

Precursors of state transitions in stochastic systems with delay

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Abstract Ecosystem dynamics may exhibit alternative stable states induced by positive feedbacks between the state of the system and environmental drivers. Bistable systems are prone to abrupt shifts from one state to another in response to even small and gradual changes in external drivers. These transitions are often catastrophic and difficult to predict by analyzing the mean state of the system. Indicators of the imminent occurrence of phase transitions can serve as important tools to warn ecosystem managers about an imminent transition before the bifurcation point is actually reached. Thus, leading indicators of phase transitions can be used either to prepare for or to prevent the occurrence of a shift to the other state. In recent years, theories of leading indicators of ecosystem shift have been developed and applied to a variety of ecological models and geophysical time series. It is unclear, however, how some of these indicators would perform in the case of systems with a delay. Here, we develop a theoretical framework for the investigation of precursors of state shift in the presence of drivers acting with a delay. We discuss how the effectiveness of leading indicators of state shift based on rising variance may be affected by the presence of delays. We apply this framework to an ecological model of desertification in arid grasslands.

Keywords Bistable ecosystems · Resilience · Delayed dynamics · Leading indicators · State shift · Precursors · Tipping point

Introduction

In the last four decades, research in ecology has investigated the emergence of multiple stable states in ecosystems. Shifts between states often occur as abrupt and somewhat irreversible transitions (e.g., Noy-Meir 1975; May 1977; Walker et al. 1981; Carpenter 2005; Rietkerk and Van de Koppel 1997; Scheffer et al. 2001; Runyan et al. 2012). Bistable dynamics can be observed in a variety of environments and their emergence typically occurs in nonlinear systems as the result of positive feedbacks with process controlling, for instance, resource availability or the disturbance regime (e.g., Walker and Salt 2006; Scheffer 2009). In most cases, the response of bistable systems to changes in environmental conditions is discontinuous because of the existence of a first-order phase transition evidenced by a fold-type bifurcation. Thus, small changes in environmental drivers can lead to a sudden shift in the state of the system. Eutrophication, desertification, and deforestation are just some of the examples of possible abrupt ecosystem shifts to a less desirable state (Carpenter 2005; D’Odorico et al. 2013; Runyan et al. 2012); they typically occur over relatively short time scales and are hard to revert. To prepare for or prevent shifts to undesirable states, environmental managers are interested in finding some criteria to identify warning signs of imminent transitions before they occur (Brock and Carpenter 2006; Carpenter and Brock 2006; van Nes and Scheffer 2007; Guttal and Jayaprakash 2008; Carpenter et al. 2011).

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Linear stability analyses indicate that as the system approaches a critical transition, its response to small perturbations of its stable state(s) tends to become slower (Strogatz 1994). Known as critical slowing down, this phenomenon can be used as a leading indicator of state shifts in ecosystems (van Nes and Scheffer 2007). It can be shown that this effect is associated with an increase in the autocorrelation and the variance in systems driven by additive noise (Carpenter and Brock 2006; Scheffer et al. 2009; Dakos et al. 2012). Because the estimation of changes in autocorrelation and variance requires relatively long time series that are seldom available, other leading indicators of state shift try to capitalize on changes in the spatial configuration of the system. For instance, an increase in spatial autocovariance (Dakos et al. 2010) or changes in the geometry of spatial patterns (van de Koppel et al. 2002) can be interpreted as precursors of state shifts.

Despite these recent contributions to the study of leading indicators of state shifts, it is still unclear how the existing theories would perform in the case of systems affected by a delay. A number of systems in biology, earth sciences, engineering, and economics are affected by processes that act with a delay (e.g., Just et al. 2010). In other words, these systems respond to external drivers with a delay after an initial incubation period, τ , has elapsed. Typical examples include the spread of infectious diseases (e.g., Thomas et al. 2009), delayed population dynamics (Gurney et al. 1980; May 1980; D'Odorico et al. 2012), the behavior of commodity markets (MacKey 1989), and the response of excitable systems (Lefebvre et al. 2010).

Delayed processes may induce a variety of interesting behaviors in dynamical systems even without invoking the effect of interactions with nonlinearities and noise. A linear dependence on a delayed variable may lead to the emergence of instabilities, oscillations, and Hopf bifurcations in deterministic systems (e.g., Gyori 1991), while the interaction of delayed dynamics with a random forcing may induce noise-sustained fluctuations and other counterintuitive behaviors (D'Odorico et al. 2013). Despite recent advances in the study of stochastic systems with a delay (MacKey and Nechaeva 1995; Frank and Beek 2001; Frank et al. 2003; Frank 2005, 2006; Guillouzic et al. 1999), a theory of precursors of state shifts in delayed nonlinear dynamics is still missing. In this paper, we develop a theoretical framework to investigate leading indicators of state transition in univariate delayed systems driven by additive noise.

Methods

We consider the case of a spatially implicit (i.e., zero dimensional) dynamical system with only one state variable, x . The system is forced by a state-dependent process that acts

on the temporal dynamics of $x(t)$ with a delay, τ . Thus, the delayed dynamics depend in general on $x_\tau = x(t - \tau)$, i.e., the value of x at time $t - \tau$. The system is forced by a zero-average additive white Gaussian noise, ξ with unit intensity. Thus, the overall dynamics of x can be expressed as

$$\frac{dx(t)}{dt} = f(x, x_\tau, a) + \sigma \xi(t) \quad (1)$$

where a is a parameter. Because at equilibrium $x(t) = x(t - \tau) \equiv x^*$, the equilibrium states of the underlying deterministic dynamics are obtained as the solutions of $f(x^*, x^*, a) = 0$. The additive character of the noise term in Eq. 1 ensures (see Horsthemke and Lefever 1984; Ridolfi et al. 2011) that these states are also the preferential configurations (i.e., the modes) of the stochastic dynamics (Eq. 1). $f(x^*, x^*, a)$ is, in general, a nonlinear function of x^* . We focus on dynamics with multiple equilibria within a certain range of the parameter, a , and with a first-order phase transition at $a = a_c$.

In systems with no delays, as the bifurcation point is approached (i.e., $a \rightarrow a_c$), precursors of phase transitions from an attractor to the other (e.g., from x_1^* to x_2^*) are typically sought in changes (increase) in the variance or in the autocorrelation function of fluctuations of $x(t)$ about the stable equilibrium state, x_1^* (Carpenter and Brock 2006; Held and Kleinen 2004). The increase in variance and autocovariance is associated with the phenomenon of critical slowing down, whereby, as the system approaches the bifurcation point, the recovery of a stable equilibrium configuration after a small perturbation, ϵ , becomes slower and slower. Similarly, here, we focus on infinitesimal fluctuations, $\epsilon(t)$, of $x(t)$ about x_1^* (i.e., $\epsilon(t) = x(t) - x_1^*$) and use a Taylor's expansion to linearize Eq. 1 in the neighborhood of x_1^* :

$$\frac{d\epsilon(t)}{dt} = -A\epsilon(t) - B\epsilon_\tau + \sigma \xi, \quad (2)$$

where $\epsilon_\tau = x_\tau - x_1^*$, and the coefficients A and B are functions of the parameter a :

$$A = -\left. \frac{\partial f(x, x_\tau, a)}{\partial x} \right|_{x, x_\tau = x_1^*} \quad B = -\left. \frac{\partial f(x, x_\tau, a)}{\partial x_\tau} \right|_{x, x_\tau = x_1^*}. \quad (3)$$

In the absence of delays (i.e., $\tau = 0$), Eq. 2 is an Ornstein–Uhlenbeck process and its variance is (e.g., Gardiner 1986, p. 103)

$$\sigma_\epsilon^2(t) = \frac{\sigma^2}{2(A+B)} \left[1 - e^{-2(A+B)t} \right] \quad (4)$$

where, in this case, $A + B = -(\partial f / \partial x)_{x=x_1^*}$ is the eigenvalue of Eq. 1. Because $x = x_1^*$ is a stable state, $A + B$ is positive. Moreover, as $a \rightarrow a_c$, $A + B$ tends to zero and the convergence to zero of a small perturbation, $\epsilon(t)$, of the

equilibrium state x_1^* becomes increasingly slow. This phenomenon is known as “critical slowing down” (van Nes and Scheffer 2007). Thus, based on Eq. 4, the variance σ_ϵ^2 of the fluctuation ϵ increases ($\sigma_\epsilon^2 \rightarrow \infty$) as a tends to the bifurcation point, a_c . The effect of rising variance is often considered as a suitable precursor of a phase transition in systems driven by additive noise. This leading indicator of state shift has been used both in economics and ecosystem science (Brock and Carpenter 2006; Carpenter et al. 2011; Dakos et al. 2008).

We now generalize this framework in the case of a delayed process (i.e., $\tau \neq 0$) and investigate whether the rising variance remains a consistent precursor of state transition in the presence of a delay. To this end, we use the expression of the steady-state variance of $\epsilon(t)$ obtained from Eq. 2 (Frank et al. 2003):

$$\sigma_\epsilon^2 = \begin{cases} \frac{\sigma^2}{2} \left(\frac{1+B\omega^{-1}\sin(\omega\tau)}{A+B\cos(\omega\tau)} \right) & A < B \quad (5a) \\ \frac{\sigma^2}{2} \left(\frac{1+B\omega^{-1}\sinh(\omega\tau)}{A+B\cosh(\omega\tau)} \right) & A > B \quad (5b) \\ \frac{\sigma^2}{2} \left(\frac{1+B\tau}{A+B} \right), & A = B \quad (5c) \end{cases} \quad (5)$$

with $\omega = \sqrt{|B^2 - A^2|}$. This expression of σ_ϵ^2 (Eq. 5) is here used to investigate the increase in variance as a leading indicator of state shift in delayed dynamics. Similarly to the case of Eq. 4, because as $a \rightarrow a_c$ $A + B$ tends to zero, the variance of the fluctuations $\epsilon(t)$ has to increase ($\sigma_\epsilon^2 \rightarrow +\infty$) as the system approaches the bifurcation point $a \rightarrow a_c$. Thus, rising variance appears to be a leading indicator of state shift even in systems with a delay.

To evaluate how the effectiveness of this indicator is affected by the delay, we take the limit for $A + B \rightarrow 0$ of $\sigma_\epsilon^2(\tau = 0)/\sigma_\epsilon^2(\tau)$. We find that if $A > 0 > B$,

$$\frac{\sigma_\epsilon^2(\tau = 0)}{\sigma_\epsilon^2(\tau)} \rightarrow (1 + A\tau) > 1 \quad (\text{if } A > 0 > B) \quad (6)$$

In this case (i.e., $A > 0 > B$), the effect of the delay is to decrease the variance of ϵ with respect to the case with no delay. Thus, the ability of σ_ϵ^2 to serve as a leading indicator of a state shift is reduced as discussed in the example presented in the following section. Conversely, if $A > B > 0$,

$$\frac{\sigma_\epsilon^2(\tau = 0)}{\sigma_\epsilon^2(\tau)} \rightarrow \frac{1}{1 + A\tau} < 1 \quad (\text{if } A > B > 0). \quad (7)$$

In this case, the delay increases the variance of ϵ with respect to the case with no delay (in fact, $\sigma_\epsilon^2(\tau) > \sigma_\epsilon^2(\tau = 0)$). Thus, σ_ϵ^2 becomes a better leading indicator of state shift.

The effect of the delay in systems with $B > A$ is more complex because, in this case, the state x^* becomes unstable when the delay exceeds a critical value $\tau_1 = \frac{\arccos(-A/B)}{\sqrt{B^2 - A^2}}$ (e.g., D’Odorico et al. 2012). If $\tau < \tau_1$, x^* is stable and σ_ϵ^2 is a precursor of state shift as shown by Eq. 5a. The analysis of

the limit for $A + B \rightarrow 0$ shows that $\frac{\sigma_\epsilon^2(\tau=0)}{\sigma_\epsilon^2(\tau)} \rightarrow (1 + A\tau) < 1$ if $B > 0 > A$. Thus, the effectiveness of the precursor is enhanced by the delay. Conversely, if $B > A > 0$, the limit becomes $\frac{\sigma_\epsilon^2(\tau=0)}{\sigma_\epsilon^2(\tau)} \rightarrow (1 - A\tau) > 1$ and the phenomenon of rising variance is weakened.

A case study

To show how the delay may affect the variance of $x(t)$ and its ability to serve as a precursor of state shift, we consider as an example the dynamics of desert grasslands, with grass biomass, x , growing logistically:

$$\frac{dx}{dt} = \beta x (x_{cc} - x) + \sigma \xi \quad (8)$$

where ξ is an additive Gaussian noise with unit intensity, β is the reproduction rate of the logistic process, and x_{cc} is the carrying capacity, i.e., the maximum value of x that is sustainable with existing resources (e.g., water, soil nutrient content). In arid landscapes, grass cover plays a crucial role in sheltering the soil surface from erosion agents (wind and water). Loss of vegetation cover may lead to soil erosion and land degradation, thereby inducing a decrease in carrying capacity. Thus, x_{cc} can be expressed as an increasing function of the grass cover, x . However, we notice that a loss in grass biomass does not immediately lead to a decrease in x_{cc} because erosion processes do not instantaneously remove the soil resources. In other words, a delay, τ exists in the process of land degradation; thus, at time t , the carrying capacity of x depends on the value of $x_\tau = x(t - \tau)$.

Moreover, because other factors beside erosion-induced depletion of soil resources are likely to limit grass productivity, x_{cc} is a nonlinear function of x , which asymptotically tends to a maximum for high values of the grass cover. Thus, we use an s-shaped function (Fig. 1) to express the dependency of x_{cc} on x_τ :

$$x_{cc} = \frac{ax_\tau^2}{(1 + ax_\tau^2)} \quad (9)$$

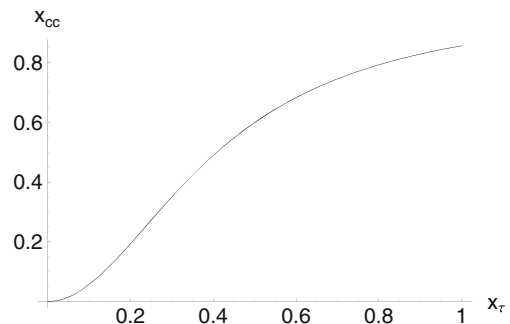


Fig. 1 Carrying capacity, x_{cc} , as a function of grass cover, x (Eq. 9) calculated for $a = 6$

where a is a shape parameter. The stable and unstable states of the dynamics expressed by Eqs. 8 and 9 are the solutions of $dx/dt = 0$, namely,

$$\begin{aligned}
 x_1^* = 0 \quad & x_2^* = \frac{1}{2} \left(1 - \sqrt{\frac{a-4}{a}} \right) \\
 & x_3^* = \frac{1}{2} \left(1 + \sqrt{\frac{a-4}{a}} \right)
 \end{aligned}
 \tag{10}$$

For small values of a , the carrying capacity (Eq. 9) is small and the grass density tends to zero regardless of the antecedent grass cover conditions (x_τ). In this case, the grass-soil erosion feedback is too weak to allow for the stabilization of the system in a vegetated state. In other words, even in the presence of a full grass cover, vegetation would not be able to prevent the loss of soil resources and the system would soon converge toward an unvegetated and degraded state. When a is greater than a critical value (a_c), the feedback is strong enough to lead to the emergence of an alternative state with a stable grass cover. In this case, if the system is in a vegetated state, grasses can stabilize the soil surface, prevent soil erosion, and maintain an adequate pool of soil resources. Conversely, unvegetated conditions are associated with soil degradation, which prevents grass establishment. These properties of the dynamics are shown in Fig. 2: the state ($x_1^* = 0$) is stable for any value of a . Moreover, a bifurcation occurs at $a_c = 4$. As a increases above a_c , two new equilibria emerge: a stable equilibrium (x_3^*) and an unstable one (x_2^*). Thus, a first-order phase transition occurs for $a_c = 4$.

The coefficients of the linearized model around x_3^* are

$$A = \frac{1}{2} \left(1 + \sqrt{\frac{a-4}{a}} \right) \quad B = -\frac{2}{a}
 \tag{11}$$

and their dependence on a is shown in Fig. 3. Thus, $A + B > 0$ (hence, x_3^* is a stable state) and $A^2 > B^2$ (hence, x_3^* remains stable for any value of τ (e.g., D’Odorico et al. 2012).

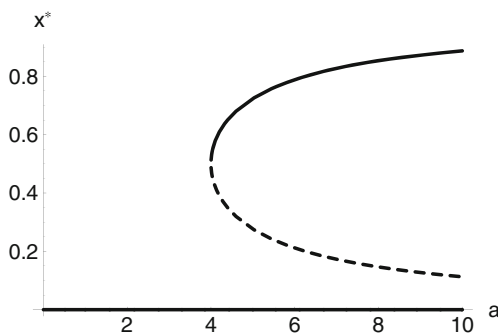


Fig. 2 Stable (solid) and unstable (dashed) states of the system (Eq. 10) as a function of the parameter a

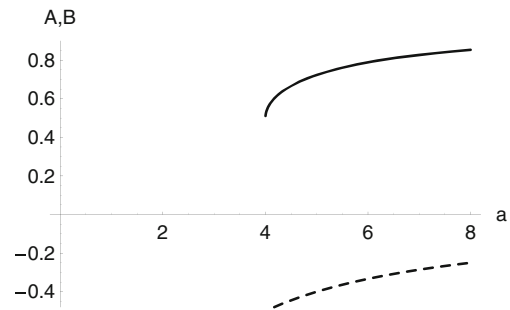


Fig. 3 A plot of the parameters A (solid) and B (dashed) (Eq. 11) as a function of the parameter a

Moving along the upper branch, $x = x_3^*$, of the bifurcation diagram (Fig. 2), the variance of x increases as $a \rightarrow a_c^+ = 4$ (Fig. 4). However, in this case ($A > 0 > B$), as the delay, τ , increases, the increase in variance occurs when the system is closer to the transition point. As an effect of the delay, the rising variance becomes less effective as a leading indicator state shift (Fig. 4, see also “Methods” section).

Discussion and conclusions

This manuscript developed a theoretical framework for the study of leading indicators of state shift in ecosystems affected by delayed processes. The framework is used to evaluate whether the variance of fluctuations of the state variable increases as the system approaches the bifurcation point. We find that the variance of the state variable does increase when the system is close to a critical transition. This result provides a generalization to variance-based theories of precursors of state shift. Thus, the rising variance can be used as a leading indicator of imminent state changes also in delayed systems driven by additive noise. It is important to stress, however, that this result applies only to univariate systems driven by additive noise. In the case of systems with multiplicative noise (i.e., with a noise term

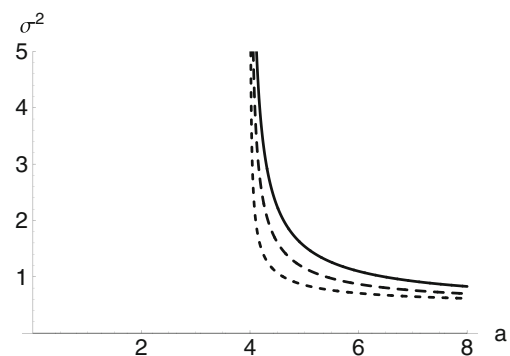


Fig. 4 Variance of the fluctuation, ϵ , of $x(t)$ about the stable state x_3^* (upper branch of the bifurcation diagram, Fig. 2) for $\tau = 0$ (solid line), $\tau = 1$ (longer dashed line), and $\tau = 5$ (shorter dashed line)

multiplying a function of the state variable x), the rising variance is not necessarily a leading indicator of state shift (Dakos et al. 2012).

This study has also shown that the delay has an impact on the effectiveness of the rising variance as a leading indicator of state shift. In fact, depending on the parameter values, the delay may either cause an increase or a decrease in the variance, thereby enhancing or weakening the effectiveness of this leading indicator of state shift with respect to the case with no delay. In other words, the delay can either increase or reduce the ability of the rising variance to anticipate the occurrence of the transition when the system is still far from the bifurcation point. More specifically, if the dependency of the linearized dynamics on the current state of the system, x , is stronger than that on x_τ (i.e., $A^2 > B^2$), the delay reduces or enhances the effectiveness of raising variance as a leading indicator, depending on whether these dependencies have a concurrent (i.e., $A > B > 0$) or an opposite (i.e., $A > 0 > B$) effect on the dynamics, respectively. Conversely, if the dependency on the past state is stronger than that on the present configuration of the system (i.e., $B^2 > A^2$), the effectiveness of this precursor is enhanced by the delay if B and A have opposite sign, while it is reduced, otherwise.

In most empirical applications, it will be difficult to discern whether the system is driven by additive or multiplicative noise. Moreover, the sign and magnitude of the dependency of the linearized dynamics on the system's present and past conditions are hard to evaluate. Regardless of these limitations, the theory presented in this manuscript supports the use of the rising variance as a leading indicator of state shift in delayed ecosystem dynamics driven by additive noise.

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