Regime shifts in ecological systems can occur with no warning

Abstract
Predicting regime shifts – drastic changes in dynamic behaviour – is a key challenge in ecology and other fields. Here we show that the class of ecological systems that will exhibit leading indicators of regime shifts is limited, and that there is a set of ecological models and, therefore, also likely to be a class of natural systems for which there will be no forewarning of a regime change. We first describe how nonlinearities in combination with environmental variability lead to model descriptions that will not have smooth potentials, concluding that many ecological systems are described by systems without smooth potentials and thus will not show typical leading indicators of regime shifts. We then illustrate the impact of these general arguments by numerically examining the dynamics of several model ecological systems under slowly changing conditions. Our results offer a cautionary note about the generality of forecasting sudden changes in ecosystems.

Keywords
Chaos, dynamics, potential, predator–prey, regime shifts, Ricker model.

INTRODUCTION
A key problem in ecology and population biology is both to understand and to predict the sudden shifts that occur in a variety of ecological systems (Scheffer et al. 2001; Conners et al. 2002; Bond et al. 2003; Foley et al. 2003; Scheffer & Carpenter 2003; Scheffer & van Nes 2004; van Nes & Scheffer 2005; Brock & Carpenter 2006; Carpenter & Brock 2006; Guttal & Jayaprakash 2007, 2008; Carpenter et al. 2008; Biggs et al. 2009; Contamin & Ellison 2009; Chisholm & Filotas 2009; Takimoto 2009). Current research has focused on the possibility of determining leading indicators that would precede these regime shifts in both ecological and other more general settings (Scheffer et al. 2009). There is a wide variety of natural systems that can exhibit sudden changes in their state (Folke et al. 2004), with dramatic shifts possible in both the levels of different variables, such as vegetation, or shifts in the kinds of observed dynamics. Often the sudden changes lead from a more desirable ecosystem state to a less desirable one, such as eutrophication in lakes (Carpenter 2005; Amemiya et al. 2007) or desertification (Guttal & Jayaprakash 2007). In most cases, it would be beneficial to predict when a change is going to occur before it does so, in order to allow for preventative management solutions or for ameliorative steps to lessen impacts.

Studies (Brock & Carpenter 2006; Carpenter & Brock 2006; Carpenter et al. 2008) that have tried to determine likely leading indicators of regime shifts have typically begun with a description of an ecosystem using a dynamic model that includes both slowly changing underlying conditions (a slowly changing parameter) and some form of stochasticity. It has been argued that there is an increase in variance (Carpenter & Brock 2006) or skew (Guttal & Jayaprakash 2008, 2009) or slowing down in dynamics (Chisholm & Filotas 2009) prior to a regime shift. The change in variance would be an increase in the variance around the mean population size or some other measure, a change in skew would be a change in the third statistical moment, and a slowing in dynamics would be reflected by a shift in the power spectrum toward lower frequencies. In some instances the presence of leading indicators has been supported by the behaviour of entire distributions of solutions. We suggest that real systems only present one case history for study, so any successful leading indicator that would be used in practice must be able to accurately predict a regime shift from the results using only one initial condition in a single model simulation.
We take a different approach here and argue that for classes of ecological systems which exhibit several important features, including complex dynamics and multiple possible outcomes, the search for leading indicators of regime shifts will generally fail. Our argument first begins with the underlying mathematical reasons for the lack of leading indicators of regime shifts for this class of model systems. Clearly, our general approach does not rule out the presence of leading indicators of regime shifts in those cases where natural systems are well described by models that have smooth potentials, and our work therefore suggests the importance of a better understanding of which models of ecological systems can provide a reasonable description of natural dynamics.

We then confirm and illustrate the predicted lack of leading indicators in a series of examples. In these models, we make two kinds of small changes in the parameters that produce regime shifts: we either change underlying parameters by a small amount or we vary the size of the (stochastic) perturbations. Although we clearly only present simulation results for a selected set of models, we argue that these models are a fairly general representation of many ecological systems. Since essentially any non-spatial model with strong enough overcompensatory density dependence will show the period doubling cascade to chaos and any spatially coupled model will inherit this trait, the spatially explicit, overcompensatory (i.e. period doubling) models we choose here are in fact adequate, or at least plausible, characterizations of a large set of real ecological settings. In none of the cases we simulate are the proposed leading indicators of regime shifts found. Obviously preceding any regime shift there has to be some form of change in dynamics, but here these do not appear to be those that have been used to predict a regime shift.

**GENERAL ARGUMENT**

Suggestions that there are leading indicators of regime shifts have been largely based on the assumed properties of a potential (Graham & Tel 1984), which is essentially the mathematical abstraction of the physical notion of potential energy and acts as a guide for the type of expected dynamics. It is typically represented by ‘ball and landscape’ diagrams such as found in Hastings (1997, p. 123). If the potential exists, depends smoothly on the underlying state of the ecosystem, and changes smoothly as underlying conditions change, then the prior arguments for the existence of leading indicators of regime shifts (summarized in Scheffer et al. 2009) are valid and in fact have been confirmed empirically. Simple ecological models based on Lotka-Volterra equations can satisfy the conditions for the existence of a smooth potential, and in these cases leading indicators are found.

However, models for ecological systems can easily exhibit complex dynamics, and systems like this do not, in general, have smooth potentials (Graham & Tel 1984, 1986; Graham et al. 1991). In many cases the description of a system undergoing a regime shift in the terminology used by ecologists is the one which undergoes a crisis (Grebogi et al. 1983), which is defined to be a sudden change in (long-term) system behaviour as a parameter is varied. For most types of crises to occur, a system must be capable of producing complex dynamics and thus will not have a smooth potential. For example, if a chaotic attractor exists, then the potential has a non-smooth fractal structure (down to the level of the noise) similar to the fractal structure of the attractor (Graham et al. 1991). These are precisely the types of systems for which the presence of leading indicators have not been studied, as indicated in (Scheffer et al. 2009).

The models that display chaotic or complex dynamics are only a subset of the systems for which the potential will not be smooth. If multiple attractors of any type are present, which is exactly the situation often modelled when looking to understand regime shifts, then the potential is likely to be non-smooth precisely in the transition area between two attractors. The physical meaning of the points where the potential has discontinuous derivatives is that the stochastic effects, which must be included in any realistic ecosystem model, causes there to be several most probable paths the system may take out of the bottom of any local potential well. The consequence of only piecewise smooth potentials for a system is that we would not in general expect that there would be obvious precursors to a regime shift (or crisis) as parameters are varied.

The reason for the discrepancy between our results and those that have been previously reported is subtle. If one writes down a given model, derives a potential, concludes it is smooth, and then adds noise during simulation, then this invariably points to the probable existence of leading indicators. Whereas, if one writes down a model that includes a stochastic term, and then derives the (non-equilibrium) potential using the methodology as presented in (Graham & Tel 1984), then one will see that this potential is in fact generically non-smooth and that the proposed leading indicators will generally no longer apply.

**SPECIFIC MODELS AND METHODS**

We numerically simulate several models that are likely to lack a smooth potential in order to illustrate the characteristics of systems prior to, or during, regime shifts. Our general argument shows there are broad classes of ecological systems that we would expect to lack a smooth potential and therefore we would expect to fail to have leading indicators of regime shifts, namely those that have either multiple attractors or have at least the possibility of chaotic
The power spectrum for a signal is computed by first approximating $f(t)$ as a truncated Fourier series:

$$f(t) = \sum_{k=-N}^{N} c_k e^{2\pi i k t}$$

The size of the Fourier coefficients $c_k$ then gives the amount of power that the signal has at each frequency from $k = 0, \ldots, N$. The theory of leading indicators (Scheffer et al. 2009) has thus far concluded that immediately prior to a shift, the parameter $\zeta_1$ is now randomly distributed in $(-\sigma, \sigma)$. We scale the suitable habitat to be of length one, with all individuals falling outside the suitable habitat dying. The results will be presented below in Fig. 2.

In the first model for the local dynamics, we use a Ricker map, and consider the case where local population dynamics alternates with diffusive movement among eight coupled spatial locations,

$$\tilde{N}(t) = N_i(t) e^r (1 - N_i(t) + \varepsilon)$$

$$N_i(t+1) = \sum_{j=1}^{8} \alpha_{ij} \tilde{N}_j(t)$$  \hspace{1cm} (1)

Here $N_i(t)$ is the population size at location $i$ and time $t$, $\tilde{N}(t)$ is the population size after reproduction, but before dispersal, $\varepsilon_j$ is a uniformly distributed random variable in $(-0.001, 0.001)$, and $a$ is a positive constant. The parameters $\alpha_{ij}$ describe the passive dispersal among the patches and are uniformly distributed in $(0.02, 0.03)$ when $\zeta_1 > 0$, and distributed in $(0.01, 0.02)$ when $\zeta_1 < 0$.

We will present results below for this first model in Fig. 1. The model, as expected, can produce complex dynamics, and in fact chaos. The parameter $a = 2.216$ for Fig. 1c,f, and $a = 2.228$ for and the remaining panels of Fig. 1. This small increase in the value of $a$ increases the dominant Liapunov exponent from $\sim 3 \times 10^{-2}$ to $\sim 3 \times 10^{-1}$ and results in the destruction of a three-part chaotic attracting region, one component of which is clearly visible in the first 200 generations of Fig. 1a,b.

The second model is an extension of the first, with an alternation between local population dynamics given by the Ricker model with movement in continuous space, described by a Gaussian dispersal kernel $f(x,y)$. $N(x,y)$ is now a density function on $x$ for the population size at time $t$, $\varepsilon_j$ is now randomly distributed in $(-\sigma, \sigma)$. We scale the suitable habitat to be of length one, with all individuals falling outside the suitable habitat dying. The results will be presented below in Fig. 2.

The third model is a three species food chain in continuous time with Type II functional responses at a single spatial location (McCann & Yodzis 1994), or at three or six locations coupled by movement. The model is made stochastic by adding a perturbation to the carrying capacity each time the first level consumer passes through a Poincare section. For a perturbation strength $\sigma$ of approximately $\sigma = 0.0045$, the top level predator will always eventually become extinct (see Fig. 3).

As a way to compare with earlier results and demonstrate the lack of leading indicators we compute possible leading indicators for our models. For our first two models, we compute the variance and skew (Figs 1c–f and 3b,d,e), and the power spectrum in Fig. 1g,h by passing sliding windows of varying widths over the time series, computing either the statistical moments or the Fourier representation from the data within that window. The species within the food web model follow nearly cyclic patterns. For this reason, we used simulations in which the top predator survived for a minimum number of cycles in order to compute the leading indicators in Fig. 4, and the data in Fig. 5 was computed using a sliding window of width ten cycles.

SIMULATION RESULTS

The systems we consider here always fail to show leading indicators of a regime shift. Simulations of the eight-patch Ricker system in Fig. 1a,b show a period of nearly laminar motion for 200 generations before the population densities unexpectedly shift to a much more erratic pattern, and there is no accompanying change in either the variance or the skew before the abrupt change (Fig. 1c,d). In fact, the
Figure 1 Populations, both at one location and summed over the entire lattice (eight locations), the computed values of the variance and skew for parameters that give both bursting and non-bursting dynamics, and the power spectrum for the coupled Ricker model. (a) Five simulations showing the single population $N(t)$ for 200 generations before a burst away from the attracting region and for 48 generations thereafter. Every third generation is plotted. (b) The total population across the lattice for the same five simulations as in (a). (c) The variance (upper curve in each case) and skew (lower curve) of $N(t)$ for the first 40 windows of each of the five simulations in (a). Computations were carried out using a sliding window of width 10 generations. (d) As (c), but the variance and skew are shown for the last 50 windows before bursting ensues. In (c, f), For comparison with (c, d) the variance (upper curve, each panel) and skew (lower curves) computed over sliding windows of width 10 generations for each of five simulations for which there is no bursting. In (g, h), the power spectrum for one of the time series in (a). The height of the surface for each $k$ gives the amount of that frequency that is found in the windowed time series (height colour coded by the colour bar). We see that there is no shift in the spectrum to blue frequencies (smaller $k$) as the system approaches regime change. The magnitudes of the Fourier coefficients $c_k$ for small $k$ are approximately the same for the first 40 windows of length 32 generations (left panel) as they are for the last 40 generations before the shift (right panel). If anything, the power corresponding to longer wavelengths (smaller $k$) has decreased over the course of the time series.
magnitudes of the variance and skew, as well as their temporal pattern (due to the model’s underlying near-periodicity), are nearly identical in the generations that immediately precede the shift to the magnitudes and patterning found some 200 generations prior (Fig. 1c,d). No parameters were changed during the course of the simulations shown in Fig. 1a–d, and at future times the densities settle back into the simpler dynamic until another abrupt burst ensues. Further, if the growth rate is reduced by only the smallest fraction (less than 0.4%), then the variance and skew change only imperceptibly, as seen if one compares Fig. 1c,d to Fig. 1e,f, and yet the populations now behave predictably for all time, i.e. the slight reduction in the growth rate causes any time series to forever appear nearly identical to the first 200 generations of Fig. 1a,b. We have also included computations of the power spectrum, both for the initial 40 generations of the time series and for the 40 generations immediately prior to the burst, showing that there is no shift to lower frequencies as the regime shift is approached (Fig. 1e,f). This first example is particularly important because the dynamics represent intermittency, a common behaviour in coupled systems, and yet all the leading indicators fail to warn of the shift. We note that intermittency is a dynamical behaviour that in many ways corresponds to the somewhat irregular behaviour of insect outbreaks in space and time (Økland & Bjørnstad 2006).

Similarly, the values of the variance and skew give no prior indication of imminent shifts in the continuous-space model (Fig. 2). Here, the parameters are chosen to be close to values for which the system has sustained complex dynamics, but the asymptotic behaviour is simple at low perturbation strengths (Fig. 2a). The system is highly effected by the presence of the nearby (in parameter space)

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**Figure 2** Simulations showing regime shifts in the total population for the Hastings–Higgins model. Shifts are marked with vertical blue lines. (a) A regime shift in the presence of small external perturbation (σ = 0.01) occurs, and wildly oscillatory behaviour is replaced by nearly periodic motion. (b) The standard deviation (square root of the variance) plotted in black, green, and skew shown in red, purple for windows of widths 50 and 10, respectively. (c) Multiple regime shifts occur in the presence of large noise (σ = 0.1), as the perturbation strength is strong enough to cause attractor switching. (d) The variance and skew shown in the same format as in (b), but around the first large shift in (c). (e) The variance and skew around the second shift in (c).
complex motion, and mimics those dynamics for long ecological times. The type of oscillations preceding the eventual relaxation to a more predictable pattern produces constant fluctuations of varying magnitudes in the variance and skew (Fig. 2b,d), and so there is little evidence that these measurements can give a true forecast of a shift. We do see that the variance reaches a relative maximum right as the shift occurs; however, larger maxima had been reached previously in the time series when no shift took place. Also, when the perturbations are larger, stochastic effects will push the system back into the regime of complex patterning and large oscillations (Fig. 2c), and the existence or final selection of any asymptotic state depends upon the noise strength. As shown in Fig. 2e, the time frame preceding the transitions from one state to another does not show any leading indicators either, and it is only after the regime change has occurred that one notices any change in the variance or skew.

The data in Figs 4 and 5 is confirmation that leading indicators do not necessarily exist even for the most dramatic class of regime shift. The three-species food chain modelled here is spatially explicit, with one, three or six patches, and the parameters are chosen to satisfy constraints reflecting biological realism (McCann & Yodzis 1994), so that with no environmental fluctuations the top predator exists indefinitely in all patches. As the strength of the perturbations is slowly increased, there is a critical value after which the top predator will always eventually become extinct (Fig. 3). This is a case where the environmental forcing is undergoing an increase in variance, and yet we see in Fig. 4 that there are only generally small, random fluctuations in the values of the populations’ variance and skew before the critical perturbation strength is surpassed, and while occasional, nearly linear trends in the data do exist there is no abrupt increase in leading indicators as the critical perturbation strength is approached or surpassed. There is also no clear trend in the data when we make different choices of the migration rate. The conclusion is that the proposed leading indicators once again fail to predict a regime shift.

**DISCUSSION**

The potential for regime shifts has been well recognized both empirically and in models. However, whether and how an impending shift can be predicted in advance has been the subject of intense recent study. A number of recent papers have proposed different leading indicators (Takimoto 2009), primarily based on careful studies of particular models. Yet, the search for universal indicators of impending regime shifts with no warning...
Figure 4 Variance and skew as a function of perturbation strength for each of the three species in the food web. Each data point represents the average value over five simulations for which the top predator survived for at least 25 annual cycles. Colours and line types correspond to different choices of the number of patches and coupling strengths: a single patch (black, solid); three patches (orange, light green, light blue and grey, solid lines) with coupling taken to be $10^{-4}$, $5 \times 10^{-4}$, $10^{-3}$ and $5 \times 10^{-3}$, respectively and six patches (red, dark green, dark blue and black, dashed lines) with the same respective values of the coupling.

Figure 5 The variance (left panel) and skew (middle) for single simulations with varying dispersal and perturbation strength. Shown are the data for three-patch systems with $\epsilon = 0.001$, $\sigma = 0.005, 0.0075$ (species x: light blue; y: light green; z: orange; solid, dashed, respectively), and $\epsilon = 0.0001$, $\sigma = 0.005, 0.0075$ (species x: dark blue; y: dark green; z: red; solid, dashed, respectively). The data for which the trajectories have left the attractor but for which the top predator has not yet begun a monotonic decrease are shown in black, and the right panel is a phase space representation showing the same portion of the trajectory in black for $\epsilon = 0.0001$, $\sigma = 0.005$. 

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Letter

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shifts has proved difficult. Therefore we have used a different approach, one that utilizes general dynamical systems arguments and starts from the viewpoint that typical ecological models are likely to embody nonlinear complexities that arise from density dependence and strong interspecific interactions. This approach implies that any underlying potential for an ecosystem cannot a priori be assumed to be smooth.

Non-equilibrium potential theory implies that ecological systems which can exhibit complex dynamics or multiple outcomes will typically not have leading indicators of regime shifts. Since ecosystems with complex dynamics are certainly at least some of the ones likely to exhibit regime shifts, drastic changes can appear in nature without warning. Although there have been surveys that have suggested that chaos in particular is uncommon in ecological systems, this work has been based on the failure to find positive Lyapunov exponents (Hastings et al. 1993). However, since many ecological models, such as the food chain model (Hastings & Powell 1991) we simulate here have positive Lyapunov exponents on the order of $10^{-2}$, it will be very difficult to demonstrate positive Lyapunov exponents in natural systems. Thus, we suggest that the classes of natural systems that would in fact fail to show leading indicators is large, but recognize that this is to some extent an open question.

Since it can be difficult to understand what kinds of ecological models will typically satisfy our general conditions, we have also undertaken simulations of specific models drawn from an important and broad class to confirm that they lack leading indicators. Using a range of models that have strong nonlinearities, we demonstrate the absence of leading indicators before regime shifts.

How can our results be explained in the light of work that has shown the presence of leading indicators? Our arguments do not contradict prior evidence (Scheffer et al. 2009) demonstrating that leading indicators are likely to be observed in a particular class of systems, namely those with smooth potentials. Unfortunately, it is not likely to be easy to identify which systems in natural or managed ecosystems are well described by models with smooth potentials. Our work therefore does not unequivocally rule out the appearance of leading indicators of regime shifts in a variety of systems.

In terms of management decisions, we would argue that rather than act on the basis of leading indicators (Biggs et al. 2009), it may often be necessary to act extremely quickly in response to observations of shifts. Our findings also indicate that predicting shifts in many natural systems may require efforts similar to the first exit time approach that has proved successful in other fields, but, most importantly, much further work will be needed to understand which classes of models can best represent natural system dynamics.


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