same system’s size values (see upper-left inset) used in figure 4(a). For each value of $C$ we have represented the potential with $\epsilon=\bar{\epsilon}^c(C)+10^{-8}$. For the sake of visualisation and comparison, we have overlapped the 5 curves using the same range amplitude (2 units) of the y-axis, since different potential values are obtained for each case analysed. This is why the values in the y-axis are not shown. Then, we have marked with a transparent rectangle the length of the flatter region of each potential. This has been quantified by means of rectangles with the same vertical amplitude, making coincide the values of each curve intersecting the left-up and right-down corners of each rectangle. The length of the flattest regions (transparent rectangles) for each value of $C$ are displayed with histograms, which have been re-sized keeping their relative differences.

We want to notice that the scaling region of interest is the one closer to the critical transition value, found as $\phi(x) \rightarrow 0$. In the presence of intrinsic noise, the resulting scaling is more complex than the simple power-law exhibited by mean field systems. In our case, $\bar{T}_e \sim C^{-b}G(\phi(x)C^a)$, with exponents $a=0.45$ and $b=0.81$, and $G(x)$ being the scaling function shown in figure 4(d). This indicates that the mechanism generating scaling behaviour in the stochastic system is fundamentally different than the one producing the $-1/2$-power law behaviour in the deterministic case.
3. Two-dimensional dynamical system

In the previous sections we analysed the impact of intrinsic noise in a one-variable dynamical system suffering a s-n bifurcation. In order to gain more intuition of this phenomenon in further dimensions we here investigate a two-dimensional system following the previous steps.

3.1. Mean field dynamics

A two-variable system also considering catalytic processes is here analysed to investigate if our previous results hold in the phase plane. Specifically, we use the so-called hypercycle model [25, 26, 48]. Hypercycles are closed, catalytic cycles where each of the molecular species $S_1, 2$ provides catalytic assistance to the reproduction of the other one. Figure 6(a) displays a diagram of a two-member hypercycle formed by two replicators (e.g. RNA molecules with catalytic activity). In this section we provide a brief summary of the mean field dynamics of these replicators that cooperate heterocatalytically, at rates $k_{12}$ and $k_{21}$, and undergo exponential degradation at rates $\epsilon_{1,2}$, respectively. These processes obey the following set of reactions ($A$ for species $S_1$ and $B$ for species $S_2$):

\begin{align}
  s + A + B & \xrightarrow{k_{12}} 2A + B, \\
  s + B + A & \xrightarrow{k_{21}} A + 2B, \\
  A & \xrightarrow{\epsilon_1} s, \\
  B & \xrightarrow{\epsilon_2} s,
\end{align}

$s$ also being some resources needed for reproduction, not explicitly considered. The reactions above, including a logistic like constraint now considering intra- and inter-specific competition are given by:

\begin{align}
  \frac{dx_i}{dt} &= k_{12} x_1 x_2 \left( 1 - \frac{x_1 + x_2}{\eta} \right) - \epsilon_1 x_1,
\end{align}

\begin{align}
  \frac{dx_2}{dt} &= k_{21} x_1 x_2 \left( 1 - \frac{x_1 + x_2}{\eta} \right) - \epsilon_2 x_2.
\end{align}
Figure 7. Mean population equilibria (±SD) obtained from the Gillespie simulations using $C = 500$ (a) and $C = 4000$ (b), with $k = 1$. Each data point is the mean of the normalized (over the system’s size) populations averaged over $10^5$ replicas for species 1 (solid black circles) and 2 (open blue circles) shown overlapped. The transparent, grey thick line is included to ease the visualization of the stochastic data. Overlapped in red we plot $x_+^{*}$ (solid) and $x_-^{*}$ (dashed) from the mean field model setting $k = \eta = 1$ and using $x_1(0) = 0.75 \cdot C$. The regions of monostability are indicated with light blue (stochastic case) overlapped to the deterministic case (red). We also display stochastic orbits in a phase space for each case with degradation rates close to the s-n bifurcation from above: (a) $\epsilon = 0.1157622$; (b) $\epsilon = 0.1249515$. The thick orbits travel directly to extinction without being trapped by the ghost.

$$\frac{dx_2}{dt} = k_{21} x_2 x_1 \left( 1 - \frac{x_1 + x_2}{\eta} \right) - \epsilon_2 x_2,$$  \hspace{1cm} (18)

$\eta$ being also the carrying capacity. Equations (17) and (18) have been investigated in references [25, 26].

Next, for the sake of clarity, we provide a brief summary of the dynamics. Since we are mainly interested in the effect of the dimension on dynamics close to the s-n bifurcation, we will focus in the so-called symmetric hypercycle i.e. $k_{12} = k_{21} = k$ and $\epsilon_1 = \epsilon_2 = \epsilon$. This system has the following equilibrium points: $(0, 0)$, $(x_+, x_+)$, and $(x_-, x_-)$, with

$$x_{\pm} = \frac{1}{4} \left( 1 \pm \sqrt{1 - \frac{8\epsilon}{k}} \right).$$ \hspace{1cm} (19)

Such dynamical system has a bifurcation point at $\epsilon_c = k/8$: if $\epsilon < \epsilon_c$, the three fixed points live in the phase space, but at $\epsilon = \epsilon_c$, the saddle and the node collide in a s-n bifurcation. If this critical condition is overcome, the equilibrium point $(0, 0)$ becomes the only attractor in phase space, being globally asymptotically stable. Such a bifurcation also leaves a ghost in phase space [25]. In order to analyse the ghost we solve numerically equations (17) and (18) using a fourth order Runge–Kutta method (with a constant time step size $\delta = 10^{-2}$). Figure 6 illustrates the behaviour of this hypercycle. In panel (b) we display three phase portraits with the orbits achieving the different equilibrium points (in black for the origin; in blue for the node $(x_+, x_+)$). The first two portraits use $\epsilon < \epsilon_c$, while the value of $\epsilon$ for the third one is taken above the bifurcation value (the ghost region is indicated with a transparent green ellipse).

Figure 6(c) displays the scaling law computed numerically, while panel (d) displays the transients and the bottleneck just found after the bifurcation for each of the hypercycle species.
3.2. Stochastic dynamics

3.2.1. Reactions

We also introduce a Markovian stochastic model now consisting of three elementary processes for each hypercycle species: quadratic heterocatalysis, binary (cubic) annihilation (with the purpose of including both intra- and inter-specific competition), and (linear) degradation [50]:

\[
\begin{align*}
A + B & \xrightarrow{k/C} A + B + A, \quad r_1 = +1, \\
A + B + A & \xrightarrow{k/C} B + A, \quad r_2 = -1, \\
A + B + B & \xrightarrow{k/C} B + B, \quad r_3 = -1, \\
A & \xrightarrow{\epsilon} \emptyset, \quad r_4 = -1, \\
B + A & \xrightarrow{k/C} B + A + B, \quad r_5 = +1, \\
B + A + A & \xrightarrow{k/C} A + A, \quad r_6 = -1, \\
B + A + B & \xrightarrow{k/C} A + B, \quad r_7 = -1, \\
B & \xrightarrow{\epsilon} \emptyset, \quad r_8 = -1,
\end{align*}
\]

Here \(r_i\) are also the components of the corresponding stoichiometric vector. The propensities (transition rates) using the law of mass action read:

\[
\begin{align*}
W_1 &= (k/C) n_1 n_2, \\
W_2 &= (k/C^2) n_1 n_2 (n_1 - 1), \\
W_3 &= (k/C^2) n_1 n_2 (n_2 - 1), \\
W_4 &= \epsilon n_1, \\
W_5 &= (k/C) n_2 n_3, \\
W_6 &= (k/C^2) n_1 n_2 (n_1 - 1),
\end{align*}
\]
Figure 9. (a) Mean stochastic bifurcation values (±SD) for different sizes of the system averaged over 50 evaluations of \( \epsilon(s) \) using the Gillespie simulations. (b) Time series (displaying 25 realisations without normalisation) with \( C = 500 \) and \( \epsilon = 0.1139499 \) (upper panel) and with \( C = 4000 \) and \( \epsilon = 0.12378394 \) (lower panel). (c) Mean extinction times, \( \bar{T}_e \) (±SEM), as a function of the distance to bifurcation, \( \phi(s) = \epsilon - \epsilon(s) \), computed using different carrying capacities: \( C = 250 \) (black), \( C = 500 \) (red), \( C = 1000 \) (green), \( C = 2000 \) (orange), \( C = 4000 \) (blue). The inset display the curves in log-log scale. Mean values have been obtained by averaging the extinction times over \( 10^3 \) realisations. (d) Scaling and collapse of the mean extinction times shown in panel (c). The phenomenon studied here takes place close to the bifurcation, where the curves collapse. In all these analyses we used \( k = 1 \) and \( x_{1,2}(0) = 0.75 \cdot C \).

\[
W_7 = \frac{k}{C^2} n_1 n_2 (n_2 - 1)
\]

\[
W_8 = \epsilon n_2,
\]

where \( n_1 \) and \( n_2 \) are the number of particles of hypercycle species 1 and 2 respectively, and \( C \) the system’s size.

3.2.2. Gillespie simulations

The stochastic dynamics of the two-member hypercycle is here explored numerically using the Gillespie algorithm. To compute \( \epsilon(s) \) we used \( 10^7 \) iterations of the Gillespie algorithm (see section 2.2.2). As we did for the one-dimensional system, we first study how the stochastic bifurcation value changes at increasing the noise magnitude (recall we do so decreasing the system’s size, \( C \)). Figure 7(a) also displays how the stochastic bifurcation value is lower than the one predicted by the deterministic model, here setting \( C = 500 \), as we found for the autocatalytic replicator model. The phase portrait on the right displays different realisations: the ones starting above the ghost region get trapped by it and strongly fluctuate for a long period of time before going to extinction. Some of the realisations starting below the ghost region directly travel to the origin without suffering any delay. Figure 7(b) displays the same results for \( C = 4000 \). Here note that the stochastic bifurcation value is very close to the deterministic one and that the fluctuations around the ghost are narrower. Figure 8 shows similar results to figure 3. Panel (a) shows how low system’s size (large noise) displaces the bifurcation value below the one predicted by the mean field model. Panels (b) show the mean stationary populations and standard deviation for one of the hypercycle species in the parameter space \((C, \epsilon)\). The same diagrams for the other species remain very similar due to the symmetry. Two time series in the parameter space close (white number 2) and far (white number 1) are shown on the right. Note that panel (b2) displays a long transitory with the characteristic bottleneck as compared to the time series of panel (b1).

3.2.3. Stochastic delayed transitions and scaling behaviour

Following the same approach developed for the one-dimensional system, we here study how extinction times behave above the stochastic bifurcation value. The table in figure 9(a) shows the stochastic bifurcation
values used in the numerical simulations. Panel (b) displays 25 realisations overlapped using $C = 500$ (upper panel) and $C = 4000$ (lower panel). Notice how extinction transients are typically longer at lower system’s size. The same scaling behaviour is recovered by the two-dimensional system following the method of parametric scaling described in section 2.2.4 (see reference [54]), although the scaling exponents slightly differ from the ones of the autocatalytic system. Here we obtained $T_e \sim C^{-a} \mathcal{G}(\phi^{1/3} C^b)$, with exponents $a = 0.35$ and $b = 0.7$. $\mathcal{G}(x)$ also being the scaling function shown in figure 9(d). Despite a good collapse of the curves has been obtained with these scaling exponents, the case $C = 4000$ remained a little below the other systems’ sizes. However, the scaling still remains robust at large noise intensities and close to stochastic bifurcation threshold.

In summary, these results suggest that the mechanism generating the scaling behaviour in stochastic systems with a s-n bifurcation may be universal. Despite these two systems analysed gave similar results, further research should check if this may be the case for other systems with s-n bifurcations under stochasticity, especially in mechanistically different systems (i.e., systems without catalytic or cooperative couplings).

4. Conclusions

Determinism and its mathematical approaches provide a neat and clear understanding of phenomena occurring in different dynamical systems. Of note is its role in the comprehension of nonlinear dynamics arising in multitude of natural and artificial systems. In this sense, bifurcations become extremely important since they can explain transitions between alternative states (phase transitions e.g., survival from extinction, active from inactive, among others). Bifurcation theory has shed light on the mechanisms involving such transitions, being currently identified in many experiments in physical [3–6], chemical [1, 2], and biological [7, 8] systems. Despite extensive research has been done in bifurcations and their properties in deterministic systems, many nonlinear systems are largely noisy. In this article we investigate two systems suffering a s-n bifurcation, focusing on the impact of demographic noise. The studied systems describe the dynamics of catalysis with exponential decay and competition [24–26].

We have revisited the phenomenon of delayed transitions (or ghosts) in the vicinity of s-n bifurcations regarding the effects of intrinsic fluctuations. In such bifurcation, the dynamics suffers an extremely long delay just after the transition has occurred. This phenomenon, known as delayed transition [23, 41], occurs because a saddle-remnant (or ghost) appears in the phase space. This ghost acts as a bottleneck and transients get trapped into the region where the saddle and the node collided, spending a large amount of time. Interestingly, bottlenecking has been experimentally observed in an electronic circuit [4]. Although delayed transitions have extensively analysed in deterministic systems [23–26, 41–44], little is known about the effect of intrinsic noise in the delaying capacity of the ghost.

To the end of analysing the status of such phenomenon in stochastic systems, we have analysed one- and two-dimensional dynamical systems whose stochastic dynamics exhibits a first-order phase transition. Somehow counterintuitively, not only have we found that the ghost phenomenon is robust in the presence of noise, but also that noise stabilizes the corresponding delayed transition. We have observed a phenomenon of noise-induced stabilization of the ghost, whereby, as the system’s size decreases (and therefore, noise levels increase), the delay to pass across the region of the saddle-remnant also increases. For the one-dimensional system we have studied this phenomenon numerically, by computing the extinction time above (but very close) to the transition, and analytically, where we have ascertained that the plateau exhibited by the effective potential, associated with the presence of the delay, is enlarged as the system’s size decreases.

One of the outstanding features of s-n ghosts in deterministic systems is the universal scaling law regarding the dependence of the time delay, $t_d$, on the quantity $\phi = \epsilon - \epsilon_c$, meaning distance to bifurcation, which is given by $t_d \sim \phi^{-1/2}$. Inspired by this result, we have looked for similar scaling properties in the behaviour of our stochastic models. Specifically, we have shown that the mean extinction times, $T_e$, satisfy a scaling law of the form: $T_e \sim C^{-a} \mathcal{G}(\phi^{1/3} C^b)$. This scaling law is much more complex than its deterministic counterpart, $t_d \sim \phi^{-1/2}$. For one dimensional systems we have obtained a ratio of $b/a = 1.8$, while for the two-dimensional one this ratio was $b/a = 2$. This suggests that, mechanistically, the origin of the stochastic scaling law should be different from that of the deterministic scaling behaviour. Furthermore, we have found the same scaling behaviour with slightly different exponents. This could indicate a universal feature between the times to extinction and the distance to stochastic bifurcation.

Taken together, our results show that the effects of intrinsic noise close (but after) to first-order phase transitions is far from trivial. Our present analyses suggest that further investigation regarding the dynamics of the system and their scaling properties should be conducted, specifically on the mechanisms leading to scaling behaviour and the impact of high-dimensional systems in the scaling properties under noise.
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