

Early warning signals: The charted and uncharted territories

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Abstract

The realization that complex systems 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 definitely 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. We review the literature that explores these edge cases and highlight the need for both (a) new early warning indicators that can be used in cases where rapid shifts do not exhibit critical slowing down, and (b) the development of methods to identify which indicator might be appropriate when encountering a novel system; bearing in mind that a positive indication for some systems is a negative indication in others.

Introduction

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

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The idea that complex systems such as ecosystems could change suddenly and without warning goes back to the 1970s (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, Jones, and Holling 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 (Hastings and Wysham 2010; Schreiber and Rudolf 2008; Bel, Hagberg, and Meron 2012; Schreiber and Rittenhouse 2004), or are observed in the absence of any transition (Kéfi 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 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, identify classes of systems where the warning signal is expected and conversely systems that may undergo shifts without such signals, and then second to determine appropriate statistical tools to detect the warning signal. In this paper we review both aspects of the overall question.

Relationships between Critical Slowing Down, Bifurcations, and Regime Shifts

CSD has been studied extensively in theoretical (Wissel 1984; Gandhi, Levin, and Orszag 1998; Carpenter, Bennett, and Peterson 2006; Hastings and Wysham 2010; Lade and Gross 2012; V. Dakos, Kéfi, et al. 2011; C. Boettiger and Hastings 2012) and empirical contexts (Drake and Griffen 2010; J. Carpenter 2011; Veraart et al. 2011; 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.

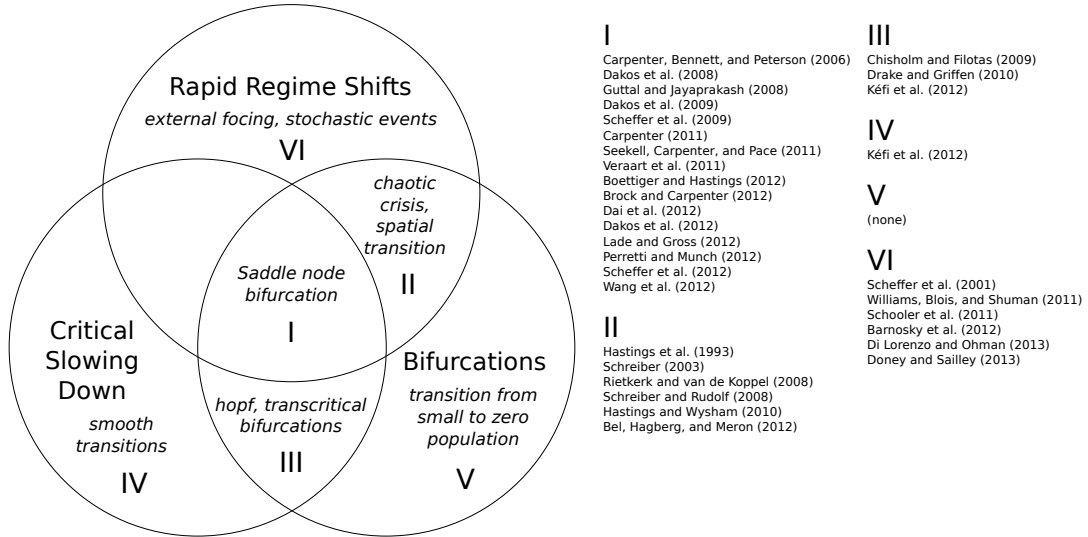


Figure 1: Venn diagram representing the intersecting domains of rapid regime shifts, bifurcations, and critical slowing down. Labels in italic are example phenomena that occur in each domain. Roman numerals indicate example literature (right) exploring each domain, and also refer to sections below describing those domains. The center domain, where all three phenomena intersect, is the most extensively researched domain of the EWS field.

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, Bennett, and Peterson 2006), increasing autocorrelation (Dakos et al. 2008), increasing skewness (Guttal and Jayaprakash 2008) can all be directly derived from the changing eigenvalue in a saddle node 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 a saddle-node bifurcation.

Dai et al. (2012) maps out the entire saddle-node bifurcation diagram empirically before presenting the corresponding decrease in recovery time (increase in variance and autocorrelation over time). Veraart et al. (2011) shows a very similar result in a similar system. 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) provides an even more ambitious 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 example, the underlying dynamics of a whole lake ecosystem are far less tractable than the laboratory controlled chemostats of microorganisms. While it is more difficult to identify the bifurcation process, 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.

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

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.

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 [Schreiber2008] and discrete time [Schreiber2003], explicitly spatial (Bel, Hagberg, and Meron 2012) and non-spatial, chaotic (Schreiber 2003,) and non-chaotic (Hastings and Wysham 2010, ,) examples. Before warning signals can be reliably applied to novel systems, research must provide a way to discern if the dynamics correspond to the more well 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, Ott, and Yorke 1983). Chaotic attractors are features of many ecological models (Hastings et al. 1993), and chaotic behavior has been shown in some ecological systems [Constantino 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). 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.

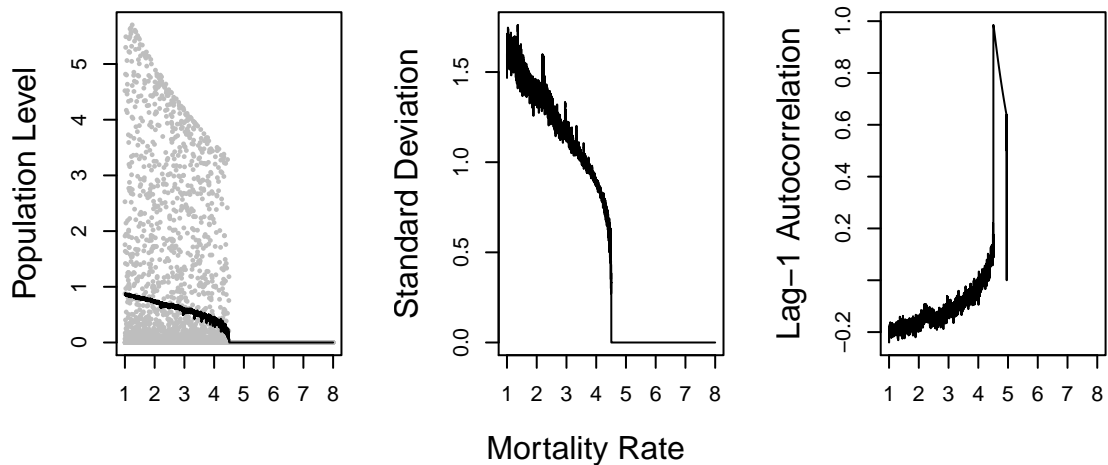


Figure 2: A system where variance decreases prior to a population collapse; adapted from Schreiber (2003). In this model, prey species with high growth rates exhibit chaotic dynamics under predation, but populations collapse when predation increases beyond a threshold value. Left: The population level as a function of predation rate. 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. Some spatially extended systems exhibit a type of bifurcation that is not accompanied by CSD. In one 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 to 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, Hagberg, and Meron 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. Another example is found in Schreiber and Rudolf (2008), in which variance is observed to decrease before a sudden transition that follow a Hopf bifurcation .

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 be 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. This bifurcation occurs in classical predator-prey systems (May 1972) and has been observed in experimental systems (Drake and Griffen 2010; J. Carpenter 2011; Veraart et al. 2011; Dai et al. 2012; Wang et al. 2012). 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. In the presence of stochasticity, system behavior may be observed on either side of the threshold may be indistinguishable.

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; Kéfi et al. 2012).

An experimental example a transcritical bifurcation 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.

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

Critical slowing down may appear in systems without any bifurcations. Kéfi 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.

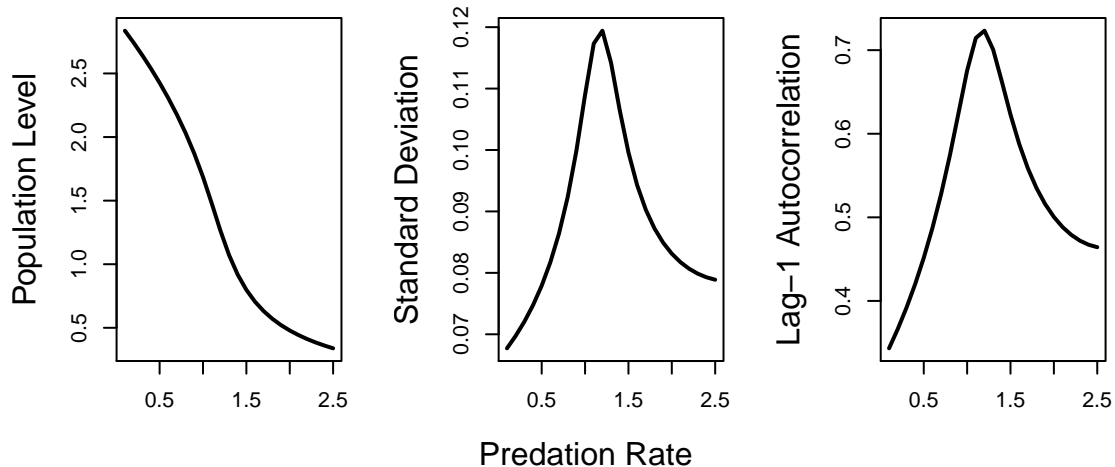


Figure 3: A system where critical slowing down is observed without a critical threshold, from Kéfi et al. (2012). In this model, prey have logistic growth and are subject to predation with a Type III functional response, but there is no bifurcation. Instead, average prey population exhibits a smooth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

Non-Catastrophic Bifurcations without CSD (V)

Some bifurcations involve neither catastrophic shifts nor patterns of critical slowing down. The transition from very small populations to zero is one such transition. System behavior after extinction is clearly different, and exhibits hysteresis. However, the transition, while not smooth, is not due to a saddle-node or similar bifurcation, and CSD would not be expected.

Catastrophic Regime Shifts without Bifurcations or CSD (VI)

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, (Barnosky et al. 2012; Scheffer et al. 2001; Scheffer et al. 2009; 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.

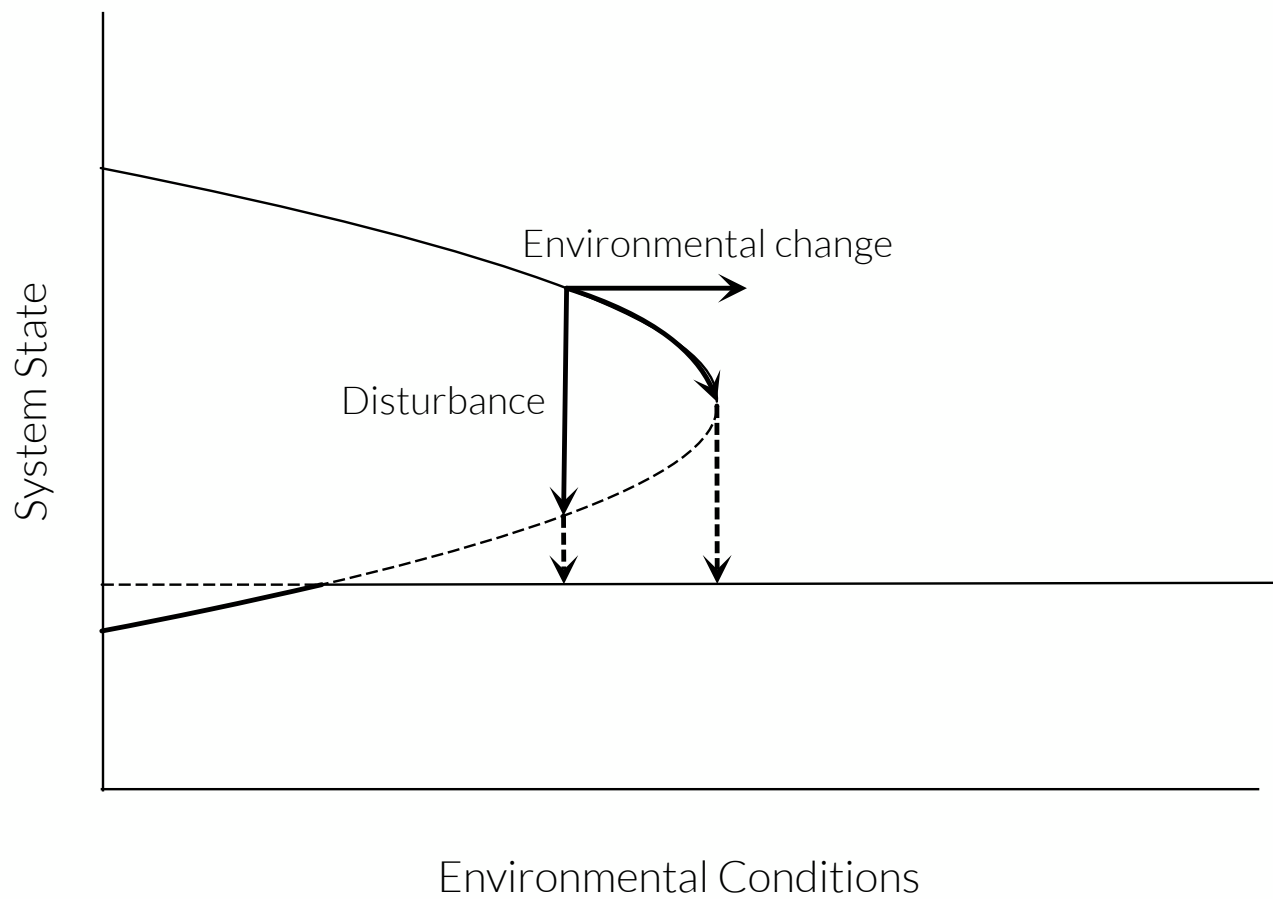


Figure 4: Difference between different types of perturbations. On the horizontal axis is the bifurcation parameter, representing the state of the environment (e.g. annual mean temperature) whose slow change could lead to a sudden shift. A direct disturbance to the system state (e.g. population size, 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, Hagberg, and Meron (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 Bølling-Allerød and end of the Younger Dryas period are thought to be responses to similarly large, rapid changes in climate (Williams, Blois, and Shuman 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 El Nino environmental dynamics through the Pacific Decadal Oscillation (PDO).

Stochastic perturbations may shift systems from one regime to another even if underlying environmental conditions remain the same. 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.

Schooler et al. (2011) found that lakes with the invasive plant *Salvinia molesta* and herbivorous weevils alternated between low- and high-*Salvinia* states driven by external disturbances from regular flooding events. 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.

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 sub-tidal 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.

Statistical problems in detecting early warning signals

The above cases show that behavior providing an early warning signal before regime shifts may only be present in certain types of ecological systems. An additional important consideration is whether these behaviors will be *detectable* in those domains where they are expected. To be usable as an 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, Carpenter, and Pace 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 (Perretti and Munch 2012; Lindegren et al. 2012; V. Dakos, van Nes, et al. 2011; Dakos et al. 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 (Stephen R. Carpenter 2011; 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,). Carl Boettiger and Hastings (2012) 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 (C. Boettiger and Hastings 2012)

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. Carl Boettiger and Hastings (2012) 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 in which cases EWS can be useful.

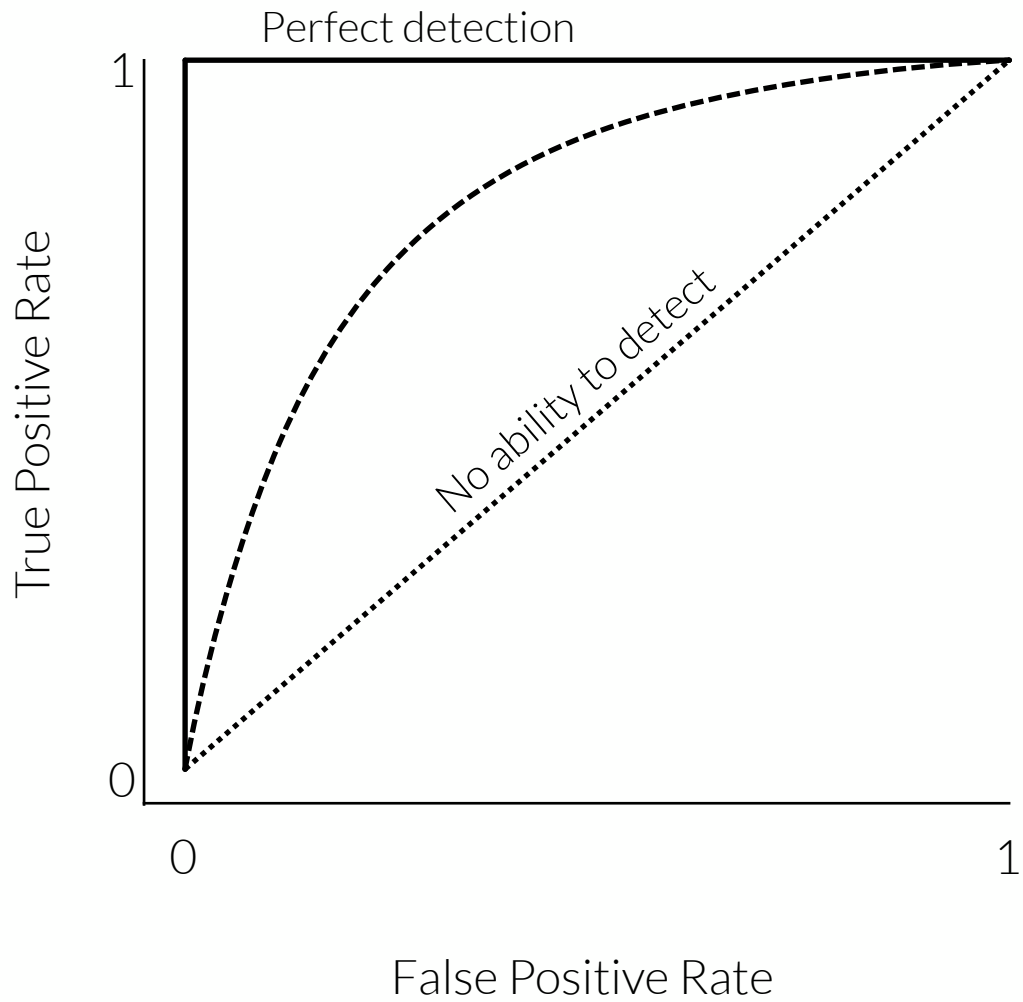


Figure 5: Receiver-operating characteristic (ROC) curves illustrate the trade-off between false positive and true positive detection rates of an EWS. Perfect warning signals (solid curve) would identify all thresholds while generating no false positives, while very poor signals would have no ability 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

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 (also called fold) 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. J. Carpenter 2011; 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.

Thus, establishing the saddle node mechanism a necessary condition of using CSD as a warning signal. This can be done via manipulation in simple experimental systems (Veraart et al. 2011; Dai et al. 2012), but this is impractical in nature. Another approach is to assume the saddle-node mechanism applies to a limited set of systems that have well-studied examples, such as lakes undergoing eutrophication (Scheffer et al. 2001), or forest/savannah transitions may also (Staver, Archibald, and Levin 2011; Hirota et al. 2011; Bel, Hagberg, and Meron 2012). Fitting simplified saddle-node models, following Carl Boettiger and Hastings (2012) to past regime shifts 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 regime shift. 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. 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 best signal to use.

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 (Alliance 2010; Fischer et al. 2009; Polasky et al. 2011).

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 bi-modality 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 (van Nes and Scheffer 2005; Kéfi et al. 2007,). Other spatial signals may apply where systems include both saddle nodes and positive feedbacks across space (Guttal and Jayaprakash 2008; Litzow, Urban, and Laurel 2008; Dakos et al. 2009; Bailey 2010; V. Dakos, van Nes, et al. 2011; Bel, Hagberg, and Meron 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.

Acknowledgments

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References

- Alliance, Resilience. 2010. *Assessing Resilience in Social-Ecological Systems : Workbook for Practitioners. Version 2.0*. <http://www.resalliance.org/3871.php>.
- Bailey, R. M. 2010. "Spatial and temporal signatures of fragility and threshold proximity in modelled semi-arid vegetation." *Proceedings. Biological sciences / The Royal Society* (October) (oct). doi:10.1098/rspb.2010.1750. <http://www.ncbi.nlm.nih.gov/pubmed/20943693>.
- Barnosky, Anthony D., Elizabeth a Hadly, Jordi Bascompte, Eric L. Berlow, James H. Brown, Mikael Fortelius, Wayne M. Getz, et al. 2012. "Approaching a state shift in Earth's biosphere." *Nature* 486 (7401) (jun): 52–58. doi:10.1038/nature11018. <http://dx.doi.org/10.1038/nature11018>.
- Bel, Golan, Aric Hagberg, and Ehud Meron. 2012. "Gradual regime shifts in spatially extended ecosystems." *Theoretical Ecology* 5 (4) (jan): 591–604. doi:10.1007/s12080-011-0149-6. <http://dx.doi.org/10.1007/s12080-011-0149-6>.

- Boettiger, C., and A. Hastings. 2012. "Early warning signals and the prosecutor's fallacy." *Proceedings of the Royal Society B: Biological Sciences* 279 (1748) (oct): 4734–4739. doi:10.1098/rspb.2012.2085. <http://dx.doi.org/10.1098/rspb.2012.2085>.
- Boettiger, Carl, and Alan Hastings. 2012. "Quantifying limits to detection of early warning for critical transitions." *Journal of the Royal Society, Interface / the Royal Society* 9 (75) (oct): 2527–39. doi:10.1098/rsif.2012.0125. <http://dx.doi.org/10.1098/rsif.2012.0125> <http://www.ncbi.nlm.nih.gov/pubmed/22593100>.
- Brock, William A., and Stephen R. Carpenter. 2010. "Interacting Regime Shifts in Ecosystems: Implication for Early Warnings." *Ecological Monographs* 80 (3) (aug): 353–367. doi:10.1890/09-1824.1. <http://www.esajournals.org/doi/abs/10.1890/09-1824.1> <http://www.esajournals.org/doi/abs/10.1890/09-1824>.
- Brock, William a, and Stephen R. Carpenter. 2012. "Early Warnings of Regime Shift When the Ecosystem Structure Is Unknown." Ed. Ricard V. Solé. *PLoS ONE* 7 (9) (sep): 45586. doi:10.1371/journal.pone.0045586. <http://dx.plos.org/10.1371/journal.pone.0045586>.
- Carpenter, J. 2011. "May the Best Analyst Win." *Science* 331 (6018) (feb): 698–699. doi:10.1126/science.331.6018.698. <http://www.sciencemag.org/cgi/doi/10.1126/science.331.6018.698>.
- Carpenter, S. R., and W. a Brock. 2010. "Early warnings of regime shifts in spatial dynamics using the discrete Fourier transform." *Ecosphere* 1 (5) (nov): 10. doi:10.1890/ES10-00016.1. <http://www.esajournals.org/doi/abs/10.1890/ES10-00016.1>.
- Carpenter, Stephen R. 2011. "Early warnings of unknown nonlinear shifts : a nonparametric approach." *Ecology* 92 (12): 2196–2201. <http://www.esajournals.org/doi/pdf/10.1890/11-0716.1>.
- Carpenter, Stephen R., Elena M. Bennett, and Garry D. Peterson. 2006. "Scenarios for ecosystem services: An overview." *Ecology and Society*. [http://apps.isiknowledge.com/full\char"005C\relax{} _record.do?product=WOS\char"005C\relax{}&search\char"005C\relax{} _mode=AdvancedSearch\char"005C\relax{}&qid=1\char"005C\relax{}&SID=U1ADlMa62oB3pn11jce\char"005C\relax{}&page=1\char"005C\relax{}&doc=18](http://apps.isiknowledge.com/full\char).
- Carpenter, Stephen R., J. J. Cole, M. L. Pace, R. Batt, W. a Brock, T. Cline, J. Coloso, et al. 2011. "Early Warnings of Regime Shifts: A Whole-Ecosystem Experiment." *Science* 1079 (April) (apr). doi:10.1126/science.1203672. <http://www.sciencemag.org/cgi/doi/10.1126/science.1203672>.
- Carpenter, Stephen R., D. Ludwig, and W. A. Brock. 1999. "Management of eutrophication for lakes subject to potentially irreversible change." *Ecological Applications* 9 (3): 751–771. [http://www.esajournals.org/doi/full/10.1890/1051-0761\(1999\)009%5B0751:MOEFLS%5D2.0.CO%3B2](http://www.esajournals.org/doi/full/10.1890/1051-0761(1999)009%5B0751:MOEFLS%5D2.0.CO%3B2).
- Chisholm, Ryan a, and Elise Filotas. 2009. "Critical slowing down as an indicator of transitions in two-species models." *Journal of theoretical biology* 257 (1) (mar): 142–9. doi:10.1016/j.jtbi.2008.11.008. <http://www.ncbi.nlm.nih.gov/pubmed/19084025>.

- Dai, L., D. Vorselen, K. S. Korolev, and J. Gore. 2012. “Generic Indicators for Loss of Resilience Before a Tipping Point Leading to Population Collapse.” *Science* 336 (6085) (may): 1175–1177. doi:10.1126/science.1219805. <http://www.sciencemag.org/cgi/doi/10.1126/science.1219805>.
- Dakos, Vasilis, Stephen R. Carpenter, William a Brock, Aaron M. Ellison, Vishwesh Guttal, Anthony R. Ives, Sonia Kéfi, et al. 2012. “Methods for Detecting Early Warnings of Critical Transitions in Time Series Illustrated Using Simulated Ecological Data.” Ed. Bülent Yener. *PLoS ONE* 7 (7) (jul): 41010. doi:10.1371/journal.pone.0041010. <http://dx.plos.org/10.1371/journal.pone.0041010>.
- Dakos, Vasilis, Sonia Kéfi, Max Rietkerk, Egbert H. van Nes, and Marten Scheffer. 2011. “Slowing down in spatially patterned ecosystems at the brink of collapse.” *The American naturalist* 177 (6) (jun): 153. doi:10.1086/659945. <http://www.ncbi.nlm.nih.gov/pubmed/21597246>.
- Dakos, Vasilis, Egbert H. Nes, Raúl Donangelo, Hugo Fort, and Marten Scheffer. 2009. “Spatial correlation as leading indicator of catastrophic shifts.” *Theoretical Ecology* (nov): 163–174. doi:10.1007/s12080-009-0060-6. <http://www.springerlink.com/index/10.1007/s12080-009-0060-6>.
- Dakos, Vasilis, Egbert H. van Nes, Paolo D’Odorico, and Marten Scheffer. 2011. “Robustness of variance and autocorrelation as indicators of critical slowing down.” *Ecology* (oct). doi:10.1890/11-0889.1. <http://www.esajournals.org/doi/abs/10.1890/11-0889.1>.
- Dakos, Vasilis, Marten Scheffer, Egbert H. van Nes, Victor Brovkin, Vladimir Petoukhov, and Hermann Held. 2008. “Slowing down as an early warning signal for abrupt climate change.” *Proceedings of the National Academy of Sciences* 105 (38) (sep): 14308–12. doi:10.1073/pnas.0802430105. <http://www.ncbi.nlm.nih.gov/pubmed/18787119>.
- Di Lorenzo, Emanuele, and Mark D. Ohman. 2013. “A double-integration hypothesis to explain ocean ecosystem response to climate forcing.” *Proceedings of the National Academy of Sciences of the United States of America* (jan). doi:10.1073/pnas.1218022110. <http://www.ncbi.nlm.nih.gov/pubmed/23341628>.
- Ditlevsen, Peter D., and Sigfus J. Johnsen. 2010. “Tipping points: Early warning and wishful thinking.” *Geophysical Research Letters* 37 (19) (oct): 2–5. doi:10.1029/2010GL044486. <http://www.agu.org/pubs/crossref/2010/2010GL044486.shtml>.
- Doney, Scott C., and Sevrine F. Sailley. 2013. “When an ecological regime shift is really just stochastic noise.” *Proceedings of the National Academy of Sciences of the United States of America* 110 (7) (feb): 2438–2439. doi:10.1073/pnas.1222736110. <http://dx.doi.org/10.1073/pnas.1222736110>.
- Drake, John M., and Blaine D. Griffen. 2010. “Early warning signals of extinction in deteriorating environments.” *Nature* 467 (sep): 456–7. doi:10.1038/nature09389. <http://dx.doi.org/10.1038/nature09389>.
- Fischer, Joern, Garry D. Peterson, Toby A. Gardner, Line J. Gordon, Ioan Fazey, Thomas Elmqvist, Adam Felton, Carl Folke, and Stephen Dovers. 2009. “Integrating resilience thinking and optimisation for conservation.”

Trends in ecology & evolution 24 (10): 549–554. doi:10.1016/j.tree.2009.03.020. <http://www.ncbi.nlm.nih.gov/pubmed/19665820>.

Gandhi, A., S. Levin, and S. Orszag. 1998. “‘Critical slowing down’ in time-to-extinction: an example of critical phenomena in ecology.” *Journal of theoretical biology* 192 (3) (jun): 363–76. doi:10.1006/jtbi.1998.0660. <http://dx.doi.org/10.1006/jtbi.1998.0660>.

Grebogi, C., E. Ott, and J. A. Yorke. 1983. “Crises, sudden changes in chaotic attractors, and transient chaos.” *Physica D: Nonlinear Phenomena*. <http://www.sciencedirect.com/science/article/pii/0167278983901264>.

Guttal, Vishwesh, and C. Jayaprakash. 2008. “Spatial variance and spatial skewness: leading indicators of regime shifts in spatial ecological systems.” *Theoretical Ecology* 2 (1) (dec): 3–12. doi:10.1007/s12080-008-0033-1. <http://www.springerlink.com/index/10.1007/s12080-008-0033-1>.

Guttal, Vishwesh, and Ciriya Jayaprakash. 2008. “Changing skewness: an early warning signal of regime shifts in ecosystems.” *Ecology letters* 11 (5) (may): 450–60. doi:10.1111/j.1461-0248.2008.01160.x. <http://www.ncbi.nlm.nih.gov/pubmed/18279354>.

Hare, S. R., and N. J. Mantua. 2000. “Empirical evidence for North Pacific regime shifts in 1977 and 1989.” *Progress in oceanography* 47 (2000): 103–145. <http://www.sciencedirect.com/science/article/pii/S0079661100000331>.

Hastings, Alan. 1998. “Transients in spatial ecological models.” Ed. Jordi Bascompte and Ricard V. Solé. *Modeling spatiotemporal dynamics in ecology*: 189–198. [http://scholar.google.com/scholar?hl=en&char"005C\relax{}&btnG=Search\char"005C\relax{}&q=intitle:Transients+in+spatial+ecological+models\char"005C\relax{}#0](http://scholar.google.com/scholar?hl=en&char).

Hastings, Alan, C. L. Hom, Stephen Ellner, Peter Turchin, and H. C. J. Godfray. 1993. “Chaos in ecology: is mother nature a strange attractor?” *Annual Review of Ecology and Systematics* 24 (1993): 1–33. <http://www.jstor.org/stable/10.2307/2097171>.

Hastings, Alan, and Derin B. Wysham. 2010. “Regime shifts in ecological systems can occur with no warning.” *Ecology letters* 13 (4) (apr): 464–72. doi:10.1111/j.1461-0248.2010.01439.x. <http://www.ncbi.nlm.nih.gov/pubmed/20148928>.

Hirota, Marina, Milena Holmgren, Egbert H. Van Nes, and Marten Scheffer. 2011. “Global resilience of tropical forest and savanna to critical transitions.” *Science (New York, N.Y.)* 334 (6053) (oct): 232–5. doi:10.1126/science.1210657. <http://www.ncbi.nlm.nih.gov/pubmed/21998390>.

Holling, C. S. S. 1973. “Resilience and Stability of Ecological Systems.” *Annual Review of Ecology and Systematics* 4 (1) (nov): 1–23. doi:10.1146/annurev.es.04.110173.000245. <http://arjournals.annualreviews.org/doi/abs/10.1146/annurev>
<http://www.jstor.org/stable/2096802>.

- Jackson, J. B., M. X. Kirby, W. H. Berger, K. a Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, et al. 2001. "Historical overfishing and the recent collapse of coastal ecosystems." *Science (New York, N.Y.)* 293 (5530) (jul): 629–37. doi:10.1126/science.1059199. <http://www.ncbi.nlm.nih.gov/pubmed/11474098>.
- Kéfi, Sonia, Max Rietkerk, and Gabriel G. Katul. 2008. "Vegetation pattern shift as a result of rising atmospheric CO₂ in arid ecosystems." *Theoretical population biology* 74 (4) (dec): 332–44. doi:10.1016/j.tpb.2008.09.004. <http://www.ncbi.nlm.nih.gov/pubmed/18930071>.
- Kéfi, Sonia, Vasilis Dakos, Marten Scheffer, Egbert H. van Nes, and Max Rietkerk. 2012. "Early warning signals also precede non-catastrophic transitions." *Oikos* (June) (sep): 1–8. doi:10.1111/j.1600-0706.2012.20838.x. <http://doi.wiley.com/10.1111/j.1600-0706.2012.20838.x>.
- Kéfi, Sonia, Max Rietkerk, Concepción L. Alados, Yolanda Pueyo, Vasilios P. Papanastasis, Ahmed Elaich, Peter C. de Ruiter, L. Alados, and Peter C. De Ruiter. 2007. "Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems." *Nature* 449 (7159) (sep): 213–7. doi:10.1038/nature06111. <http://www.ncbi.nlm.nih.gov/pubmed/17851524>.
- Lade, Steven J., and Thilo Gross. 2012. "Early Warning Signals for Critical Transitions: A Generalized Modeling Approach." Ed. Mercedes Pascual. *PLoS Computational Biology* 8 (2) (feb): 1002360. doi:10.1371/journal.pcbi.1002360. <http://dx.plos.org/10.1371/journal.pcbi.1002360>.
- Lenton, Timothy M., V. N. Livina, V. Dakos, Egbert H. van Nes, and Marten Scheffer. 2012. "Early warning of climate tipping points from critical slowing down: comparing methods to improve robustness." *Philosophical transactions. Series A, Mathematical, physical, and engineering sciences* 370 (1662) (mar): 1185–204. doi:10.1098/rsta.2011.0304. <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3261433&char=005C\relax{}&tool=pmcentrez&char=005C\relax{}&rendertype=abstract>.
- Lindgren, Martin, Vasilis Dakos, Joachim P. Gröger, Anna G\aa rdmark, Georgs Kornilovs, Saskia a Otto, and Christian Möllmann. 2012. "Early Detection of Ecosystem Regime Shifts: A Multiple Method Evaluation for Management Application." Ed. Simon Thrush. *PLoS ONE* 7 (7) (jul): 38410. doi:10.1371/journal.pone.0038410. <http://dx.plos.org/10.1371/journal.pone.0038410>.
- Litzow, M. A., J. D. Urban, and B. J. Laurel. 2008. "Increased spatial variance accompanies reorganization of two continental shelf ecosystems." *Ecological Applications* 18 (6): 1331–1337. <http://www.esajournals.org/doi/pdf/10.1890/07-0998.1>.
- Ludwig, D., D. D. Jones, and C. S. Holling. 1978. "Qualitative Analysis of Insect Outbreak Systems: The Spruce Budworm and Forest." *The Journal of Animal Ecology* 47 (1) (feb): 315. doi:10.2307/3939. <http://www.jstor.org/stable/3939?origin=crossref>.
- May, R. M. 1972. "Limit cycles in predator-prey communities." *Science (New York, N.Y.)* 177 (4052) (sep): 900–2. doi:10.1126/science.177.4052.900. <http://www.ncbi.nlm.nih.gov/pubmed/17780991>.

- May, Robert M. 1977. "Thresholds and breakpoints in ecosystems with a multiplicity of stable states." *Nature* 269 (5628) (oct): 471–477. doi:10.1038/269471a0. <http://www.nature.com/doifinder/10.1038/269471a0>.
- Mumby, Peter J., Alan Hastings, and Helen J. Edwards. 2007. "Thresholds and the resilience of Caribbean coral reefs." *Nature* 450 (7166) (nov): 98–101. doi:10.1038/nature06252. <http://www.ncbi.nlm.nih.gov/pubmed/17972885>.
- van Nes, Egbert H., and Marten Scheffer. 2005. "Implications of Spatial Heterogeneity for Catastrophic Regime Shifts in Ecosystems." *Ecology* 86 (7) (jul): 1797–1807. doi:10.1890/04-0550. <http://dx.doi.org/10.1890/04-0550>.
- Perretti, Charles T., and Stephan B. Munch. 2012. "Regime shift indicators fail under noise levels commonly observed in ecological systems." *Ecological Applications* 22 (6) (sep): 1772–1779. doi:10.1890/11-0161.1. <http://www.esajournals.org/doi/abs/10.1890/11-0161.1>.
- Polasky, Stephen, Stephen R. Carpenter, Carl Folke, and Bonnie Keeler. 2011. "Decision-making under great uncertainty: environmental management in an era of global change." *Trends in ecology & evolution* 26 (8) (aug): 398–404. doi:10.1016/j.tree.2011.04.007. <http://www.ncbi.nlm.nih.gov/pubmed/21616553>.
- Rietkerk, Max, and Johan van de Koppel. 2008. "Regular pattern formation in real ecosystems." *Trends in ecology & evolution* 23 (3) (mar): 169–75. doi:10.1016/j.tree.2007.10.013. <http://www.ncbi.nlm.nih.gov/pubmed/18255188>.
- Scheffer, Marten, Jordi Bascompte, William A. Brock, Victor Brovkin, Stephen R. Carpenter, Vasilis Dakos, Hermann Held, Egbert H. van Nes, Max Rietkerk, and George Sugihara. 2009. "Early-warning signals for critical transitions." *Nature* 461 (7260): 53–9. <http://www.ncbi.nlm.nih.gov/pubmed/19727193>.
- Scheffer, Marten, Stephen R. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. "Catastrophic shifts in ecosystems." *Nature* 413 (6856) (oct): 591–6. doi:10.1038/35098000. <http://www.ncbi.nlm.nih.gov/pubmed/11595939>.
- Scheffer, Marten, Stephen R. Carpenter, Timothy M. Lenton, Jordi Bascompte, William Brock, Vasilis Dakos, Johan van de Koppel, et al. 2012. "Anticipating Critical Transitions." *Science* 338 (6105) (oct): 344–348. doi:10.1126/science.1225244. <http://www.ncbi.nlm.nih.gov/pubmed/23087241> <http://www.sciencemag.org/cgi/doi/10.1126/science.1225244>.
- Schooler, Shon S., Buck Salau, Mic H. Julien, and Anthony R. Ives. 2011. "Alternative stable states explain unpredictable biological control of *Salvinia molesta* in Kakadu." *Nature* 470 (7332) (feb): 86–89. doi:10.1038/nature09735. <http://www.nature.com/doifinder/10.1038/nature09735>.
- Schreiber, Sebastian J. 2003. "Allee effects, extinctions, and chaotic transients in simple population models." *Theoretical Population Biology* 64 (2) (sep): 201–209. doi:10.1016/S0040-5809(03)00072-8. <http://linkinghub.elsevier.com/retrieve/pii/S0040580903000728>.
- Schreiber, Sebastian J., and Seth Rittenhouse. 2004. "From simple rules to cycling in community assembly." *Oikos* 93 (2) (may): 430–358. doi:10.1111/j.0030-1299.2004.12433.x.

- Schreiber, Sebastian, and Volker H. W. Rudolf. 2008. "Crossing habitat boundaries: coupling dynamics of ecosystems through complex life cycles." *Ecology letters* 11 (6) (jun): 576–87. doi:10.1111/j.1461-0248.2008.01171.x. <http://www.ncbi.nlm.nih.gov/pubmed/18371091>.
- Seekell, David A., Stephen R. Carpenter, and Michael L. Pace. 2011. "Conditional heteroscedasticity as a leading indicator of ecological regime shifts." *The American naturalist* 178 (4) (oct): 442–51. doi:10.1086/661898. <http://www.ncbi.nlm.nih.gov/pubmed/21956023>.
- Staver, A. Carla, Sally Archibald, and Simon Levin. 2011. "Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states." *Ecology* 92 (5) (may): 1063–72. <http://www.ncbi.nlm.nih.gov/pubmed/21661567>.
- Veraart, Annelies J., Elisabeth J. Faassen, Vasilis Dakos, Egbert H. van Nes, Miquel Lüring, and Marten Scheffer. 2011. "Recovery rates reflect distance to a tipping point in a living system." *Nature* (dec): 2–5. doi:10.1038/nature10723. <http://www.nature.com/doifinder/10.1038/nature10723>.
- Wang, Rong, John a Dearing, Peter G. Langdon, Enlou Zhang, Xiangdong Yang, Vasilis Dakos, and Marten Scheffer. 2012. "Flickering gives early warning signals of a critical transition to a eutrophic lake state." *Nature* (nov): 1–4. doi:10.1038/nature11655. <http://www.ncbi.nlm.nih.gov/pubmed/23160492>.
- Williams, John W., Jessica L. Blois, and Bryan N. Shuman. 2011. "Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary." *Journal of Ecology* 99 (3) (may): 664–677. doi:10.1111/j.1365-2745.2011.01810.x. <http://doi.wiley.com/10.1111/j.1365-2745.2011.01810.x>.
- Wissel, C. 1984. "A universal law of the characteristic return time near thresholds." *Oecologia* 65 (1) (dec): 101–107. doi:10.1007/BF00384470. <http://dx.doi.org/10.1007/BF00384470> .