Robustness of variance and autocorrelation as indicators of critical slowing down

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Abstract. Ecosystems close to a critical threshold lose resilience, in the sense that perturbations can more easily push them into an alternative state. Recently, it has been proposed that such loss of resilience may be detected from elevated autocorrelation and variance in the fluctuations of the state of an ecosystem due to critical slowing down; the underlying generic phenomenon that occurs at critical thresholds. Here we explore the robustness of autocorrelation and variance as indicators of imminent critical transitions. We show both analytically and in simulations that variance may sometimes decrease close to a transition. This can happen when environmental factors fluctuate stochastically and the ecosystem becomes less sensitive to these factors near the threshold, or when critical slowing down reduces the ecosystem's capacity to follow high-frequency fluctuations in the environment. In addition, when available data is limited, variance can be systematically underestimated due to the prevalence of low frequencies close to a transition. By contrast, autocorrelation always increases toward critical transitions in our analyses. To exemplify this point, we provide cases of rising autocorrelation and increasing or decreasing variance in time series prior to past climate transitions.

Key words: alternative stable states; autocorrelation; critical slowing down; early-warning signals; fold bifurcation; leading indicators; noise; resilience; variance.

Introduction

Some ecosystems may occasionally change quite abruptly to a contrasting state (Scheffer et al. 2001). Theoretical studies have suggested that such shift may occur in ecosystems with alternative stable states in which the conditions change gradually toward a critical point, called a bifurcation, where the ecosystem becomes unstable and shifts to the alternative state. It has been recently suggested that such shifts may be announced in advance by generic leading indicators for critical transitions (Scheffer 2009). This idea is based on the fact that systems tend to show a phenomenon known as "critical slowing down" as they approach bifurcation points (Wissel 1984, Strogatz 1994, Scheffer 2009) where a tiny change in conditions can lead to a marked qualitative change in the behavior of a system. The term "critical slowing down" refers to the fact that near these points the return time to equilibrium upon a small perturbation increases strongly. To illustrate the principle, consider an ecosystem that exhibits alternative stable states over a range of conditions (Fig. 1). Such ecosystems will undergo a critical transition at point F_1 when conditions (expressed by a control parameter p) cross a threshold (at

$p = p_1$), and the ecosystem shifts to an alternative state (Fig. 1a). As the ecosystem moves close to the critical threshold ($p \rightarrow p_1$), the return rate to equilibrium upon a small perturbation smoothly declines to 0 (Fig. 1b). This means that the ecosystem needs increasingly more time to recover from a small perturbation as it comes closer to this critical point (van Nes and Scheffer 2007).

Now consider what will happen if one exposes such an ecosystem to a permanent stochastic regime of perturbations. Intuitively one can imagine that the loss of the ecosystem's tendency to return to its equilibrium may cause it to be simply pushed around by the stochastic perturbations. This effect can be seen in simulations in our example where the state of the ecosystem becomes more correlated to its past and drifts farther away from its equilibrium when the bifurcation is close (Fig. 1f and d) compared to when the bifurcation is far (Fig. 1e and d). Indeed, analytical arguments as well as simulations have suggested that, close to a bifurcation, one should expect critical slowing down to cause a rise in autocorrelation (Kleinen et al. 2003, Held and Kleinen 2004) and variance (Carpenter and Brock 2006) in stochastically forced systems.

While it is an attractive idea that such changes could be used as early-warning signals (or "leading indicators") for critical transitions related to underlying bifurcations, the conditions under which this approach is reliable are still poorly understood. These leading indicators can signal an upcoming transition, only when
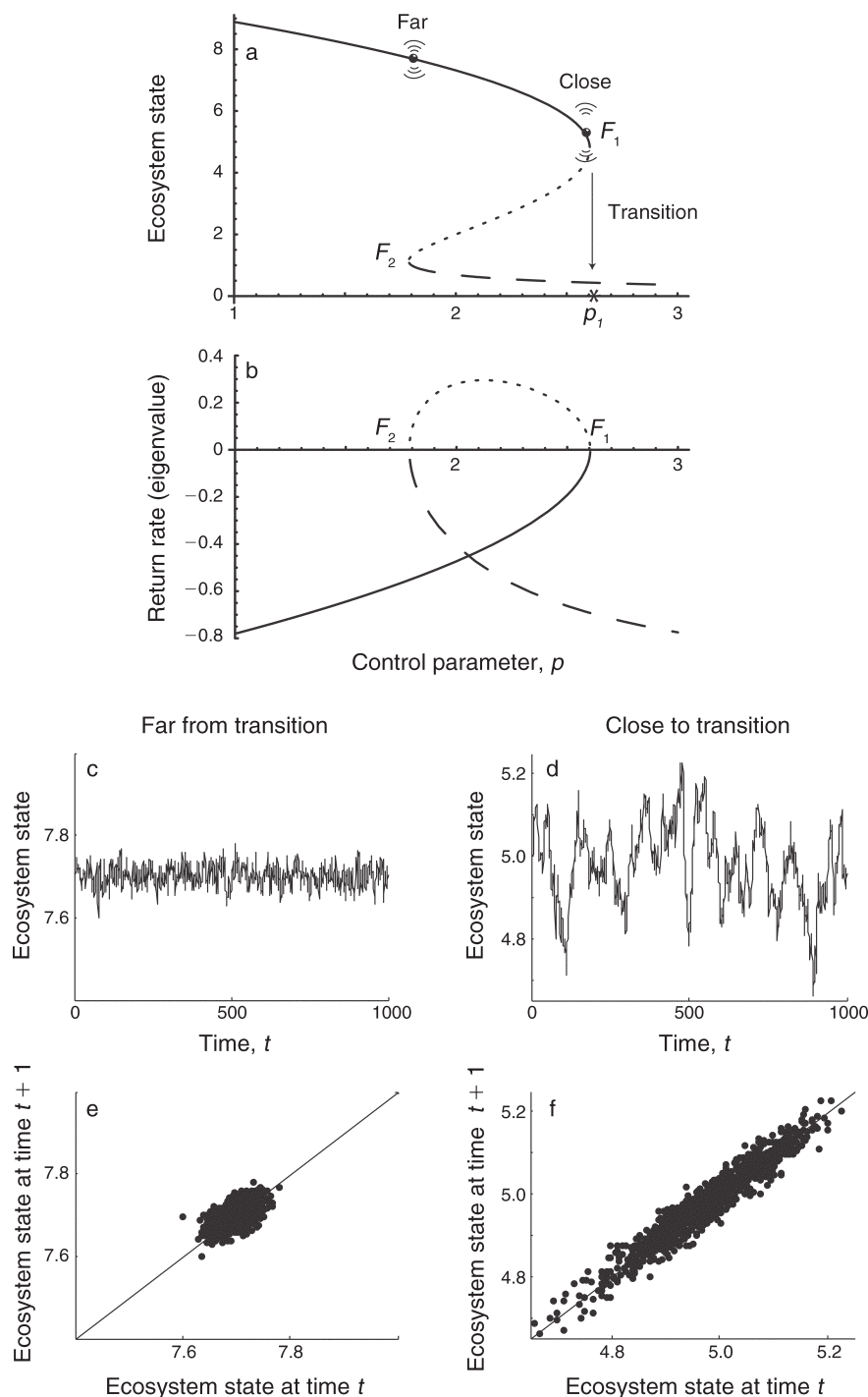
FIG. 1. An example of an ecosystem undergoing a critical transition through a fold bifurcation, F_1, when an external driver (control parameter, p) reaches a threshold value, p_1. The system undergoes a transition from the lower to the upper state through another fold bifurcation F_2. (a) Stable and unstable equilibria as function of control parameter p. The two dots denote two instances of the system (far and close to the transition), and the semicircles around them represent small disturbances. (b) Return rates of equilibria. The dotted line denotes the unstable equilibrium that separates the two basins of attraction of the stable upper (solid line) and stable lower (dashed line) equilibrium state. (c–f) Sampled realizations and their first-lag correlations of a stochastically perturbed ecosystem: (c, e) far from the transition and (d, f) close to it.

conditions gradually move the ecosystem toward a bifurcation. The indicators are unlikely to detect transitions between attractors induced by major perturbations, or chaotic dynamics far from local bifurcation points. Another obvious source of false positives or negatives would be a systematic change in the external perturbation regime over the period leading up to a shift (Scheffer et al. 2009). For instance, dynamics of an ecosystem under a regime of increasingly autocorrelated perturbations may appear increasingly autocorrelated, even if there is no approaching bifurcation. Moreover, even if the return rate decreases, statistical detection of the resulting change in dynamics can still be challenging.

Here we explore some more intricate mechanisms that may affect the way in which critical slowing down translates into changes in autocorrelation and variance in the fluctuations of an ecosystem. First, we ask whether the way in which the environmental perturbations act on an ecosystem could influence how critical slowing down translates into autocorrelation and variance in the ecosystem's dynamics. Thinking in terms of models, environmental perturbations can be applied directly to the state of the ecosystem (e.g., stochastically killing portions of a population) or to any of its parameters (e.g., temperature fluctuations affecting process rates). Most work so far has focused on the first aspect (Brock and Carpenter 2006, Brock et al. 2006, Biggs et al. 2009, Carpenter et al. 2009, Guttal and Jayaprakash 2009, Dakos et al. 2010; but see Carpenter and Brock 2006, Carpenter et al. 2008, and Guttal and Jayaprakash 2008). In this paper, we examine how perturbations on ecosystem processes may impact the behavior of the leading indicators compared to the case of direct perturbations on the state of an ecosystem. For these two situations we derive simple analytical approximations for autocorrelation and variance as functions of the proximity to a bifurcation, and we compare the results to estimates of autocorrelation and variance derived from numerical simulations. We also discuss how sensitive estimators of autocorrelation and variance may be due to limitations in our current time series techniques as well as due to the availability of data. Last, we use some examples of past climate transitions to show how patterns in autocorrelation and variance may deviate prior to a shift.

METHODS

Perturbations in the state of an ecosystem.—To derive analytical expectations for autocorrelation and variance, let us assume that the dynamics of an ecosystem are described by a continuous stochastic equation:

$$dx = f(x, p)dt + \sigma dW \qquad (1)$$

where x is the state of the system, p is the ecosystem control parameter, $f(x, p)$ is the deterministic part that governs the dynamics of the ecosystem, and dW is the stochastic driver represented by a white noise process of mean zero and intensity σ^2/dt.

When a small perturbation ε pushes the state of an ecosystem a tiny bit away from equilibrium x^* [for which $f(x^*, p) = 0$], the ecosystem returns to equilibrium with a rate approximately equal to the dominant eigenvalue $f_x(x^*, p) = \lambda(x^*, p)$ of the linearized equation of the system (Horsthemke 2006):

$$d\varepsilon = \lambda(x^*, p)\varepsilon dt + \sigma dW \qquad (2)$$

where λ is the dominant eigenvalue and $\lambda(x^*, p)$ is negative if x^* is stable. Eq. 2 has the following explicit solution (Gardiner 2003):

$$\varepsilon_t = \varepsilon_0 e^{\lambda(x^*, p)t} + \sigma \int_0^t e^{\lambda(x^*, p)(t-s)}dW(s)$$

where the temporal variable s is integrated between time 0 (when $\varepsilon_t = \varepsilon_0$) and time t. Autocorrelation ρ_ε and variance σ_ε^2 of ε_t are given by $\rho_\varepsilon = e^{\lambda(x^*, p)|t-s|}$ and $\sigma_\varepsilon^2 = [\sigma^2/2\lambda(x^*, p)](e^{2\lambda(x^*, p)t} - 1)$, respectively (Gardiner 2003). For time $t \to \infty$, we can derive approximate expressions for autocorrelation at lag 1 [$\rho_\varepsilon(1)$] and variance (σ_ε^2) (Gardiner 2003), which explicitly depend on the responsiveness of the ecosystem as determined by the dominant eigenvalue $\lambda(x^*, p)$:

$$\rho_\varepsilon(1) = e^{\lambda(x^*, p)} \qquad (3)$$

$$\sigma_\varepsilon^2 = -\frac{\sigma^2}{2\lambda(x^*, p)}. \qquad (4)$$

Perturbations of parameters representing processes.—When environmental stochasticity is affecting processes in an ecosystem, we may model that by assuming that one of the parameters p of the ecosystem $dx = f(x, p)dt$ becomes a random parameter with mean p^*. If we consider that for average p^* an equilibrium x^* exists [i.e., $f(x^*, p^*) = 0$], then the evolution of small disturbances around equilibrium x^* can be approximated by the linearized system (Ripa and Heino 1999):

$$dx = f_x(x^*, p^*)(x - x^*)dt + f_p(x^*, p^*)(p - p^*)dt. \qquad (5)$$

Assuming that $\varepsilon = x - x^*$ and $z = p - p^*$, where z is a Gaussian random variable with mean zero and magnitude σ^2, Eq. 5 can be rewritten as

$$d\varepsilon = \lambda(x^*, p^*)\varepsilon dt + f_p(x^*, p^*)\sigma dW \qquad (6)$$

where $f_x(x^*, p^*) = \lambda(x^*, p^*)$ is the eigenvalue of the ecosystem for average parameter p^*, $f_p(x^*, p^*)$ is the partial derivative of f with respect to the parameter p that is affected by environmental noise, and dW is a stochastic term of zero mean and unit variance that represents the random variable z. In this case, the effect of stochastic perturbations on the state of the ecosystem depends on $f_p(x^*, p^*)$. The factor

$$f_p(x^*, p^*) = \frac{\partial f}{\partial p}\bigg|_{x^*}$$

reflects the sensitivity of the ecosystem to changes in the

parameter p: in other words it reflects how the ecosystem is modulating (scaling) the magnitude of perturbations to produce an effect on its state. Following the same steps as above, autocorrelation at lag 1 is the same as Eq. 3. However, variance is now also a function of $f_p(x^*, p^*)$:

$$\sigma_\varepsilon^2 = -\frac{\sigma^2 f_p(x^*, p^*)^2}{2\lambda(x^*, p^*)}. \quad (7)$$

The important observation is that as $f_p(x^*, p^*)$ may change, if a control parameter brings the ecosystem closer to a bifurcation, variance may be amplified or dampened as the ecosystem approaches the bifurcation. By contrast, autocorrelation remains solely dependent on the dominant eigenvalue $\lambda(x^*, p^*)$ (Eq. 3).

Simulation experiments.—We tested these theoretical approximations of autocorrelation and variance in a well-studied ecosystem model that describes the shift of a harvested resource to overexploitation (Noy-Meir 1975, May 1977). Resource biomass x grows logistically and is harvested according to

$$dx = \left[rx\left(1 - \frac{x}{K}\right) - c\left(\frac{x^2}{x^2 + h^2}\right) \right] dt + f_p(x, p)\sigma dW \quad (8)$$

where r is the growth rate, K is the population's carrying-capacity, h is the half-saturation constant, and c is the grazing rate. When c reaches a certain threshold value ($c \approx 2.604$), the ecosystem undergoes a critical transition through a fold bifurcation. When environmental noise is affecting directly the state variable x, white noise is added through a stochastic term dW with intensity σ^2/dt. When environmental noise affects the parameters, dW is scaled by $f_p(x, p)$, which reflects how stochastic forcing translates into changes in the state; scaling factors $f_p(x, p)$ for growth rate r, grazing rate c, and carrying capacity K are $f_r(x) = x[1 - (x/K)]$, $f_c(x) = -x^2/(x^2 + h^2)$, and $f_K(x) = rx^2/K^2$, respectively.

We started simulations from equilibrium and slowly increased grazing rate c until the ecosystem shifted to overexploitation. After each stepwise change of grazing rate, we ran the model for 500 time steps. We used these 500 time steps to estimate autocorrelation at lag 1 and variance (expressed as standard deviation) for each level of grazing rate c. We estimated autocorrelation at lag 1 by fitting a first-order autoregressive model using package arfit in MATLAB (Schneider and Neumaier 2001). We repeated this for 200 simulations and used average estimates for both indicators. All simulations and statistical analyses were performed in MATLAB (The Mathworks, Natick, Massachusetts, USA), R (R Project for Statistical Computing, Vienna, Austria), and Mathematica (Wolfram Research, Champaign, Illinois, USA). We solved the stochastic equations using an Euler-Murayama integration method with Ito calculus in 36 integration steps for each time step. Parameter

values used were $r = 1$, $K = 10$, $h = 1$, $c = [1, 3]$, $\sigma = 0.1$, unless otherwise indicated.

RESULTS

Our theoretical approximations illustrate that, as an ecosystem undergoes a transition, autocorrelation at lag 1 is expected to reach 1 (Eq. 3). When perturbations affect the state of the ecosystem directly, variance is also predicted to increase gradually before the bifurcation (Eq. 4). However, when environmental stochasticity acts on a parameter of the ecosystem, the effect on variance is modulated by the system's sensitivity to that parameter:

$$f_p(x^*, p^*) = \frac{\partial f}{\partial p}\bigg|_{x^*}.$$

Therefore, under a constant environmental noise regime, variance in the fluctuations of the ecosystem state may either increase or decrease as the ecosystem approaches a bifurcation (Eq. 7). Nonetheless, at the bifurcation itself, variance should approach infinity as long as the sensitivity of the ecosystem to the disturbed parameter is not zero (i.e., $f_p(x^*, p^*)^2 > 0$). Fig. 2 illustrates this effect. If the sensitivity of the ecosystem to the disturbed parameter stays constant or increases toward the bifurcation, variance will typically increase over a range prior to transition (Fig. 2a, b). However, the opposite occurs, if the sensitivity of the ecosystem to the disturbed parameter is shrinking as the ecosystem is approaching the transition (Fig. 2c). Autocorrelation at lag 1 is insensitive to this effect (Fig. 2).

Numerical simulations support these theoretical predictions (Fig. 3). In the overgrazing model, trends in variance toward the bifurcation point depend on the way in which the sensitivity to the affected parameter [scaled by $f_p(x^*, p^*)$] changes as the ecosystem approaches the bifurcation. While noise on most parameters has a similar effect to noise applied directly to the state (Fig. 3c, d, f), noise on the carrying capacity K leads to an opposite trend in variance over much of the trajectory of the ecosystem toward the bifurcation (Fig. 3e). As the resource is moving away from its carrying capacity due to increased grazing, perturbations on K have a small effect on the equilibrium that the system is forced to track. Only very close to the transition, the effect of critical slowing down overwhelms the effect of the decreasing trend in sensitivity (cf. Fig. 2c). On the other hand, autocorrelation at lag 1 is insensitive to the way in which environmental noise affects an ecosystem (Fig. 3c, d, e, f).

Filtering effects of slowness.—In addition to the potential effect of decreasing sensitivity to parameters, there is a quite different mechanism that may in some situations mute variance as the ecosystem approaches a bifurcation. This is related to the very nature of critical slowing down. Consider an overall slow ecosystem (Fig. 4). When environmental stochasticity directly affects the ecosystem's state variables, the ecosystem is as if it were
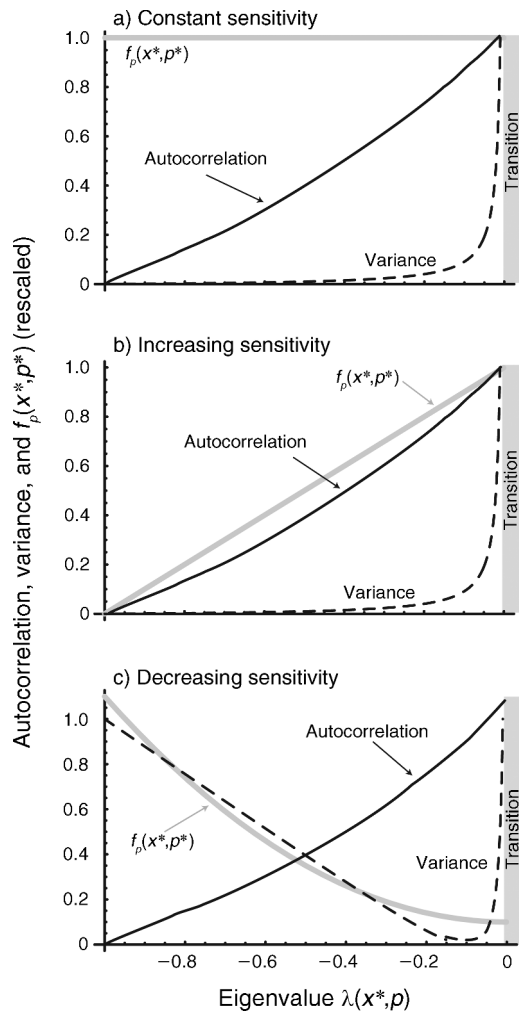
FIG. 2. Analytically predicted trends in autocorrelation at lag 1 [$\rho(1)$] and variance [σ_ε^2] prior to a zero-eigenvalue bifurcation depending on the sensitivity $f_p(x^*, p^*)$ of the ecosystem to noise. (a) Constant sensitivity $f_p(x^*, p^*)$ of the ecosystem. (b) Increasing sensitivity $f_p(x^*, p^*)$ of the ecosystem toward the transition. (c) Decreasing sensitivity $f_p(x^*, p^*)$ of the ecosystem toward the transition. (Autocorrelation is at lag 1 from Eq. 4; variance is from Eq. 8 with $\sigma^2 = 1$ rescaled to the interval 0–1.)

"pushed" around the fixed equilibrium (Fig. 4a, gray line). By contrast, when noise affects processes, one can think of the ecosystem as "tracking a fluctuating equilibrium" (in this case driven by a fluctuating carrying capacity K; Fig. 4a, black line). Now, if an ecosystem is inherently slow (i.e., has low rates of change), it will hardly follow the fluctuations in the equilibrium and as a result its state may vary only little over time (Fig. 4b, black line). As critical slowing down will only aggravate the already limited capacity of the ecosystem to track the fluctuating environment, the net effect is that the state of the ecosystem "freezes" as it approaches the bifurcation. This "freezing" may smother even the increase of variance just before the

bifurcation (Fig. 4a1, a2; gray line). Again, autocorrelation is insensitive to this effect. It will increase prior to the shift regardless of the responsiveness of the ecosystem, even though in such inherently slow ecosystems autocorrelation is obviously always very large (Fig. 4a2, b2; black line).

DISCUSSION

The use of indicators of critical slowing down to sense the risk of upcoming critical transitions in real ecosystems is an exciting prospect. Rising variance and autocorrelation are among the prime candidate indicators. However, while autocorrelation appears a relatively robust indicator, our results suggest that there can be particular conditions under which variance may decrease instead of rise prior to a transition. Specifically, this can happen if environmental stochasticity affects the "equilibrium" rather than the state of an ecosystem, and the effect can be aggravated if the ecosystem's inherent rates of change are slow relative to the frequency characteristics of the forcing regime.

It remains difficult to judge how common distortions of the basic effect of critical slowing down on variance will be in practice. As stochastic perturbations usually affect ecosystems in multiple ways simultaneously, our analysis of a one-dimensional model with a single noise source may be seen as a special case. Indeed, simulations with a lake ecosystem model subject to multiple sources of noise suggest that an increase in variance may dominate the pattern (Carpenter and Brock 2006, Carpenter et al. 2008). In such multidimensional systems, the effect of noise on variance is not approximated by a simple sensitivity function as the one we presented here, but derived from a multidimensional variance matrix (see appendix in Biggs et al. 2009). In some of such cases, variance may be either muffled or amplified (Brock and Carpenter 2010), and even autocorrelation may not be immune to changes in the magnitude of noise (S. Carpenter, *personal communication*), although examples have not been identified so far. Our results complement such general considerations in explaining specifically why we might expect deviations in trends in variance prior to regime shifts when applied to real data, as illustrated, for instance, by the contradicting trends in variance despite consistent trends in autocorrelation in the four examples of past climatic shifts we present in Appendix A.

It is interesting that, with respect to the factors we explored, rising autocorrelation appears a robust indicator of critical slowing down. Of course this is not to say that it will be a flawless indicator in practice. While we can trust that the linear approximation of Eq. 2 holds in the case of small magnitude noise (close to equilibrium dynamics), in systems with strong noise regimes this may not be true. In such systems far from equilibrium, critical slowing down is less relevant and our approximations and their consequences on the behavior of the indicators will not hold. Instead, in
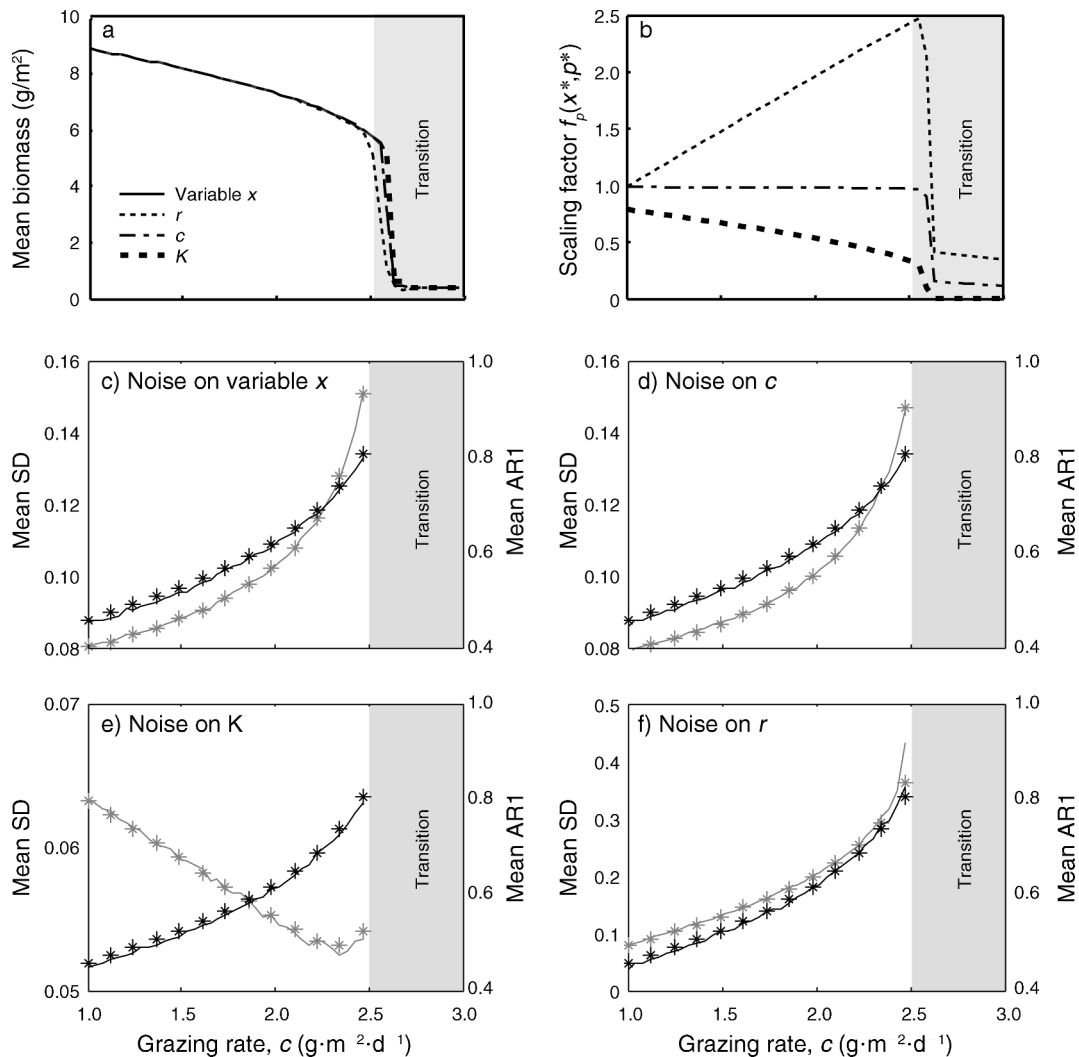
FIG. 3. Leading indicators in a model of a logistically growing population driven slowly to collapse due to increasing grazing rate. Environmental noise is affecting the state variable x, grazing rate c, carrying capacity K, or growth rate r. (a) Mean biomass at increasing grazing rate. (b) The scaling factor represents how strongly perturbations on a parameter affect the state. (c–f) Analytical (asterisks) and numerical (lines) estimates of autocorrelation (AR1, gray lines) and variance (measured as standard deviation [SD], black lines) for stochastic forcing of the state or a parameter.

such situations the behavior of the system may be used to infer emerging alternative attractors in the underlying stability landscape (Livina et al. 2010, Hirota et al. 2011), or nonparametric estimates of variance may be more reliable than estimates of autocorrelation in forewarning a transition (Carpenter and Brock 2011).

Clearly, a major challenge in applying early-warning signals in real-world situations is to accurately estimate variance and autocorrelation in the face of limited data availability. Note, for instance, that even if the real variance stays constant, the perceived variance may decrease toward a shift, as the fluctuations in an ecosystem become increasingly dominated by low frequencies. This can happen simply because our time window for estimating variance is limited, thus missing out on variance related to the lowest frequencies, and also because there is

an increasing risk that local detrending techniques filter out this slow part of the variability (Appendix B). Autocorrelation is insensitive to this effect. On the other hand, accurate estimates of autocorrelation require long and equidistant time series (see Appendix C for a discussion on time series requirements), which are not typical for most ecological records, while error estimates of variance are smaller for short data sets. As a result detectability of an increase in autocorrelation can be more difficult (Appendix C). Alternatively, the use of spatial information can sometimes help to improve the diagnosis of early warning signals (Dakos et al. 2011). For example, even if rising variance is not found prior to a transition under strong noise regimes (Hastings and Wysham 2010), an increase may be visible in spatial variance (Carpenter and Brock 2010). Also, spatial correlation may often
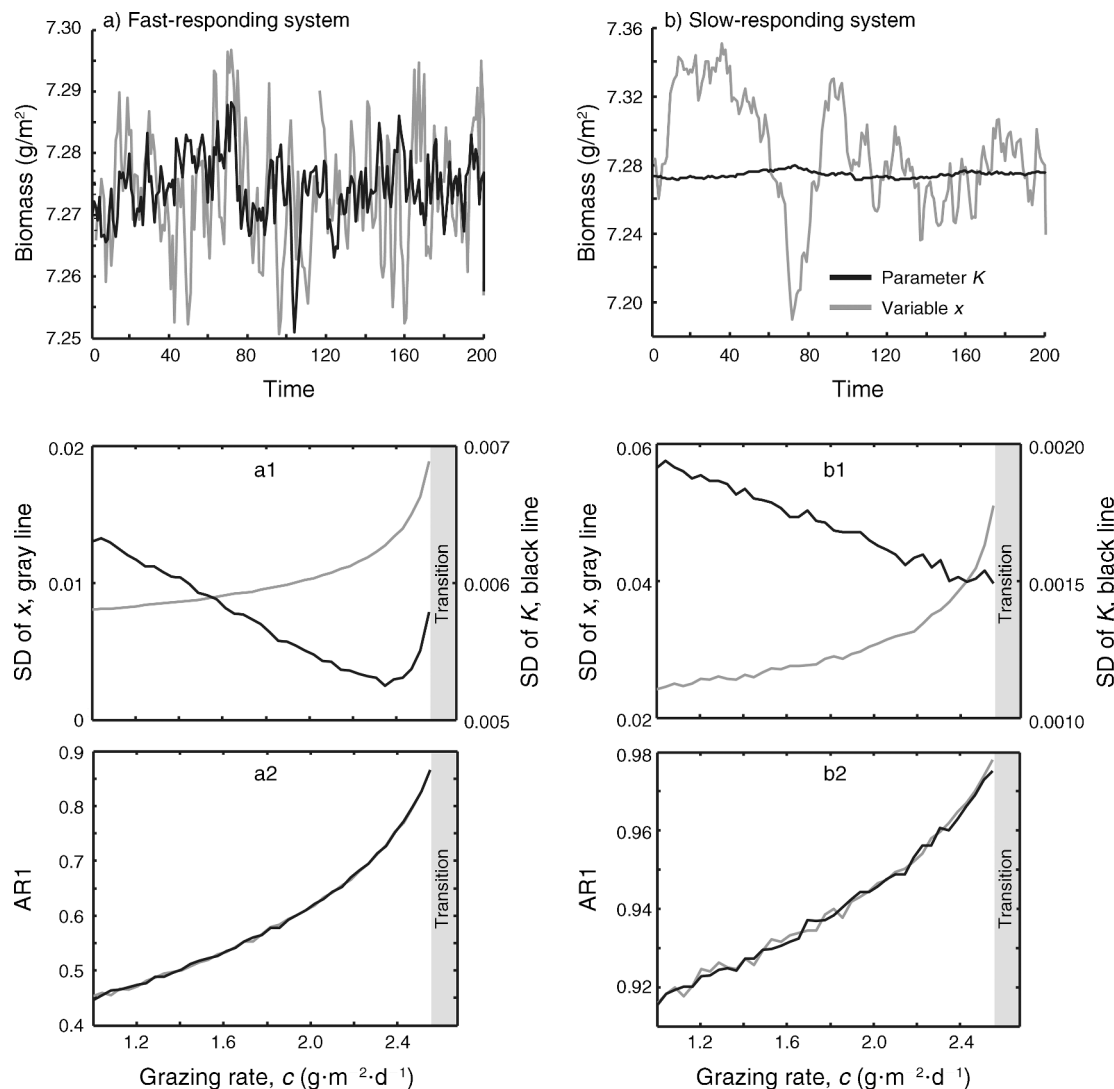
FIG. 4. Slowing down can reduce the sensitivity of an ecosystem to high-frequency fluctuations in the environment, preventing variance from rising in the vicinity of a bifurcation. (a) Fast-responding ecosystem. Noise is affecting either the state of the ecosystem (gray line) or a parameter (carrying capacity K, black line). Variance drops and rises only before the transition (a1). Autocorrelation rises independently from the source of noise (a2). (b) Slow-responding ecosystem. The ecosystem is less able to track the constantly changing equilibrium. Slowing down further "freezes" the ecosystem, preventing variance to rise in the vicinity of the bifurcation (b1). Autocorrelation at lag 1 rises independently from the source of noise (b2).

provide a stronger warning signal than temporal autocorrelation (Dakos et al. 2010). Thus, it is worth investigating whether spatial variance and spatial correlation would be robust against the factors we explored.

While the fundamental principle of critical slowing down has already been known in physics for a long time, the search for practical leading indicators of critical transitions in ecology and earth science has just started (Dakos et al. 2008, Drake and Griffen 2010, Carpenter et al. 2011). Undoubtedly, challenges of model identification and statistical estimation still affect our current ability to detect generic early-warning signals (Hastings and Wysham 2010, Carpenter and Brock 2011). Thus, it seems likely that, rather than a "silver bullet approach,"

we will need to develop a toolkit of indicators and a good understanding of when each of them might be most useful both in terms of detectability and reliability. Variance clearly remains an attractive candidate, as it is a straightforward characteristic that can in principle be easily measured. On the other hand, it may be less generic as an indicator of critical slowing down than autocorrelation, and our results provide a search image for particular situations where perceived and/or real variance may decrease rather than increase toward a bifurcation.

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Supplemental Material

Appendix A

Examples from past climate transitions (*Ecological Archives* E093-026-A1).

Appendix B

Deviations in the performance of leading indicators when measured in time series due to methodological issues (*Ecological Archives* E093-026-A2).

Appendix C

Reliability in identification of increasing trends in variance and autocorrelation (*Ecological Archives* E093-026-A3).

Reports