

LETTER

Changing skewness: an early warning signal of regime shifts in ecosystems

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Abstract

Empirical evidence for large-scale abrupt changes in ecosystems such as lakes and vegetation of semi-arid regions is growing. Such changes, called regime shifts, can lead to degradation of ecological services. We study simple ecological models that show a catastrophic transition as a control parameter is varied and propose a novel early warning signal that exploits two ubiquitous features of ecological systems: nonlinearity and large external fluctuations. Either reduced resilience or increased external fluctuations can tip ecosystems to an alternative stable state. It is shown that changes in asymmetry in the distribution of time series data, quantified by changing skewness, is a model-independent and reliable early warning signal for both routes to regime shifts. Furthermore, using model simulations that mimic field measurements and a simple analysis of real data from abrupt climate change in the Sahara, we study the feasibility of skewness calculations using data available from routine monitoring.

Keywords

Alternative stable states, catastrophic regime shifts, ecological indicators, lake eutrophication, resilience, skewness, stability, tipping points, vegetation collapse, warning signals.

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INTRODUCTION

Studies indicate that ecological systems occasionally undergo rapid shifts from one stable state to an alternative stable state with dramatically different properties, often accompanied by degradation of ecosystem services and attendant economic losses. Such abrupt transitions that occur without large external shocks but only with gradual changes in external conditions have been termed ‘catastrophic regime shifts’ (Scheffer *et al.* 2001). Well-studied examples of such drastic changes include lake eutrophication, marine ecosystems, changes in states of coral reefs, collapse of vegetation in semi-arid ecosystems, preferential states of soil moisture and trophic cascades (Knowlton 1992; Steele 1996; Hare & Mantua 2000; Scheffer *et al.* 2001; D’Odorico & Porporato 2004; Schroder *et al.* 2005; Daskalov *et al.* 2007; Narisma *et al.* 2007). Simple mechanistic models have provided useful insights into both feedback mechanisms that stabilize alternative stable states and the occurrence of critical thresholds beyond which regime shifts occur. However, to translate this theoretical insight into practically useful predictions we must calibrate the model parameters. This needs a detailed understanding of ecological processes, a

formidable task beyond our current abilities. It is therefore important to devise model-independent indicators that can be obtained from data collected with routine monitoring and use them as warning signals for impending catastrophic transitions. Such warning signals can have enormous impact on managing ecosystems by identifying the threatened systems permitting initiation of suitable management strategies.

Several indicators that can potentially determine the proximity to a transition point have been recently suggested in simple models. These models exhibit bifurcations, i.e. sudden changes in the topology of the long-time behaviour, such as the number of possible stable states when small, smooth changes occur in a parameter value. Kleinen *et al.* (2003) consider the power spectrum of the dynamical variable, i.e. its intensity (squared amplitude) per unit frequency interval and show that there is a ‘reddening’ near the threshold. Increases in the system variability, i.e. the amplitude of oscillations, near a bifurcation point have been observed in variety of ecological models (Strogatz 1994; van Nes & Scheffer 2003; Obórny *et al.* 2005; Carpenter & Brock 2006). In a spatial population model, Obórny *et al.* (2005) found that even as the average density

decreases as the threshold is approached its variance over a large spatial region increases in a scale-invariant manner and this can serve as an indicator of a potential species extinction on large spatial scales. In addition, several indicators based on patch formation in spatially extended models have been suggested (Rietkerk *et al.* 2004; Obórny *et al.* 2005; Kéfi *et al.* 2007). In a relatively complex, but non-spatial model of lake eutrophication, Carpenter & Brock (2006) showed that increases in variance near a bifurcation can be observed in the presence of exogenous noise. Reddened spectrum and the rise in the variance near a threshold arise from the flattening of the potential (often referred to as the landscape picture or the ball in a cup picture; Scheffer *et al.* 2001) that determines the dynamics as the bifurcation point is approached in one-variable models. Additionally, this flattening leads to a substantial reduction in the recovery rate of the system from a perturbation. This is a generic phenomenon observed near all threshold points and is related to 'critical slowing down' in physics literature (Ma 1976; Strogatz 1994). Signatures of critical slowing down near a threshold have been reported in ecological model systems as well (Wissel 1984; Rietkerk *et al.* 1996; Gandhi *et al.* 1998; Held & Kleinen 2004; van Nes & Sheffer 2007). Various studies have suggested that increase in the recovery time can be used as an indicator of a nearby transition (Wissel 1984; Held & Kleinen 2004; van Nes & Sheffer 2007).

As one approaches a regime shift, the landscape picture of the ecosystem dynamics exhibits a pronounced asymmetry around the stable state, in addition to flattening of the potential landscape, i.e. decrease in curvature. In contrast to the flattening of the landscape which is obtained by a linear analysis, the asymmetry arises due to nonlinear effects and hence presents a new way of devising an early warning signal. In this paper, we exploit the impact of large external fluctuations and asymmetry in the landscape on the dynamics of the ecosystem and show that a changing skewness (a measure of the changing asymmetry) of the time series probability distribution can be an effective early warning signal of a regime shift. In general, regime shifts can occur either due to the approach to a threshold point as an external parameter is varied (studied traditionally in the theory of dynamical systems and in various ecological studies mentioned above) or due to increased width of the external noise distribution (Scheffer *et al.* 2001; Guttal & Jayaprakash 2007). Whereas the existing set of indicators can serve as warning signals typically only for the former scenario, it is shown that a changing skewness is a promising indicator for both routes to regime shift. We show these results demonstrating the utility of skewness as an early warning signal by studying different model systems including a parameterized lake eutrophication model where we simulate a plausible scenario for collection of field data and

show that a trend of changing skewness can be detected several years in advance of an impending regime shift. We provide an intuitive understanding of these results and discuss the issues related to the feasibility of computing skewness in empirical data sets by analysing data from climatic shift in the Sahara and total phosphorus concentration data from a tributary to Lake Erie.

MODELS AND METHODS

We consider three well-studied ecological model systems showing alternative stable states and regime shifts: two of vegetation collapse in semi-arid regions and another, a parameterized model of lake eutrophication (Noy-Meir 1975; May 1977; Carpenter 2005; Guttal & Jayaprakash 2007). Table 1 lists the models along with brief definitions of the various symbols used. A short description of the models and the ecological motivation for various terms is presented in the Appendix S1 in Supplementary Material. A common aspect of all the models is that they show a regime shift via a saddle node bifurcation in which a stable fixed point disappears by merging with an unstable fixed point as we vary one of the model parameters. Saddle node bifurcations are widely employed to model regime shifts in ecology. These three models, however, differ in the nature of the noise and in the details of ecological feedback mechanisms. This allows us to check the utility of asymmetric indicator in different contexts and at different levels of modelling approximations.

We do a variety of numerical and analytical calculations to establish the changing skewness as an early warning signal. The stochastic differential equations (eqns T1–T6) are solved numerically by a simple Euler algorithm which is first order accurate in time assuming the rules of Ito calculus (Risken 1984; Gardiner 2003). The solution for a particular time sequence of noise values obtained by our numerical simulation corresponds to the time series data of the ecological variable collected in field. Simulations were performed using the MATLAB and C++.

The skewness, denoted by γ , is a dimensionless measure of the degree of asymmetry of a probability distribution. Given a probability distribution $P(x)$, with mean μ and standard deviation σ , the skewness is defined as the scaled third moment about the mean:

$$\gamma = \frac{\int (x - \mu)^3 P(x) dx}{\sigma^3} \quad (1)$$

The skewness vanishes for distribution symmetric about the mean and is positive or negative for an asymmetric distribution with a tail above or below the mean respectively. For the vegetation models, we calculate skewness for a time series of length 2000 time units. We then average the skewness over 100 such realizations.

Table 1 Description of models and parameters

Models and/or parameters	Description and/or values
$\frac{dV}{dt} = rV \left(1 - \frac{V}{K} \right) - c \frac{V^2}{V^2 + V_0^2} + \sigma_V \eta_V(t) \quad (T1)$	Ref: Noy-Meir (1975), May (1977)
V	Vegetation biomass; the dynamical variable
r	Growth rate, $r = 1$
K	Carrying capacity, $K = 10$
c	Maximum grazing rate; the control parameter (range: 1–3)
V_0	Biomass at which the grazing rate is half maximum, $V_0 = 1$
σ_V	SD of external noise (range: 0–1)
$\eta_V(t)$	Uncorrelated Gaussian noise, i.e. $\langle \eta_V(t) \eta_V(t') \rangle = \delta(t-t')$
$\frac{dw}{dt} = R - \alpha w - \lambda w B + \sigma_w \eta_w(t) \quad (T2)$	Ref: Guttal & Jayaprakash (2007)
$\frac{dB}{dt} = \rho w B \left(1 - \frac{B}{w B_c} \right) - \mu \frac{B}{B + B_0} + \sigma_B \eta_B(t) \quad (T3)$	Coupled dynamics of water and vegetation
B	Vegetation biomass; dynamic variable of interest
w	Soil water
R	Rainfall rate; control parameter (range: 0–3)
α	Rate of soil water loss; $\alpha = 1.0$
λ	Consumption rate of water by biomass, $\lambda = 0.12$
σ_w	SD of fluctuations in rainfall rate R (range: 0–1)
ρ	Maximum biomass growth rate (for $w = 1$), $\rho = 1$
B_c	Carrying capacity of biomass (for $w = 1$), $B_c = 10$
μ	Maximum grazing rate, $\mu = 2$
B_0	Biomass at which the grazing rate is half maximum, $B_0 = 1$
σ_B	SD of external noise (range: 0–1)
$\eta_w(t), \eta_B(t)$	Uncorrelated Gaussian noise, i.e. $\langle \eta_i(t) \eta_j(t') \rangle = \delta_{ij} \delta(t-t')$ where $i, j = w$ or B .
$\frac{dP}{dt} = l - (s + b)P + rMR(P) + \sigma_r \eta_r(t) rMR(P) + \sigma_l \eta_l \quad (T4)$	Ref: Carpenter & Brock (2006)
$\frac{dM}{dt} = sP - bM - rMR(P) - \sigma_r \eta_r(t) rMR(P) \quad (T5)$	Lake eutrophication model
$R(P) = \frac{P^q}{P_0^q + P^q} \quad (T6)$	Recycling term
P	Phosphorus density in water; g m^{-2}
M	Phosphorus density in sediments; g m^{-2}
l	Phosphorus loading rate; control parameter (range: 0.5–1.0 $\text{g m}^{-2} \text{ year}^{-1}$)
s	Phosphorus sink rate, $s = 0.7 \text{ year}^{-1}$
b	Outflow rate, $b = 0.15 \text{ year}^{-1}$
r	Recycling rate, $r = 0.019 \text{ year}^{-1}$
b	Permanent burial rate, $b = 0.001 \text{ year}^{-1}$
P_0	Phosphorus concentration at which recycling rate is half maximum; $P_0 = 2.4 \text{ g m}^{-2}$
q	Hill coefficient, $q = 8$
σ_l	SD of fluctuations in loading term l ; $\sigma_l = 0.01$
σ_r	SD of fluctuations in recycling rate r ; $\sigma_r = 0.01$
$\eta_l(t), \eta_r(t)$	Uncorrelated Gaussian noise, i.e. $\langle \eta_i(t) \eta_j(t') \rangle = \delta_{ij} \delta(t-t')$ where $i, j = l$ or r

In all of our calculations, we choose the parameters so that the skewness is zero when the system is far from a regime shift. Thus we choose the magnitude of the skewness

(for a single time series data) or the magnitude of the average skewness (for repeated simulations of time series data) denoted by $|\langle \gamma \rangle|$, as a measure of proximity to a

regime shift and hence we show that an increase in the magnitude of skewness is a potential indicator of regime shift. More generally, however, it is the change in skewness which acts as an early warning signal of an impending ecological transition. Depending on the ecological system under consideration, the change can be from zero skewness to either positive or negative values or from one sign of skewness to the other.

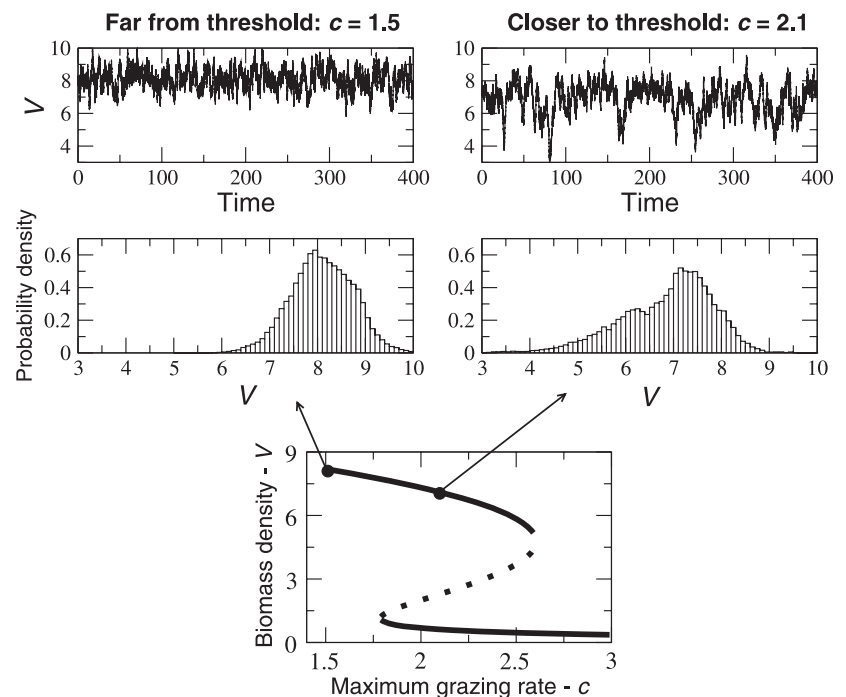
We explain the origin of asymmetry in one-variable stochastic models using the concept of effective potential. Consider a model of an ecosystem governed by the stochastic differential equation $\dot{x} = f(x) + g(x)\eta(t)$ where $\eta(t)$ is an uncorrelated Gaussian noise with standard deviation of σ . The intuitive ball in a potential landscape picture can be rendered mathematically precise by defining the effective potential $U(x)$ in terms of f and g . The steady-state time series distribution is then given by $P_s(x) \propto \exp(-\frac{2}{\sigma^2} U(x))$. These results are obtained by solving the Fokker–Planck equation for the evolution of probability density of the dynamical variable x (see Appendix S2 and Horsthemke & Lefever (1984)). For May’s model, we have calculated the skewness by performing the integration (eqn 1) in the region $\mathbf{R} = (x_b, x_m)$ around the stable fixed point x^* such that $x_l = x^* - 5\sigma_V$ and x_r is determined by solving the equation $P_s(x_l) = P_s(x_r)$. We compare this analytical result with the results of numerical simulations. No such potential $U(x)$ can be obtained for the two variable models we have studied and hence they were studied through numerical simulation alone.

RESULTS

We begin this section by showing that qualitative changes in the shape of the distribution are observed in the time series of the state variable as one approaches a threshold point. We illustrate this using the results of numerical simulations of the one-variable vegetation model of eqn T1. The bifurcation diagram for the deterministic limit of the model is shown in Fig. 1. As the maximum grazing rate c is increased the system goes from a (stable) high-density vegetated state, to a bistable region with coexisting bare and vegetated states for $1.8 < c < 2.6$. For $c > c^* = 2.6$ the system collapses to a single low-density vegetated state. We are interested in predicting the vegetation collapse that occurs as we approach the bifurcation at $c^* = 2.6$. So we consider values of $c < c^*$ with the system in the desirable state of high vegetation biomass and move towards the bifurcation threshold by varying c keeping the strength of the external noise (i.e. its variance) constant. The plots of time series of the state variable, the vegetation biomass density, and the corresponding probability distributions are shown in Fig. 1. The distribution is symmetric at $c = 1.5$ far from the threshold. As the threshold value is approached, the distribution develops a visible asymmetric tail. For this specific model, substantial asymmetry is observed even at $c = 2.1$, relatively far away from the bifurcation ($(c^* - c)/c^* \approx 20\%$).

In the rest of this section we present detailed results exploiting this asymmetry to find a warning signal of an impending regime shift. The calculated skewness increases

Figure 1 The plot at the bottom of the panel shows the bifurcation diagram for May’s single-variable model (eqn T1) of vegetation collapse due to increase in grazing. The thick lines indicate stable ecological states whereas the dotted line represents the unstable equilibria. Four subplots at the top of the panel show representative numerical simulation results for the time series and its probability density (i.e. histogram) when the ecosystem is far from and close to the threshold of collapse ($c^* = 2.6$). The asymmetry in the distribution that is clearly visible underlies the indicator of regime shift proposed in the paper. Simulations were started with the vegetation in the high density state. We choose $\sigma_V = 0.75$, a time step of $dt = 0.01$ for numerical integration and rest of the parameters are as in Table 1.



in the two routes to a regime shift discussed in the introduction: (i) approaching the ecological threshold by changing a parameter with fixed external noise distribution and (ii) increasing the variance of the external noise holding the other parameters fixed so that in the deterministic limit the system is far from the bifurcation. By studying a plausible field measurement scenario as simulated in the lake eutrophication model parameterized for Lake Mendota (Carpenter 2005), we show that changing skewness is a useful measure of proximity to a regime shift. We report on our analysis of real data sets of sediment in the Sahara and total phosphorus concentration from a tributary to Lake Erie.

Skewness as a measure of asymmetry and an indicator of a regime shift

We compute the skewness from the time series for the model of eqn T1. In Fig. 2, we plot the absolute value of the

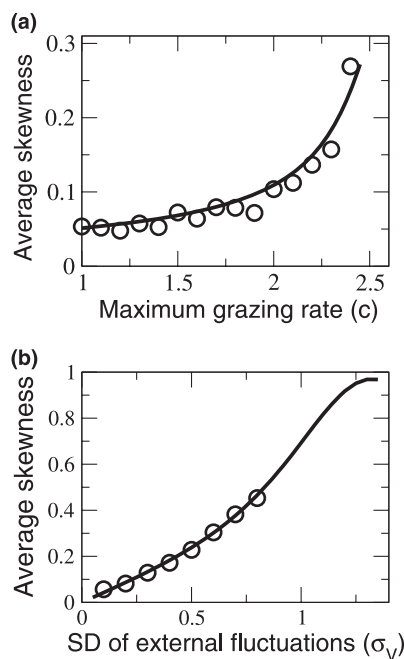


Figure 2 Increase in skewness as the ecosystem approaches regime shift via different routes for May's model of vegetation collapse considered in Fig. 1. The thick line is the analytical result obtained directly from the stationary probability distribution. The open circles are the average values of skewness obtained by the numerical simulations. Note that we have plotted the absolute value of the average skewness. (a) Approaching the threshold of vegetation collapse by increasing the grazing pressure with fixed external fluctuations $\sigma_v = 0.25$. (b) Approaching regime shift by increasing (noise) fluctuations in the system at $c = 2.0$ (far from threshold). We choose $dt = 0.1$ and rest of the parameters are as in Table 1.

average skewness in the two scenarios corresponding to different routes to a regime shift. In both the plots, the solid line represents the analytical calculations obtained by a direct evaluation of skewness of the corresponding stationary probability distributions. The open circles represent the average values of skewness obtained by numerical simulations.

In the first scenario the variance of the external noise is held constant and the grazing rate c is varied. The skewness of the time series distribution as a function of the bifurcation parameter c , shown in Fig. 2a, increases slowly up to $c = 2.0$. However, as the grazing rate is tuned closer to the threshold value from $c = 2.0$ to 2.6, the skewness increases substantially. Thus, an increase in skewness foreshadows the vegetation collapse and serves as an early warning signal of the regime shift.

In the second route, increasing the external noise by increasing the standard deviation, σ , of the Gaussian noise distribution, leads to a regime shift even if the system is far from the bifurcation (Guttal & Jayaprakash 2007). In Fig. 2b, we plot the skewness, with a fixed grazing rate at $c = 2.0$, as σ is varied. Clearly, the skewness increases as the noise level increases. This is an intrinsic dynamical effect as the noise distribution is Gaussian and symmetric. We do not show data for $\sigma > 0.8$ in Fig. 2b because the significant reduction in the average collapse time to low-density vegetation precludes an accurate estimate of the skewness. We have studied this more carefully as follows: Starting from the vegetated state the system will eventually make a transition to the bare state in the presence of Gaussian noise. In a random process with a given initial condition the first occurrence of an event such as reaching a specific value is known as the 'first passage time' (Gardiner 2003; Drury 2007). The mean first passage time in our problem is the average time interval over which the system remains in the vegetated state. In all of our calculations if the mean first passage time is smaller than a certain length of time interval we have chosen (2000 time units for May's model), we do not compute skewness. For details on the mean first passage time calculations, see Appendix S3.

We have checked that the features reported above hold for the model with no additive noise but noise in either the growth rate r or the grazing rate c . In the former case the skewness though large far from equilibrium, increases substantially as the bifurcation is approached, thus serving as an early warning signal. We also check the applicability of our proposal in a more complex ecological model of vegetation dynamics described in eqns T2–T3. See Appendix S4 for detailed results. We comment on the limitations imposed by the nature of the noise on using skewness as an indicator in the Discussion section and present details in Appendices S7–S9.

Skewness calculations for a parameterized lake model

In this section we consider a parameterized lake eutrophication model and mimic a plausible scenario of field measurements. We show that a trend of increasing skewness can be detected well in advance of a regime shift despite constraints of sparse data availability. Our results allow us to make useful observations and provide insights on the analysis of real data sets.

We choose a slightly modified version of the lake eutrophication model which has been parameterized for Lake Mendota, Wisconsin (see eqns T5–T6 and Carpenter 2005). Appendix S5 contains the bifurcation diagram and the results for the skewness. We consider a scenario in which the mean nutrient inputs increase as a function of time which can occur with economic growth. We perform a dynamic simulation to see if we can observe a trend of increasing skewness under such conditions. In our numerical calculations the mean nutrient loading is increased from 0.5 to 1.28 $\text{g m}^{-2} \text{year}^{-1}$ in 40 years time with constant increments every year and kept constant thereafter. We

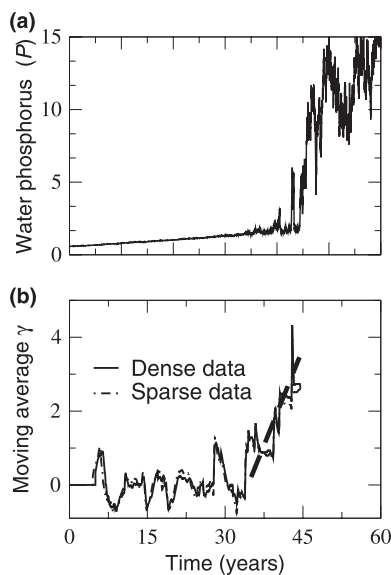


Figure 3 The figures show that changes in the skewness (denoted by γ) can be detected well in advance for a model system which mimics a field measurement scenario. These results are obtained by numerical simulation for the lake model (eqns T4–T5) when the nutrient inputs are increased as a function of time towards the eutrophication threshold as described in the text. All parameters are defined in Table 1; the initial conditions $P(t=0) = 0.58 \text{ g m}^{-2}$ & $M(t=0) = 410 \text{ g m}^{-2}$ and a time step of $dt = 0.01$. The moving average skewness has been calculated from data for the previous 5 years. The dense and the sparse data sets correspond to 100 and 33 measurements of lake water phosphorus concentration (P) per year respectively.

solve eqns T5–T6 to obtain the phosphorus concentration and compute a simple moving average skewness from the data for the previous 5 years.

The results of the model calculations are presented in Fig. 3a,b. The phosphorus concentration data indicates that a regime shift occurred around year 45. Moving average skewness shows an increasing trend starting from year 34 and by the beginning of year 40 the trend is unmistakable (around 100% increase) and hence, this can serve as an early warning signal nearly 5 years in advance. We added a practical constraint of limited data sets by comparing the results of a dense data set (100 water phosphorus measurements per year) with those for a sparse data set of 33 measurements per year. We find that thinning the data set had negligible effect on the trend of changing skewness, thus providing confidence in its utility as an early warning signal. We note that for a specific set of parameters values (nutrient loading taken to be constant at $1 \text{ g m}^{-2} \text{year}^{-1}$ with the initial conditions $P_0 = 1 \text{ g m}^{-2}$ and $M_0 = 800 \text{ g m}^{-2}$), the skewness failed to detect a regime shift in nearly 30% of the cases.

More importantly, these model calculations suggest that skewness can fluctuate for short time periods and then relax to the background value; such behavior, observable far from a regime shift, should not be misinterpreted as signalling an impending transition. However, significant changes on a time scale larger than the background fluctuation time scale act as reliable early warning signals of an impending regime shift.

Analysis of Sahara data

We consider a well-dated record of terrigenous sediment deposition at Ocean Drilling Program Site 658C off Cap Blanc, Mauritania which indicates an abrupt termination of North African (Sahara region) humid periods resulting in collapse of vegetation and desertification (deMenocal *et al.* 2000). See Appendix S6 for the analysis of the complete Sahara data set from 25 000 years before present (BP) to the present. An abrupt change in the sediment concentration corresponding to the most recent regime shift in Sahara is found around year 5500 BP as shown in Fig. 4a. Our interest is to determine whether skewness of the data showed any reliable trends prior to the regime shift. We note that the data are relatively sparse and have errors both in the determination of the time and the sediment. Nevertheless, in an effort to illustrate the difficulties encountered in the prediction of regime shifts from available data we have performed a simple analysis of the data. The moving average skewness (calculated for the previous 10 data points) up to the year of the shift is shown in Fig. 4b. An increasing trend of moving skewness is clearly identifiable and occurred around 1000 years prior to the collapse. However, we need

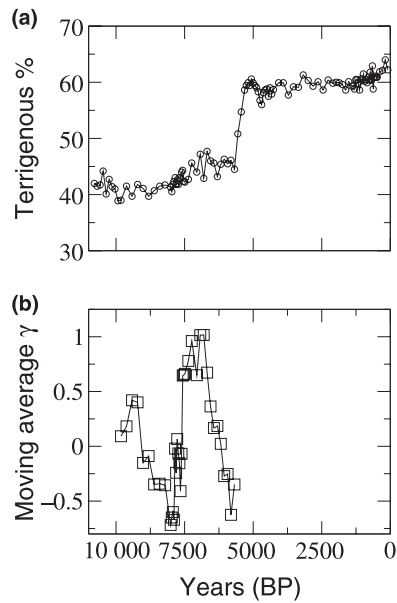


Figure 4 Analysis of terrigenous sediment data indicating climatic shift in Sahara (a) Time series of terrigenous sediment percentage record from Site 658C off Cap Blanc, Mauritania (deMenocal *et al.* 2000). Circles represent data while connecting line is meant to guide the eye. Note the regime shift which occurred around 5500 years before the present day (BP). (b) The moving average skewness: for any given time, skewness is calculated from the previous 10 data points. Squares represent computed skewness values with the connecting line meant to guide the eye.

to establish that this change is statistically significant in order to interpret it as an early warning signal. To do so we perform a simple diagnostic test based on the idea that an AR(1) process defined by $x(t+1) = \beta x(t) + \sigma \eta(t)$ (where $\eta(t)$ is a Gaussian white noise) acts as a null model for measuring changes in skewness. This is reasonable because an AR(1) process follows from a linear analysis around the fixed point and therefore, yields zero (long-time average) skewness. For finite-sized time series, the moving skewness of an AR(1) process can therefore act as a reference to measure changes in skewness near a bifurcation.

We fit the data prior to the regime shift to the AR(1) process to obtain coefficients β and σ to be 0.59 and 1.51 units respectively. We then generated 100 time series each of length comparable to the real data (66 data points) and computed the moving skewness. In a typical simulation we find, unfortunately, that the changes in skewness are comparable to those in the Sahara data set. Hence we are unable to conclude that the changes in skewness observed in the Sahara data set arise from the proximity to a regime shift. These results however do not mean that the indices of regime shifts will always fail, but indicate the limitations involved in applying to an extremely sparse data set such as

this one. A possible reason could be the lack of finer resolution data. As we show in the Appendix S6, with a finer resolution data such as the phosphorus concentration data available from Sandusky Bay (Heidelberg-College 2007) one can calculate changes in skewness more reliably. We further note that we have not considered a variety of statistical data analysis issues such as missing data, effects of seasonality, obtaining confidence intervals and detrending the data. One may also need to consider a dynamic AR(1) model in which parameters β and σ are time-varying. See Discussion section for issues with analysing real data sets.

ORIGIN OF ASYMMETRY

In this section, we explain the origin of the asymmetry and the rise in skewness as the transition is approached based on the ball in a potential landscape picture (Scheffer *et al.* 2001). In general, the ecosystem evolves towards the local minimum of the potential, analogous to a ball rolling towards the bottom of a cup. For an ecosystem with alternative stables states the potential contains multiple minima.

Figure 5 shows how the asymmetry arises in two different routes to regime shift. As one approaches the vicinity of the transition point, two noteworthy changes occur in the qualitative nature of the effective potential. The basin of attraction shrinks and flattens and the asymmetry in the bowl becomes pronounced. Therefore, for a fixed small variance of an additive noise term the measured asymmetry will increase. On the other hand, consider the case in which the system is relatively far from the threshold. For small noise, the system explores a relatively narrow region which is symmetric around the minima. However, as the external fluctuations increase, the asymmetric effects of the effective potential on the dynamics can become measurable.

Next, we argue that the asymmetry in the effective potential leads to asymmetry in the time series distribution of the state variable. Using the analogy of a ball rolling in a landscape with minima, if we include external noise the ball fluctuates in the region around a minimum. The time spent in the vicinity of different minima depends on the curvature of the potential and the strength of the external fluctuations. The system is more likely to explore the flatter regions in the cup than the steeper parts. Thus for an asymmetrically shaped landscape the ball spends more time in the flatter directions resulting in an asymmetry in the probability distribution of the time series. The probability distribution can be calculated exactly by solving the Fokker-Planck equation to obtain $P_s(x) = N \exp(-\frac{2}{\sigma^2} U(x))$, where N is a normalization constant. This formula clearly shows that an asymmetric potential, $U(x)$, leads to an asymmetric stationary time series distribution.

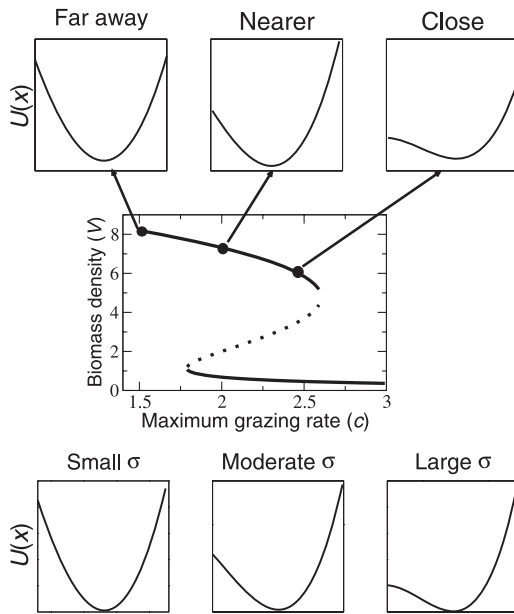


Figure 5 The panels of figures show how the asymmetry in the potential landscape picture evolves in the different pathways to regime shifts. At the centre of the plot is the bifurcation diagram for May's model of vegetation collapse in semi-arid regions. The top row shows the change in landscape potential as one approaches the threshold (for fixed additive external fluctuations σ_{V_1} in eqn T1) by varying the control parameter c . The bottom row of figures shows the alternative route to regime shift in which increase in the additive external fluctuations σ_{V_1} , for fixed c , causes a regime shift to occur. As σ increases, the extent of the region around the minimum explored by the system widens leading to asymmetry in the time series distribution.

A linear analysis around the fixed point yields a symmetric potential and flattening landscape near the threshold. Indicators such as reddened power spectrum, increase in the variance and recovery time rely on this feature of the landscape. They do not include the effects of asymmetry discussed in this paper. However, for the system to explore the asymmetric part of the landscape the external fluctuations should be sufficiently large. We have exploited the fact that ecological systems are often influenced by large environmental variations in conjunction with the contribution of the nonlinear terms to devise a measure that serves as a warning signal for a nearby regime shift. It is to be noted that such asymmetry in time series distribution has been employed as an indicator of nonlinearity in studies of climate and forecasting (Sugihara *et al.* 1999).

In case of two-variable systems an effective potential does not exist in general (it does not in the models described by eqns T2–T6). It is nevertheless possible to devise an intuitive understanding of how the asymmetry arises by considering the vector field that represents the 'forces' that

determine the rate of the change of the dynamical variables (see Appendix S7).

DISCUSSION

Our analysis of simple ecological models shows that changes in the asymmetry, quantified by changes in the skewness of the time series data, can be a generic indicator of an impending regime shift. We have shown that the skewness of the time series data increases as we approach a regime shift in one-variable and more complex ecological models. Although we have illustrated the case of skewness increasing from zero to non-zero values, in general, changing skewness (from non-zero skewness to even larger skewness, etc.) can serve as an indicator of regime shifts. The origin of asymmetry lies in the contribution of nonlinear terms to the dynamics of the system and hence changing skewness may be referred to as a 'nonlinear indicator' of regime shift; in contrast variance, recovery time and reddened power spectra can be derived by a linear analysis, and constitute 'linear indicators' of regime shift.

We discuss the utility of skewness in understanding ecosystem stability in the context of 'resilience' (Holling 1973), defined as the maximum shock an ecosystem can absorb without undergoing a regime shift. As the external conditions affecting ecosystems (such as nutrient inputs and rainfall) gradually change, systems move closer to a threshold of instability. Such ecosystems are prone to regime shifts even when stochastic events of moderate amplitude affect them and hence, are said to have low resilience. Both the linear and nonlinear indicators can be used to identify this reduction of resilience. Many empirical studies indicate frequent shifts between alternative stable states (Blindow *et al.* 1993; Hargeby *et al.* 2007) and theoretical studies indicate that persistent stochastic events of large magnitude can cause such shifts even when the system is far away from threshold (Guttal & Jayaprakash 2007). This route to regime change due to increased amplitude of the external noise is often ignored and is not easily detected by the previously proposed set of indicators (see Appendix S8). We have shown that rise in skewness can be an indicator for both routes to regime shifts making this a potentially more versatile indicator.

We present scenarios in which skewness fails as an early warning signal of a regime shift. If the regime shift occurs too rapidly then skewness fails to provide an early warning just as other indicators fail. In this case the observed increase in skewness reflects the regime shift itself rather than being an early indicator. Next we discuss a less obvious example of a model situation in which skewness does not perform well. Consider the two-variable vegetation model with increasing variance of the fluctuations in the rainfall rate. Our results show that in this route to a regime shift,

there is no detectable increase in skewness (see Appendix S9). In general, it is difficult to provide advance warning of regime shifts caused by increasing noise. Our results have shown that even in such cases, though not in all cases as evidenced by the example cited above, skewness can be useful as an early warning signal.

A recurrent issue in ecology is the lack of sufficiently long and finely resolved data sets for many ecosystems. We have explicitly demonstrated this drawback for indicators using data from Sahara climatic shift. One may wonder whether model calculations yielding as long and finely resolved a series as needed are representative of real systems. We emphasize that even in model calculations the system undergoes a regime shift (for the parameter values considered in this study) on finite time scales: thus, only time series of limited length is available even for theoretical calculations. In addition, for all of the model calculations presented in this paper, the skewness has been calculated for a time span less than the mean escape time to an alternative regime. Furthermore, our calculations demonstrate that even when the driving force (nutrient concentration) is changing as a function of time and the data available are made sparse the necessary skewness calculations are feasible and can be useful. A finely resolved and long data set (for example, the total phosphorous concentration data from a tributary to Lake Erie) can yield reliable evaluation of indicators.

An important assumption in our calculations is that the stochastic dynamics of the model systems are a complete representation of the ecological data. Real ecological data are prone to multiple sources of errors including external and observational errors in addition to the uncertainty involved in identifying and modelling the dynamical processes. One possible pitfall is that the observed changes in asymmetry in the time series do not necessarily imply proximity to a regime shift as it may not be due to intrinsic dynamics but due to asymmetry in the exogenous noise, for example. Technically, this means that modelling all the uncertainties and errors by a simple Gaussian white noise is an oversimplification. This problem has to be addressed on a case-by-case basis by various statistical methods: If data are available for the noisy external variable that drives the system (such as nutrient input and rainfall data), we can remove associated trends from the time series of the state variable. It has been shown that one can successfully separate true variance from other sources of noise by using dynamical linear modelling techniques of time series data (Carpenter & Brock 2006) and such a calculation, at least in principle, can be extended to extract true skewness as well. More generally, the problem of detecting regime shifts as well as distinguishing environmental fluctuations from the true dynamics of the system is an issue of immense practical

importance and has also been addressed by other techniques (Ives 1995; Held & Kleinen 2004; Mantua 2004; Rodionov 2004; Hsieh *et al.* 2005; Mayer *et al.* 2006; Rodionov 2006).

CONCLUDING REMARKS AND FUTURE DIRECTIONS

In summary, given the growing evidence for the existence of tipping points in many large-scale ecosystems as well as climatic and complex social systems (Rial *et al.* 2004; Schroder *et al.* 2005; Brock 2006), devising a set of early indicators is clearly valuable. No single indicator is likely to be sufficient due to different limitations and sources of uncertainty thereby making it necessary to have multiple indicators. Our work makes an important contribution by devising a new indicator of an impending transition based on nonlinearity and large external fluctuations influencing ecological systems, establishing its effectiveness and identifying situations in which it can fail. Future research work on the theoretical analysis of skewness under non-stationary conditions, the statistical issues of estimation and errors and developing simple methods to extract true skewness from an error-prone data are needed which make this indicator further useful for practical applications. Other indices of nonlinearities such as S-maps and anisotropic variances in the time-1 return map (Sugihara *et al.* 1999) can also be explored as measures of changing asymmetry. Another area for future investigations is the study of early warning signals in spatially explicit models of regime shift and elucidating the relative merits of different indicators.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

- Appendix S1** Description of models.
- Appendix S2** Derivation of effective potential.
- Appendix S3** Mean first passage time calculations.
- Appendix S4** Results for the two-variable vegetation model.
- Appendix S5** Results for the parameterized lake model.
- Appendix S6** Analysis of real data sets.

Appendix S7 Asymmetric arguments for multivariable models.

Appendix S8 Relative merits of indicators.

Appendix S9 Analysis of failure of skewness.

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