Abstract

The realization that complex systems such as ecological communities can collapse or shift regimes suddenly and without rapid external forcing poses a serious challenge to our understanding and management of the natural world. The potential to identify early warning signals that would allow researchers and managers to predict such events before they happen has therefore been an invaluable discovery that offers a way forward in spite of such seemingly unpredictable behavior. Research into early warning signals has demonstrated that it is possible to define and detect such early warning signals in advance of a transition in certain contexts. Here we describe the pattern emerging as research continues to explore just how far we can generalize these results. A core of examples emerges that shares three properties: the phenomenon of rapid regime shifts, a pattern of 'critical slowing down' that can be used to detect the approaching shift, and a mechanism of bifurcation driving the sudden change. As research has expanded beyond these core examples, it is becoming clear that not all systems that show regime shifts exhibit critical slowing down, or vice versa. Even when systems exhibit critical slowing down, statistical detection is a challenge. We review the literature that explores these edge cases and highlight the need for (a) new early warning behaviors that can be used in cases where rapid shifts do not exhibit critical slowing down, (b) the development of methods to identify which behavior might be an appropriate signal when encountering a novel system; bearing in mind that a positive indication for some systems is a negative indication in others, and (c) statistical methods that can distinguish between signatures of early warning behaviors and noise.
Key words: early warning signals, regime shifts, bifurcation, critical slowing down

1 Introduction

Many natural systems exhibit regime shifts - rapid changes in the state and conditions of system behavior. Such shifts include lake eutrophication (Carpenter et al. 1999), algal overgrowth of coral systems (Mumby et al. 2007), fishery collapse (Jackson et al. 2001), desertification of grasslands (Kfi et al. 2007), and rapid changes in climate (Dakos et al. 2008, Lenton et al. 2009). Such dramatic shifts have the potential to impact ecosystem health and human wellbeing. Thus, it is important to develop strategies for adaptation, mitigation, and avoidance of such shifts.

The idea that complex systems such as ecosystems could change suddenly and without warning goes back to the 1960s (Lewontin 1969, Holling 1973, May 1977). Such early work revealed that even simple models with the appropriate nonlinearities were capable of unpredictable behavior. The only way to predict the transition was to have the right model – and that meant having already had the chance to observe the transition (even then, this remains a tough problem). One cogent early example (Ludwig et al. 1978) demonstrated how knowledge of the forms and time scales of interactions among insects, birds, and trees could lead to a qualitative model that essentially predicted the possibility of regime shifts.

Management of systems that could potentially undergo shifts requires balancing the costs of adaptation, mitigation, or avoidance against the costs of the shift itself. Avoidance depends on an ability to predict regime shifts in advance, or depending on the time scale of response and response of the system, on the ability to recognize a shift as it is occurring. Adaptation and mitigation might require an ability to predict a shift in advance if the time scale of implementation is long relative to the rate at which damages occur.

An important component of this management challenge is the development of early warning signals (EWS) of impending rapid regime shifts (Scheffer et al. 2009). Since regime shifts occur in a variety of systems, and underlying mechanisms for the shifts are not always known, the development of generic signals applicable to a variety of systems would be particularly valuable. This naturally leads to the questions of when such generic signals would be valuable tools versus the need to develop system-specific approaches in all cases.

Foundational research in EWS identified certain patterns that may forecast a sudden transition in a wide variety of systems (Scheffer et al. 2009). Most extensively researched is the phenomenon of critical slowing down (CSD), which is manifested as a pattern of increasing variance or autocorrelation of a system. Subsequent work has begun to identify a growing library of cases in which these indicators are not present before a transition (Schreiber and Rittenhouse 2004, Schreiber and Rudolf 2008, Hastings and Wysham 2010, Bel et al. 2012), or are observed in the absence of any transition (Kfi et al. 2012). These examples are distinct from the more well-known case of statistical error – such as a signal that is present but too weak to detect due to insufficient available data (see Dakos et al. (2008); Scheffer et al. (2009) and Perretti and Munch (2012)). Instead, such work moves into new territory where different underlying mechanisms have lead to starkly different patterns. Determining which underlying mechanisms are present is a substantial empirical and theoretical challenge. When does critical slowing down correspond to the assumptions made?

Here we review a variety of mechanisms that may lead to rapid (or "catastrophic") regime shifts in ecological systems, as well as mechanisms that generate early warning signals. We focus on CSD and its manifestations as they are the most commonly studied warning signals. We illustrate that not all rapid shifts exhibit CSD, and not all observations of CSD involve rapid shifts. Thus the issue of determining EWS is really two-fold: first, to identify classes of systems where the warning signal is expected and conversely systems that may undergo shifts without such signals, and second, to determine appropriate statistical tools to detect the warning signal. In this paper we review both aspects of the overall question.

Critical slowing down (CSD)	A system's slowing response to perturbations as it's dominant eigenvalue approaches zero, often expressed in greater variance, autocorrelation, and return time. CSD is one possible EWS.
Early warning signals (EWS)	A general term for dynamic patterns in system behavior that precede regime shifts. Though CSD phenomena are among the best studied EWS, some shifts will require alternative signals; Figure 1.

Definitions: In this paper we refer to two closely related but different phenomena

2 Relationships between Critical Slowing Down, Bifurcations, and Regime Shifts

CSD has been studied extensively in theoretical (Wissel 1984, Gandhi et al. 1998, Carpenter and Brock 2006, Hastings and Wysham 2010, Dakos et al. 2011a, Lade and Gross 2012, Boettiger and Hastings 2012a) and empirical contexts (Drake and Griffen 2010, Carpenter 2011a, Veraart et al. 2012, Dai et al. 2012, Wang et al. 2012) as a potential EWS for regime shifts. CSD occurs as a system's dominant eigenvalue approaches zero due to a changing (possibly deteriorating) environment. As the eigenvalue approaches zero, the system's response to small perturbations slows. This change in dynamic properties of a system can be expressed in greater variance, autocorrelation, and return time of observed state variables.

In Figure 1, we illustrate the domains of overlap between three distinct phenomena. The first, *rapid regime shifts*, are abrupt changes in system behavior. The second, *bifurcations*, are qualitative changes in system behavior due to the passing of a threshold in underlying parameters or conditions. Where these two overlap, we sometimes call the phenomenon a "catastrophic bifurcation." Finally, *critical slowing down* is the observed behavior of slow system response to perturbation. The labels in italics describe examples of phenomena that fall into these various domains. Below we describe cases that fall into each of these regions.

2.1 Catastrophic Bifurcations Preceded by CSD (I)

Much of the (most visible) recent research in EWS has focused on the center of the diagram, where all three concepts intersect. The warning signal patterns postulated, such as increasing variance and coefficient of variation, (Carpenter and Brock 2006), increasing autocorrelation (Dakos et al. 2008), increas-

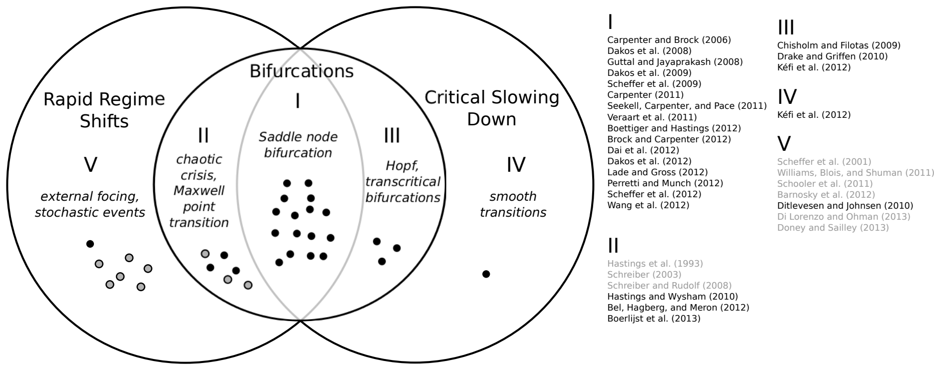

Figure 1: Venn diagram representing the intersecting domains of rapid regime shifts, bifurcations, and critical slowing down. Labels in italic are example phenomena that occur in each domain. Roman numerals and indicate example literature (right) exploring each domain, and also refer to sections below describing those domains. Each dot represents a study in the domain. Studies and dots in grey represent literature not explicitly testing EWS, but which demonstrate phenomena related to EWS. The center domain (I) where all three phenomena intersect, is the most extensively researched domain of the EWS field. Literature outside this charted region does not yet provide the needed EWS, but hints where existing signals based on CSD may be insufficient or misleading.

ing skewness (Guttal and Jayaprakash 2008a) can all be directly derived from the changing eigenvalue in a saddle node (also called fold) bifurcation. Consequently, experimental evaluations of warning signals have largely focused on this situation as well. CSD has frequently been studied in the context of models exhibiting saddle-node bifurcations.

Dai et al. (2012) studied yeast cell growth in a microcosm and demonstrated that an Allee effect created a saddle-node bifurcation in the system. When the cell density was reduced to levels near the bifurcation point, a decrease in recovery time (increase in variance and autocorrelation over time) was observed. Veraart et al. (2012) studied a system of cyanobacteria where models suggest a saddle-node bifurcation driven by light inhibition. They also found increases in autocorrelation and decreased recovery rates as the system approached the bifurcation. These important experiments are among the best demonstrations that saddle-node bifurcation dynamics really occur in natural systems, and can be accompanied by reliable detection of EWS, at least when sufficient data sampling, replicates, and controls are available.

Carpenter et al. (2011) provide a larger-scale example in which a lake ecosystem is manipulated towards a sudden transition through the introduction of a predator, while a neighboring experimental lake provides a control. In this and similar lake systems, bifurcation is thought to be driven in part by trophic interactions where adult fish prey on the competitors of their juveniles (Carpenter and Kitchell 1996, Walters2001; Carpenter et al. 2008) which leads to a saddle-node bifurcation. While the underlying dynamics of a whole lake ecosystem are less tractable than the laboratory controlled chemoststats of microorganisms, the system is understood well enough to anticipate that a sudden transition can be induced under the intended manipulation. Like the laboratory examples, this helps eliminate the options outside the circle "bifurcations," in Figure 1. The observed warning signals then place it in the center of the diagram.

These studies have provided valuable demonstrations of the potential to find early warning signals of sudden transitions. However, this literature has begun to enumerate examples of similar transitions in which no such signal is present.

2.2 Catastrophic Bifurcations *not* Preceded by CSD (II)

Saddle nodes are only one of a variety of bifurcations, which can cause rapid changes in system dynamics. Other bifurcations can cause long-term changes in system dynamics without a gradual pass through a state with zero eigenvalue, and therefore, not exhibit CSD. Many of these examples can in fact show patterns in typical early warning indicator variables such as variance or autocorrelation that are completely opposite to the patterns seen in the saddle-node case. Several of these examples are found outside the EWS literature, indicating a need to expand the range of systems studied for EWS.

These are some of the most problematic cases. They represent disruptive but potentially avoidable events, but would not be detected by using CSD as an EWS. These cases include bifurcations in continuous time (Schreiber and Rudolf 2008) and discrete time (Schreiber 2003), explicitly spatial (Bel et al. 2012) and non-spatial, chaotic (Schreiber 2003, Hastings and Wysham 2010) and non-chaotic (Schreiber and Rudolf 2008, Hastings and Wysham 2010, Bel et al. 2012) examples. Before warning signals can be reliably applied to novel systems, research must provide a way to discern if the dynamics correspond to the better understood warning signals of the saddle-node case or the more complex patterns such as the examples discussed here.

One class of bifurcations in which we would not expect to see CSD prior to regime shift are sometimes known as *crises*. Crises are sudden changes in the dynamics of chaotic attractors that occur in response to small changes in parameters (Grebogi et al. 1983). Chaotic attractors are features of many ecological models (Hastings et al. 1993), and chaotic behavior has been shown in some ecological systems (Costantino et al. 1997).

Hastings and Wysham (2010) examined a continuous model of a stochastic three-species food chain where all species migrate between six patches. When environmental stochasticity (represented as random variation in the carrying capacity) is low, all species coexist in a chaotic but stable attractor. A small increase in environmental stochasticity, though, causes extinction of the top predator and rapid shift to a non-chaotic cycle. Despite an increase in environmental variability, neither the variance nor skew of the populations of any species change as the system approaches this bifurcation.

Another example of a chaotic crisis can be found in a simple discrete-time model where a population is subject to strong density dependence (an Allee effect) and harvested by predators with a Type II (saturating) functional response (Schreiber 2003). This case is illustrated in Figure 2. When prey have high growth rates, the system has chaotic dynamics. Small increases in the predation intensity cause a bifurcation with chaotic but persistent prey populations to prey extinction. As predation intensity increases towards this threshold, the population exhibits *decreasing* variance.

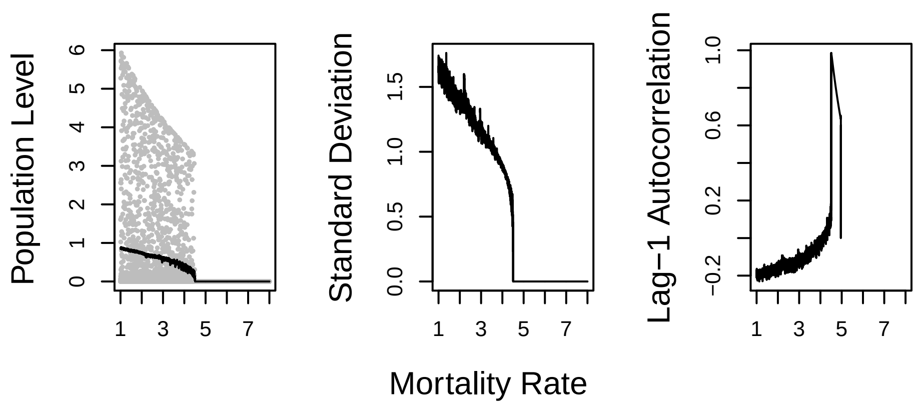

Figure 2: A system where variance decreases prior to a population collapse; adapted from Schreiber (2003). In this model, prey species with high growth rates exhibit chaotic dynamics under predation, but populations collapse when predation increases beyond a threshold value. Left: The population level as a function of predation rate. Mean dynamics shown as black line, realizations with varying initial conditions shown as grey dots; see Schreiber (2003). Middle: Variance of the prey population level. Note that it *decreases* as predation rate approaches the threshold. Right: Lag-1 Autocorrelation in prey population dynamics increases as the threshold is approached

Examples are not restricted to chaotic dynamics. An example is found in Schreiber and Rudolf (2008), in which variance is observed to decrease before a sudden transition that results in the extinction of the population.

Another non-chaotic example is found in some spatially extended systems that exhibit a type of bifurcation not accompanied by CSD. In this class of models, individual locations are subject to saddle node-type regime shifts and influence adjacent locations via short-range facilitation and long-range competition. Such models are used represent transitions between vegetation types in response to changing water availability, and reproduce naturally occurring vegetation patterns (Rietkerk and van de Koppel 2008). In such systems, a regime shift in one location can propagate spatially and transition the whole system from one regime to another. Such a transition occurs if the control parameter (e.g., rainfall), exceeds the *Maxwell point* - the value at which a local disturbance propagates outwards (Bel et al. 2012). The Maxwell point may be far from the level at which an individual location would undergo a saddle-node bifurcation, and thus the system's global dynamics would not exhibit CSD prior to such a transition. This case illustrates the importance of distinguishing between *local* and *global* system dynamics and identifying the appropriate scale of observation.

Finally, Boerlijst et al. (2013) found that indicators of CSD do not appear prior to saddle-node bifurcations when perturbations are not in the direction of a system's dominant eigenvalue, and even then may only appear in one variable of the system. In their example case, increased variance and autocorrelation only occurred when noise was applied to the juvenile population of a model with juveniles, adults, and predators, and it did not appear when identical noise was applied to all three. When CSD indicators did appear, they only did so in the juvenile population variables. This represents another under-explored area - selecting appropriate variables for early-warning detection in multivariate systems. Even where CSD is present, it may not be expressed in all system components.

2.3 Non-Catastrophic Bifurcations Preceded by CSD (III)

Not all regime shifts are rapid. Some systems undergo bifurcations between qualitatively different, but quantitatively similar regimes. These transitions may be reversible. In a management setting, such qualitative changes may insignificant, so warning signals that detect such transitions may be effective "false positives."

CSD precedes several types of these non-catastrophic bifurcations. In the subcritical form of a Hopf bifurcation, a system transitions from a stable equilibrium to a stable cycle. As a control parameter approaches the critical threshold, the system's dominant eigenvalue approaches zero and thus exhibits CSD (Chisholm and Filotas 2009, Kéfi et al. 2012). However, the mean value of the equilibrium does not change dramatically, and the transition from stable equilibrium to cycles is gradual as the cycle sizes grow from zero at the threshold value. To appreciate how this bifurcation is gradual rather than catastrophic, note that in the presence of stochasticity, the system behavior observed on either side of the threshold may be indistinguishable: on one side stochasticity bounces the system around a stable node, while on the other it bounces the system around a very small limit cycle in the same region of state space. Contrast this to a critical transition in which any stochastic fluctuation across the threshold could lead to a qualitatively different state.

The system's eigenvalue also passes through zero in the case of the transcritical bifurcation. The transcritical is a degenerate case of the saddle-node, and occurs in many of the same systems. However, when a system passes through a transcritical bifurcation, the stable equilibrium transitions smoothly from positive to zero, or the reverse. In population systems, this corresponds to a transition from an equilibrium of a very small population size to extinction

- an important but non-catastrophic, and probably directly observable, event. CSD is observed prior to the transcritical bifurcations (Chisholm and Filotas 2009, Kfi et al. 2012).

An experimental example of a transcritical bifurcation is found in Drake and Griffen (2010), where a population of *Daphnia* was forced through a transcritical bifurcation by reducing food supplies and driving population growth rates below zero. Indicators of CSD (variation, skewness, autocorrelation, and spatial correlation) increased prior to collapse of the population.

2.4 CSD in the absence of bifurcations or regime shifts. (IV)

Critical slowing down may appear in systems without any bifurcations. Kfi et al. (2012) showed that smooth transitions that modify a system's potential and decrease the value of its dominant eigenvalue would result in longer return times and greater variance and autocorrelation in system behavior (See Figure 3). When the transition between states is smooth, these measures will exhibit a smooth increase to a maximum and then a decrease, unlike the sharp peaks found in systems with bifurcations. Nonetheless, both exhibit increasing measures of CSD that may be indistinguishable.

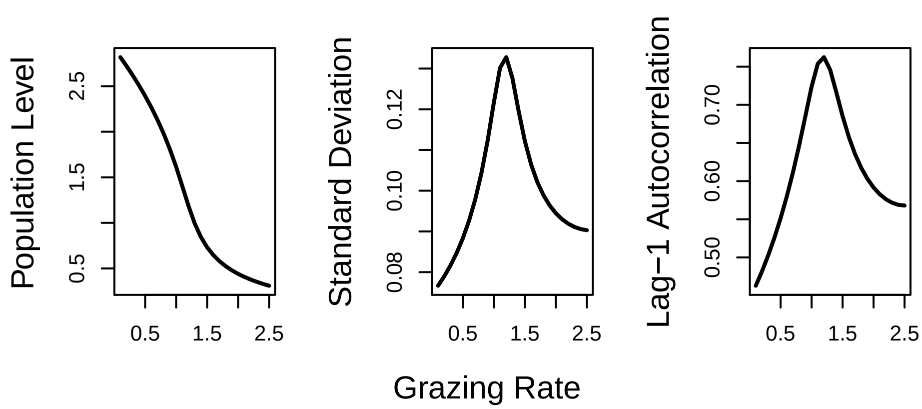

Figure 3: A system where critical slowing down is observed without a critical threshold, from Kfi et al. (2012). In this model, prey have logistic growth and are subject to predation with a Type III functional response, but there is no bifurcation. Instead, average prey population exhibits a smooth response to increased predation (grazing). Left: The population level as a function of predation rate. Middle: Variance of the prey population level. Right: Lag-1 Autocorrelation in prey population dynamics as grazing rate increases. Note that both indicators increase despite the lack of a bifurcation.

2.5 Catastrophic Regime Shifts without Bifurcations or CSD (V)

Some rapid regime shifts are not due to bifurcations at all. A large external forcing (as illustrated in Figure 4) may change the behavior of a system without any warning. This mechanism is commonly recognized, (Scheffer et al. 2001, 2009, Barnosky et al. 2012, Scheffer et al. 2012), but others are possible. An internal stochastic event may switch a system between dynamic regimes, or a change in system behavior may be the manifestation of a long-term transient. In none of these cases would CSD be expected to precede such changes. Nonetheless, it may be difficult to distinguish such cases from bifurcations.

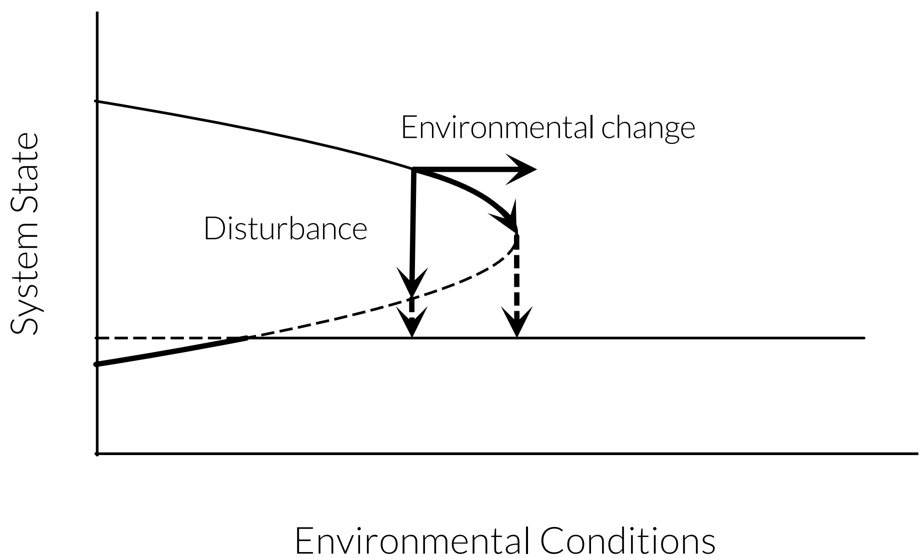

Figure 4: Difference between different types of perturbations. On the horizontal axis is the bifurcation parameter, representing the state of the environment (e.g. annual mean temperature) whose slow change could lead to a sudden shift. A direct disturbance to the system state (e.g. population size, vertical axis) could also cause a transition if it is large enough to cross the stability threshold (dashed line). Such a perturbation can come from exogenous factors such as anthropogenic pressures or occur by chance from intrinsic stochasticity. These distinct mechanisms of disturbance and environmental change are coupled – as the environment deteriorates, moving the system right on the diagram, the probability that a disturbance crosses the threshold increases. From Bel et al. (2012).

Large, rapid changes in external conditions will result in rapid changes in ecological system dynamics. For instance, rapid changes in North American vegetation at the start of the Blling-Allerd and end of the Younger Dryas period are thought to be responses to similarly large, rapid changes in climate (Williams et al. 2011). Doney and Sailley (2013) interpret a recent analysis by Di Lorenzo and Ohman (2013) as demonstrating that what were previously thought of as regime shifts in krill dynamics in the Pacific ocean (Hare and Mantua 2000) could actually be explained by a close coupling to the external forcing of El Nino environmental dynamics through the Pacific Decadal Oscillation (PDO). Schooler et al. (2011) found that lakes with the invasive plant *Salvaniai molesta* andherbivorous weevils alternated between low- and high-*Salvnia* states driven by disturbances from regular external flooding events. These examples highlight cases that involve critical transitions between regimes under circumstances that do not permit the discovery of early warning signals, as CSD is not anticipated under these mechanisms.

Internally-driven stochastic perturbations may shift systems from one state to another even if underlying environmental conditions remain the same. In such conditions EWS would not be expected. Hastings and Wysham (2010) showed that in a model where one species with stochastic Ricker dynamics disperses among eight patches, model behavior can switch stochastically between wildly oscillatory behavior and regularly cycling regimes even while parameters (including stochastic variability) remain the same. Ditlevsen and Johnsen (2010) examined 25 abrupt climate changes that occurred during the last glacial period (Dansgaard-Oeschger events) and found no evidence for CSD in high-resolution climate data from ice cores, and concluded that the events were driven by endogenous climate stochasticity rather than regime shifts (though see Cimatoribus et al. 2013 for an alternative conclusion).

Some events that appear to be regime shifts may actually be transients in some systems. Sudden changes in dynamics can occur in simple ecological models with strong density dependence that take long times to reach equilibrium. Hastings (1998) showed such dynamics in model of dispersal of inter- or subtidal organisms whose larvae disperse along a coastline. Over the thousands of years it takes the model to reach equilibrium, it may alternate between temporary regimes of regular cycles and chaos that switch in only a few years. While on long time scales these are technically not regime shifts, such changes would effectively appear to be regime shifts on shorter ones. We would not expect such regime shifts to be preceded with CSD.

Of course, stochastically-driven regime shifts may occur in systems where bifurcations are also possible, and it may be difficult to distinguish between the two. Renne et al. (2013), for example suggest that ecosystems were under near-critical stress due to climate changes just prior to the Chicxulub meteor impact, which resulted in mass extinction. In such a case, EWS may precede the regime shift even if it is ultimately triggered by a stochastic event.

3 Statistical problems in detecting early warning signals

The above cases show that behavior providing EWS before regime shifts may only be present in certain types of ecological systems (e.g. see the conditions outlined in Scheffer et al. 2009). An additional important consideration is whether these behaviors will be *detectable*. To be usable as EWS, system behavior must be detectable well enough in advance of a regime shift to serve in decision-making, and be reliably distinguishable from other patterns.

Ecological data is often sparse, noisy, autocorrelated and subject to confounding driving variables, in contrast to much of the experimental or simulated data used to test EWS. Under common levels of noise found in field data, CSD-based EWS often fail (Perretti and Munch 2012).

A wide variety of statistical summary indicators have been examined as potential detectors of CSD. The most common are variance and autocorrelation. Others include skewness [Guttal2008a] and conditional heteroscedasticity (Seekell et al. 2011). These statistics are typically calculated on sliding windows of time-series data and tested formally or informally for trends. The relative power of these tests varies considerably with context; no indicator has consistently outperformed others (Dakos et al. 2011b, 2012, Lindegren et al. 2012, Perretti and Munch 2012). Also, measuring these indicators requires making sometimes arbitrary calculations. For instance, the power of lag-1 autocorrelation to detect a regime shift may be modified by changing methods of data aggregation, de-trending, changing sliding window length, filtering signal bandwidth (Lenton et al. 2012). These choices may be optimized when enough calibration data is available, as Lenton et al. (2012) were able to do with several sets of paleoclimate data. However, such calibration may not be possible with many ecological datasets. Multiple-method (Lindegren et al. 2012) and composite indices (Drake and Griffen 2010) have been proposed, but their power relative to other indicators is unknown.

Another approach to detecting CSD has been fitting time series data to models. Two approaches have been used for these model-based methods. First, models may be used to calculate summary statistics related to CSD, such as eigenvalues (Lade and Gross 2012) or diffusion terms in jump-diffusion models (Carpenter 2011a, Brock and Carpenter 2012). These statistics are then examined for trends in the same fashion as the summary statistics above. Alternatively, models representing both deteriorating and stable conditions may be fit to the data and in order to determine which is more likely (Dakos et al. 2012,). Boettiger and Hastings (2012a) found that likelihood ratio tests were more powerful than trend-based summary statistic tests across several real and simulated ecological data sets. This approach is also more robust than summary-statistic methods to spurious correlations that arise when collapses are driven by purely stochastic events (Boettiger and Hastings 2012a).

Care is required in the criteria used to judge the power of warning signal methods. The trade-off between false negatives and false positives is a matter of not just statistical but economic efficiency. For instance, a large number of false positives may be acceptable if they reduce the probability of a false warning that would result in an otherwise avoidable catastrophic regime shift, and the costs of failing to detect such a shift exceed that of the false positives. Boettiger and Hastings (2012a) suggest the use of receiver-operating characteristic (ROC) curves to describe the performance of various EWS. ROC curves (Figure 5) represent the false positive rate at any true positive rate. The area under the curve (AUC) is a useful metric of overall performance. AUC will be one if the signal is perfect and 0.5 if the signal performs no better than random. The complete shape of the curve provides more information on the possible trade-offs under different sensitivities. This information, combined with a decision-theoretic framework, has the potential to illuminate the cases in which EWS can be useful.

4 Discussion

Recognizing the potential for early warning signals of critical transitions represents a substantial leap forward in addressing one of the most challenging questions in ecology and ecosystem management today. In the decades prior, the prospect that ecosystems could make sudden transitions into an undesirable state due to gradual, slow changes in their environment hung like a specter over both our understanding and management of natural systems. Research that points to the possibility of detecting these transitions holds the promise of meeting this challenge and has attracted justifiably widespread attention among both theoretical and empirical communities. Nonetheless, our understanding of early warning signals is still in its infancy. Thus far, our best understanding and empirical experience lies in transitions that are driven by saddle-node bifurcations.

While saddle-node bifurcations may be common, they represent only part of the potential mechanisms for rapid regime shift. Occupying the center of our diagram, Figure 1, such transitions represent our best-understood cases. Researchers have relied on existing expertise and prior research to identify empirical systems most likely to experience critical transitions through the saddle-node-like mechanism (e.g. Carpenter 2011a, Dai et al. 2012), and have achieved a close match to theoretical predictions of early warning signals. While these examples provide a much needed proof-of-principle that these signals can be detected in the real world, it is too early to apply the same methods to novel systems where the saddle-node is only one of many possible mechanisms. We are not yet able to determine if a natural system is likely to have a saddle-node bifurcation without detailed study, despite the popularity of saddle-node models.

Thus, establishing the saddle node mechanism is a necessary condition of using CSD as a warning signal. This can be done via manipulation in simple experimental systems (Veraart et al. 2012, Dai et al. 2012), but this is impractical in most natural systems. Another approach is to assume the saddle-node mech-

Figure 5: Receiver-operating characteristic (ROC) curves illustrate the trade-off between false positive and true positive detection rates of an EWS. Perfect warning signals (solid curve) would identify all thresholds while generating no false positives, while very poor signals would have no ability to distinguish false from true signals (dotted line). In reality, warning signals' have a trade-off between the two which is described by a curve (dotted line) or summarized by the area under the ROC curve

anism applies to a limited set of systems that have well-studied examples, such as lakes undergoing eutrophication (Scheffer et al. 2001), lakes with 'trophic-triangle' cascade mechanisms (Carpenter and Kitchell 1996, Walters2001; Carpenter et al. 2008), forest/savannah transitions (Staver et al. 2011, Hirota et al. 2011), and rangeland transitions (Walker1993; Anderies et al. 2002). Fitting simplified saddle-node models to past regime shifts (Boettiger and Hastings 2012a) in less well-understood systems may provide evidence for the mechanism. However, care must be taken to specify sufficient alternative models.

CSD alone cannot be used as evidence of regime shifts. In some cases, it will be present when no transition is approaching. In other cases, regime shifts occur without CSD. Though false alarms and missed events can occur in any statistical procedure, the cases discussed here demonstrate that these errors will also arise when the underlying dynamics do not correspond to our assumptions. These situations fall in the uncharted area beyond the center of Figure 1, where research has just begun to illuminate their existence and properties. A better theoretical and empirical understanding of these cases will allow us to construct novel warning signals, that may be opposite the patterns observed in the familiar saddle-node bifurcations. Before early warning signals can be applied in novel systems, additional information is needed in order to determine the best signal to use.

One area that requires further exploration is the effect of different forms of stochasticity on the existence of EWS and signal detectability. Many processes contribute to stochastic behavior in ecological systems, and different forms of stochasticity have different effects on system behavior far beyond greater variance (Melbourne and Hastings 2008). Hastings and Wysham (2010) argued that most examples of detectable CSD indicators were found in models with additive stochasticity and smooth potentials. Boerlijst et al. (2013), however, found that stochasticity had the same effects whether it was additive or included in the population growth rate. Instead, they found the *direction* of stochastic perturbations relative to the system's eigenvalue determined whether CSD indicators were detectable. The form of stochasticity may be important in the detectability of CSD indicators even where CSD is present, because stochastic perturbations are needed to explore system state-space, while at the same time can reduce the statistical power. More work such as Perretti and Munch (2012), which examined the role of noise color in detecting CSD, will be useful.

Another area that has is understanding how the relationship between the scale of observation and the scale of ecological processes affect the efficacy of EWS. As shown by the Maxwell Point example in Bel et al. (2012), EWS which detect local bifurcations may not detect global bifurcations in system behavior. The scale of observation likely also will affect the statistical power of EWS. Similarly, as illustrated in Boerlijst et al. (2013), the choice of variables to observe in multivariate systems is important, but little is known about how to select the appropriate variable for detecting EWS.

The future of early warning signals lies in the uncharted territory. For certain classes of transitions, such as stochastically-driven regime shifts, prediction may not be possible. In such cases, managing for resilience may be the only option.

Likewise, regime shifts driven by external perturbation or strong forcing are not predictable *if* the scope of management does not include the external causes. Proper scoping of the management problem can avoid this situation (Fischer et al. 2009, Alliance 2010, Polasky et al. 2011). More research is needed in methods of distinguishing such cases from those in which early detection may be possible.

For other classes of transitions, prediction may be possible but other EWS must be explored. Flickering (Brock and Carpenter 2010, Wang et al. 2012), or rapid transitions between states prior to a more permanent transition, is one signal that may apply across many types of systems. It manifests in bimodality and high variance in times series. Spatial pattern development may be a warning signal in systems with short-distance positive feedbacks but long-distance negative feedbacks, such as grassland-desert transitions (Rietkerk et al. 2004). Other spatial signals may apply where systems include both saddle nodes and positive feedbacks across space (Litzow et al. 2008, Guttal and Jayaprakash 2008a, Dakos et al. 2009, Bailey 2010, Dakos et al. 2011b, Bel et al. 2012). A critical task for EWS research is to map these signals to their domains of applicability, and create methods to establish if ecosystems fall into these domains.

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