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Resilience indicators: prospects and limitations for early warnings of regime shifts

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In the vicinity of tipping points—or more precisely bifurcation points—ecosystems recover slowly from small perturbations. Such slowness may be interpreted as a sign of low resilience in the sense that the ecosystem could easily be tipped through a critical transition into a contrasting state. Indicators of this phenomenon of 'critical slowing down (CSD)' include a rise in temporal correlation and variance. Such indicators of CSD can provide an early warning signal of a nearby tipping point. Or, they may offer a possibility to rank reefs, lakes or other ecosystems according to their resilience. The fact that CSD may happen across a wide range of complex ecosystems close to tipping points implies a powerful generality. However, indicators of CSD are not manifested in all cases where regime shifts occur. This is because not all regime shifts are associated with tipping points. Here, we review the exploding literature about this issue to provide guidance on what to expect and what not to expect when it comes to the CSD-based early warning signals for critical transitions.

1. Introduction

Real world systems occasionally undergo substantial changes triggered by just small disturbances [1]. The onset of an epidemic, the spread of a forest fire or the sudden eutrophication of a lake are examples of such unexpected behaviour. In the marine world similar cases abound. Early work on sessile fouling communities [2] and on simple food webs of rocky intertidal areas [3] demonstrated that disturbances might lead to alternative endpoint communities. Subsequent studies suggested a similar potential of shifting between alternative states (or 'regimes') also in coral reefs [4,5], kelp forests [6,7], macroalgae beds [8], fish populations [9–11], and even whole pelagic and benthic communities [12–16].

Despite the rich advances in the understanding of the mechanisms behind marine regime shifts [17–19], our ability to predict them remains poor. In recent years, this challenge has gained importance as it is unclear how marine ecosystems will respond to current trends in climate patterns and anthropogenic pressures. Interestingly enough, this situation is not unique to the marine world; it holds for a whole range of ecosystems that have experienced regime shifts in the past or may do so in the future.

A novel approach for tackling this challenge is the recently developed early warning signals for critical transitions [20]. Critical transitions are defined as abrupt qualitative changes in the state of an ecosystem that occur close to bifurcation points [21]. Below we offer a more rigorous description of a critical transition. Most early warning signals are temporal and spatial statistical signatures of the phenomenon of critical slowing down (CSD) that arises in the vicinity of bifurcations [22–24]. CSD can be interpreted as an indication of low resilience in the sense that the ecosystem could easily be tipped into a contrasting state. Indicators of CSD have been demonstrated in a variety of systems, ranging from yeast and zooplankton populations close to extinction [25,26] and collapsing phytoplankton monocultures [27], to eutrophication transitions [28] and trophic cascades in whole lakes [29].

Nevertheless, despite the strong theoretical underpinning and the growing list of empirical demonstrations, studies have also shown that CSD-based indicators are not a panacea for anticipating all types of regime shifts. Estimating such indicators in empirical data from drylands prone to desertification did not yield expected patterns [30]. In marine ecosystems, despite some indirectly derived positive results [31–33], indicators of CSD largely failed to detect known regime shifts [34].

At first read these stories may appear contradictory, raising scepticism whether CSD indicators are coincidental or idiosyncratic, and, thus, may have only limited value for management purposes. Our attempt here is to help to avoid potential misconceptions and misuses by offering possible explanations to this conundrum. In particular, we suggest that application and identification of CSD indicators are limited by at least three constraints

— *Conceptual*. CSD detection depends to a great extent on whether the regime shift in question is a critical transition and whether this transition is gradually approached. The ability to unequivocally identify an approaching regime shift is conditional on the underlying mechanism that drives the shift. If such conditions are not met, misunderstandings and misuses of CSD indicators may arise.
— *Operational*. Operationalizing CSD identification crucially depends on the temporal and spatial scales of the ecosystem in question and our ability to monitor key variables. Highly variable environments, or insufficient monitoring protocols, reduce the ability for monitoring the right variables at the right scale.
— *Methodological*. Just like any other quantitative analysis, the sensitivity and significance of CSD indicators largely depend on the quality and quantity of the data as well as the underlying assumptions of the various statistical tools employed ([35–37], www.early-warning-signals.org).

Here, we focus on the conceptual and operational constraints by showcasing examples derived from a generic model that undergoes regime shifts. We identify key limitations to detection and propose an alternative way of interpreting and using CSD indicators. Our approach is mainly theoretical, but we highlight case studies where possible. Although we focus on temporal CSD indicators in a marine context, our conclusions apply to both temporal and spatial indicators for a wide range of ecosystems.

2. The basics: critical transitions and indicators of critical slowing down as early warning signals

We define critical transitions as abrupt qualitative changes in the state of an ecosystem that occur close to bifurcation points [21]. Mathematically, critical transitions are associated with bifurcation points. At a bifurcation, the current ecosystem state becomes unstable and the system jumps to an alternative (usually radically different) state. Here, we look at local bifurcations with eigenvalues that smoothly diminish to zero, like a saddle-node, transcritical or a Hopf bifurcation. The reason why we can anticipate a critical transition in advance lies in the fact that prior to a bifurcation point small disturbances around the current ecosystem state take longer to dissipate due to CSD [38]. The early warning signals we are treating here are indirect manifestations of CSD and we will explicitly address them as CSD indicators throughout the text. Increased variance and correlation are CSD indicators and can be used to estimate ecosystem resilience (box 1).

3. Not all regime shifts are announced by critical slowing down indicators

CSD indicators are a promising tool because of their generic character [20]. Therefore, it is tempting to think that before any regime shift, one could measure a metric as simple as variance fingerprinting the upcoming event. Although a lot of regime shifts appear as critical transitions, the fact is that not all regime shifts are associated with a bifurcation [1,18,39]. Thus not all regime shifts are expected to exhibit CSD. There is a plethora of mechanisms to explain a regime shift that may not necessarily involve crossing a bifurcation [40]. For instance, abrupt changes in patterns of environmental drivers, like the Pacific Decadal Oscillation variability, may have caused big changes in North Pacific fisheries [13], although similar shifts could also have been incurred by slowly drifting ('correlated') climatic conditions alternating between extremes, or just stochastic events [41–43]. Such variability may have pushed plankton species in and out of their growth optima that shows up as a regime shift on the community level [44]. More likely, the majority of marine regime shifts documented in the North Atlantic [12] or the Baltic Sea [14] is driven by a combination of processes involving slowly changing environmental and anthropogenic pressures, climatic events and complex internal biological processes [18]. Clearly, not all regime shifts independent of their underlying mechanism will exhibit rising variance and autocorrelation.

Below we present six simple mechanisms that may trigger regime shifts of which some exhibit CSD and others not (table 1; see electronic supplementary material for model details). In all cases, we consider that the ecosystem state may shift between alternative stable states and do not treat cases where ecosystem dynamics involve shifts between irregular aperiodic dynamics that have been shown not to be preceded by CSD [45].

(a) Slow environmental change towards a tipping point

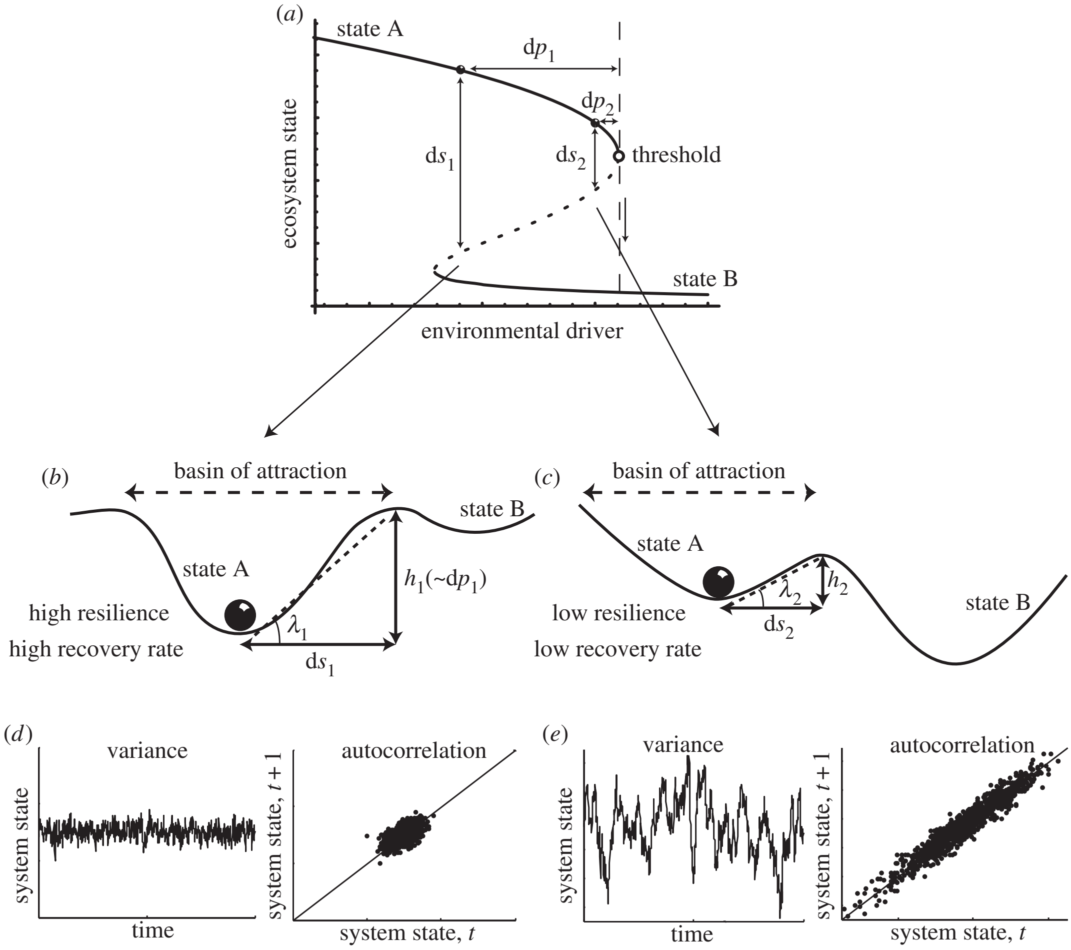
This is the basic case where an environmental driver slowly pushes the ecosystem towards the threshold at which the regime shift takes place [1]. The shift is permanent meaning that recovery to the previous state is possible only by restoring environmental conditions. In the presence of weak environmental stochasticity, the ecosystem shifts almost at the threshold and exhibits CSD expressed as an increase in variance and autocorrelation prior to the regime shift (figure 1*a*).

(b) Slow–fast cyclic transitions

Some systems have intrinsic cycles caused by the interaction between fast and slow variables. Such cycles tend to have relatively abrupt transitions but although these can be loosely attributed to tipping points, the alternative 'states' in such cycles are not stable. Instead, each time the ecosystem shifts, a negative feedback starts to operate 'moving' environmental conditions backwards till a shift to the previous state takes

Box 1. The relationship between resilience, CSD and early warnings.

Ecological resilience (*ecR*) depends on the distance to the border of the unstable manifold in state space (d*s*) and on the distance to the critical threshold (d*p*) in parameter space [$ecR = f(\mathrm{d}s,\mathrm{d}p)$] (*a*). We can approximate d*s* as the distance to the border of the attraction basin and d*p* as the height *h* of the attraction basin to the alternative state (*b*,*c*). Recovery rate (*recR*) (or engineering resilience) depends on the slope of the basin of attraction, which is defined by d*s* and d*p* [$recR = \mathrm{d}p/\mathrm{d}s$]. This slope can be approximated by the eigenvalue $|\lambda|$ which determines the stability of the current equilibrium of the system [$recR \equiv |\lambda|$]. CSD occurs as the system approaches the threshold, d*p* becomes smaller, recovery rate decreases and ecological resilience declines. Although ecological resilience is not approximated completely by $|\lambda|$, CSD indicates the progressive shrinking of the basin of attraction of the current state. Moreover, the dynamics of the monitored ecosystem differ radically far from and close to the threshold; both variance and autocorrelation increase (*d*,*e*).



place [46]. Thus, such a scenario causes a sequence of abrupt swings between the two states, as observed for instance in cyclic shifts between a vegetated and a barren state in lakes [47], in repeated outbreaks of forest pests [48], or the whelk–lobster alternate states in marine benthic communities [49]. Even though there are no formal bifurcation points within such cycles, indicators of CSD may be observed in the dynamics of the fast variable prior to the shifts (figure 1*b*).

(c) Stochastic resonance

Swinging between alternative states can also result from a combination of stochastic perturbations and a periodic change in environmental conditions. Periodic change causes the ecosystem to approach (but not cross) the tipping points while stochastic disturbances can cause swings between the two alternative states due to stochastic resonance [50]. Stochastic resonance is hypothesized to explain glaciation events in the Earth's climate past [51]. It is conceivable that in the marine environment, cyclic trends in climatic conditions, such as the decadal North Atlantic Oscillation, might have facilitated abrupt shifts in fish populations triggered by perturbations. Depending on the rate of the processes and the amplitude of stochastic forcing, it may be difficult to observe increase in variance and autocorrelation prior to the regime shift (figure 1*c*).

(d) Noise-induced transitions

Noise-induced transitions are another case of regime shifts that are unlikely to be announced by CSD indicators (figure 1*d*). In this case, a tipping point is neither crossed nor approached, but simply strong external disturbances induce the shift to the alternative state, a phenomenon termed as noise-induced flickering [52].

(e) Long transient upon extreme events

In some cases, external disturbances are exceptionally strong. As a result, an ecosystem may be pushed far away from its present

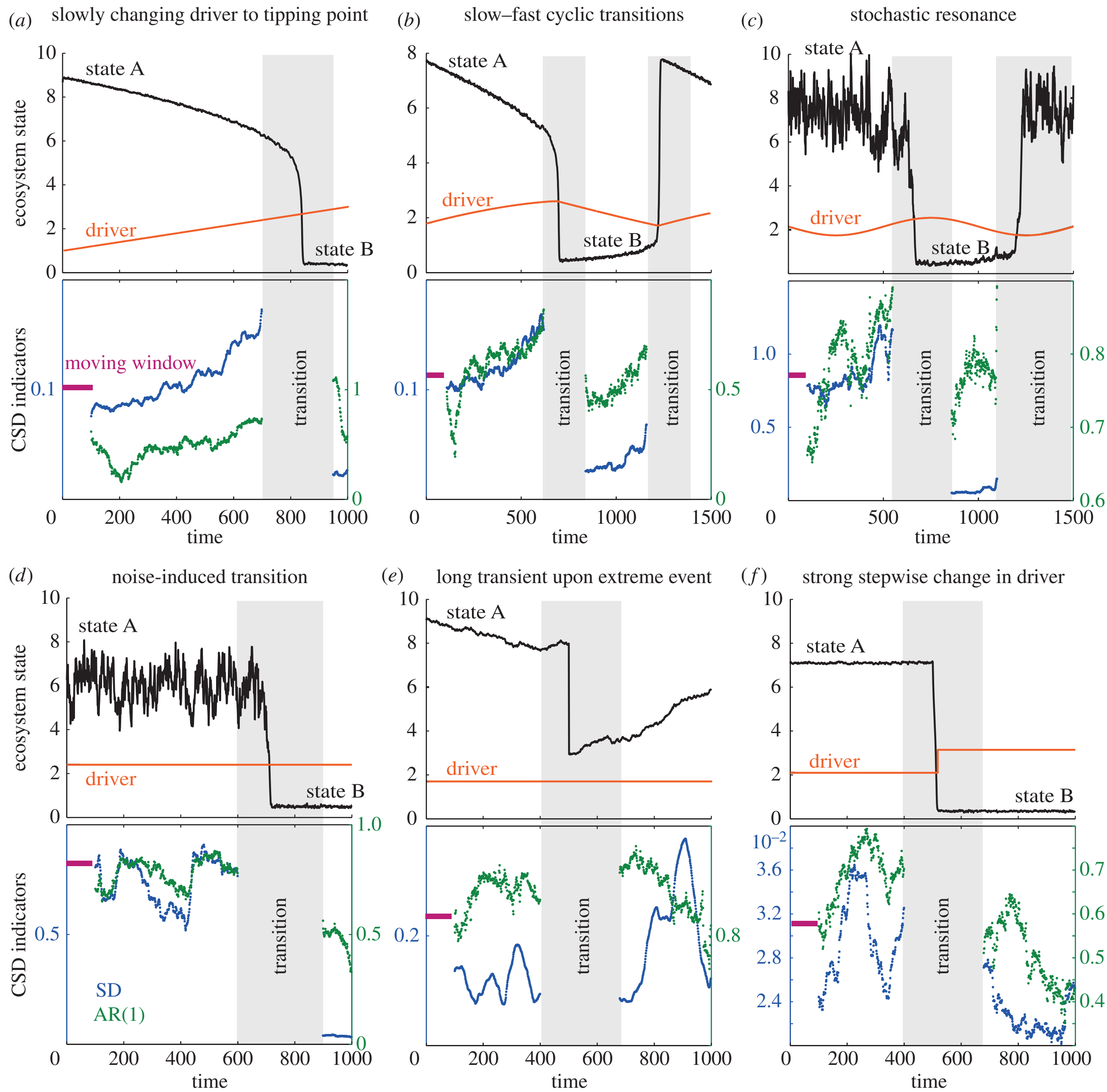


Figure 1. (*a–f*) Six different mechanisms can lead to regime shifts with or without crossing a tipping point. Based on the mechanism, early warnings may or may not indicate the approaching shift. Black lines indicate time series of the ecosystem state, red lines time series of underlying environmental conditions. Standard deviation (s.d., blue) and autocorraletion at-lag-1 (AR1, green) were estimated from the detrended time series of ecosystem state within moving windows up to the regime shift (details in the electronic supplementary material). (Online version in colour.)

state but without necessarily being trapped to an alternative state. For instance a hypoxia event or a pathogen outbreak may wipe out almost completely a fish population, but that population may rebound. Although in the short term, this change would appear as a regime shift, in reality it is only an extreme event. In that case, no CSD can be detected (figure 1*e*).

(f) Big stepwise changes in external conditions

Big stepwise changes sometimes occur in environmental conditions. If these changes are permanent, the ecosystem will move to a new state. Regardless of whether this state may be an alternative attractor or not [53], there is no reason to expect any signs of CSD prior to the regime shift (figure 1*f*).

Although the above mechanisms are fundamentally different, from a pragmatic point of view, such differences may not be all too relevant as there is typically a combination of mechanisms acting at the same time. It is the relative role of stochastic shocks and change in environmental drivers that will determine the nature of the regime shift and our ability to detect it. The bottom line is that for some combinations of mechanisms—e.g. a noise-induced transition while slowly drifting to a threshold (case 1 and 3 above) [28,52,54]—we may still detect CSD indicators, whereas for other situations early detection will be unlikely. Viewing this from another side, presence or absence of CSD may help determine the type of mechanism responsible for the regime shift.

4. Critical slowing down indicators are not only detected in bistable ecosystems

While some transitions cannot be announced by CSD indicators (figure 2*a*), there are also transitions that do exhibit

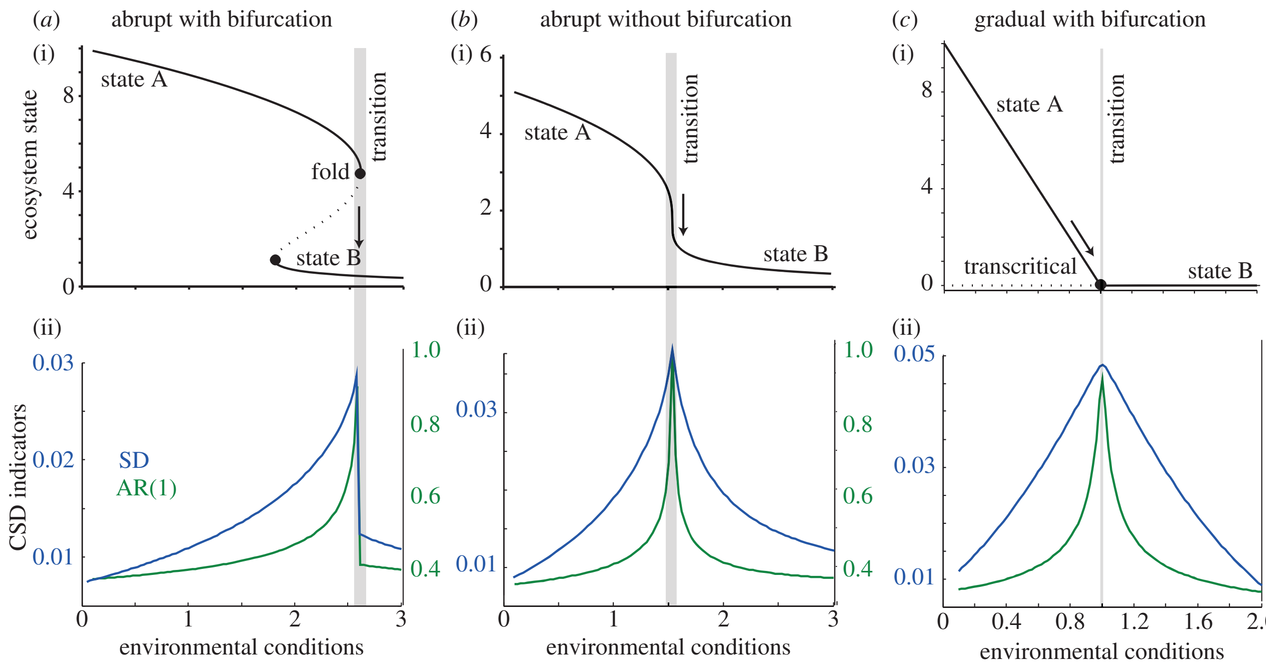


Figure 2. CSD indicators do not detect transitions only in bistable systems (*a*). Even in the absence of alternative states, with (*b*) or without (*c*) the existence of a tipping point (bifurcation), similar trends in indicators are to be expected prior to abrupt (*b*) or even gradual shifts (*c*). (Online version in colour.)

Table 1. Six mechanisms that can produce regime shifts with or without crossing tipping points, and the potential of identifying CSD-based indicators in advance.

mechanism	crossing a tipping point	CSD indicators: variance	CSD indicators: autocorrelation
slowly changing driver to tipping point	+	+	+
slow–fast cyclic transition	−	+	+
stochastic resonance	−	+/−	+/−
noise-induced transition	−	+/−	+/−
long transient upon extreme events	−	−	−
big stepwise changes in drivers	−	−	−

CSD but without switching to an alternative stable state [20,23,55]. For instance, an ecosystem may have a strongly nonlinear response to environmental change without shifting to an alternative state (figure 2*b*), or a population may gradually go extinct through a transcritical bifurcation (figure 2*c*). In both cases, CSD and its derived indicators will be detected (figure 2*b*,*c*(ii)). Therefore, the proposed indicators do not always indicate bistability. This is true not only for the CSD-related indicators, but also for indicators derived from spatial patterns [56,57]. Scheffer & Carpenter [58] have proposed that patterns such as hysteresis in the response to a control variable, or the emergence of bimodality in the frequency distribution of states in time or space (e.g. due to ‘flickering’) can be interpreted as signals of bistability. Novel approaches, such as potential analysis, may be used to assess bistability [59,60].

5. Critical slowing down indicators are not forecasting tools *per se*

In theory, exactly at the critical transition, autocorrelation reaches unity and variance blows up to infinity. Therefore, the difference between the current indicator values and the expected ones at the transition should quantify how close the ecosystem is to shifting and this distance can be used for forecasting a transition [38]. This would be true only if the transition occurred exactly at the bifurcation. In a stochastic environment, however, transitions usually occur before the actual bifurcation. Therefore, one-time measurements of CSD indicators have limited forecasting value. Instead, there is more forecasting value in their relative estimates. Once a baseline indicator value is established, then a consistent deviating trend from the baseline could indicate whether a transition is lurking. Nonetheless, even when sequences of indicator values are available, trends may still be noisy, difficult to interpret, and thus lacking the confidence needed to initiate management action [35] (figure 3). Despite the fact that this is an obstacle to the application of early warnings, recent advances in significance testing [35,36,61], model-based approaches [35,62,63] and combinations of spatial and temporal indicators [25,29,64] offer promising alternatives in identifying a nearby transition.

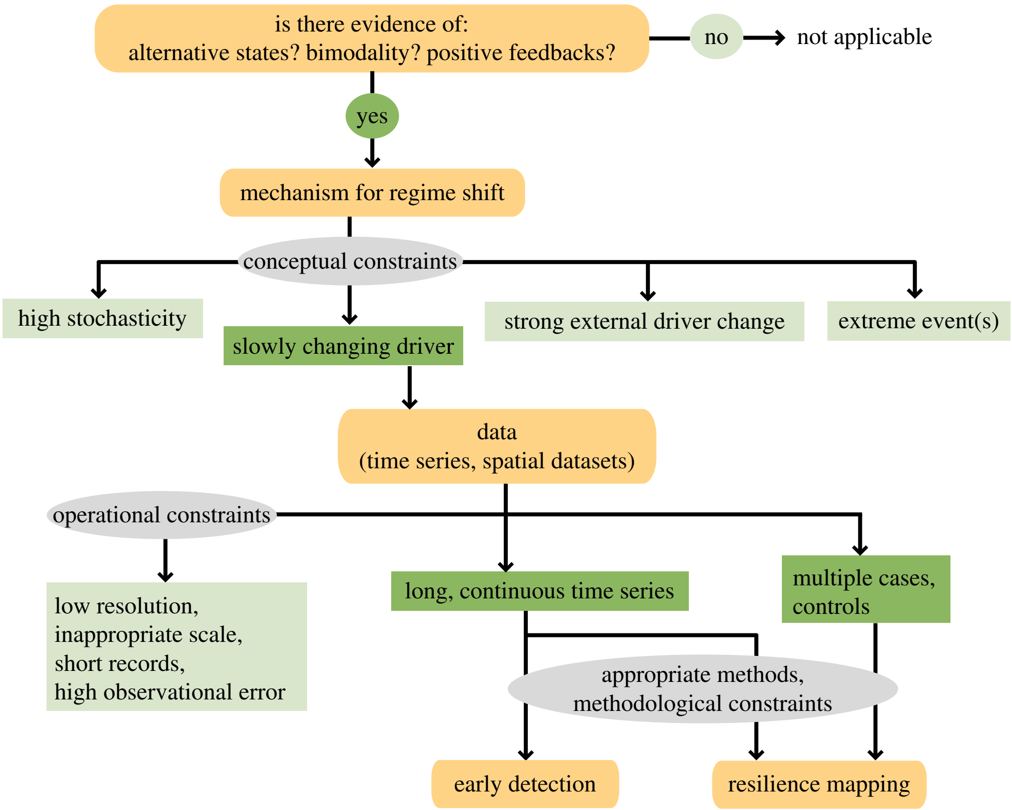


Figure 3. A map of conceptual, operational and methodological considerations when applying CSD indicators for the detection of critical transitions and resilience mapping. Light green colours indicate cases where early detection is less likely. (Online version in colour.)

6. Critical slowing down indicator detection is sensitive to false alarms

Even under the ideal case of a well-defined bistable ecosystem, a rise in variance and autocorrelation may be triggered by factors other than approaching a critical transition. The most common sources of false alarms are changes in the stochastic regime of perturbations rather than the actual dynamics [20,65]. For example, an increase in the magnitude of environmental stochasticity (like extreme events, or stronger climatic fluctuations) will cause any ecosystem response to appear more variable. As a result variance will rise, but autocorrelation should remain constant (electronic supplementary material, figure S1b,c). However, positive trends in both variance and autocorrelation can be observed when there is some memory in the temporal evolution of environmental shocks, like temperatures fluctuating around high values during hot periods (electronic supplementary material, figure S1d,e). In such cases, CSD indicators would just reflect changes in the patterns of stochasticity rather than an approaching critical transition.

7. Critical slowing down indicators may fail to announce a true transition: no alarms

While a false alarm can be a burden in terms of the costs it may incur, the absence of an alarm prior to a transition can be really disastrous. Thus, it is important to acknowledge that there is a high chance that there will be no early warning trend even if the likelihood for a transition increases. Conditions under which no alarms may occur include:

— *large process error*: the magnitude of environmental shocks may overshadow CSD. Simulations with large correlated noise have shown that indicators perform poorly when estimated from sparsely sampled time series [66].
— *large observation error*: imprecise observations make it difficult to discern CSD indicators [67].
— *multiple noise effects*: when environmental stochasticity acts both on ecosystem state (e.g. by removing biomass) and ecosystem processes (e.g. by changing growth rates) ecosystem dynamics may be amplified or dampened. Such multiple effects may result in distorted patterns in variance and autocorrelation prior to a transition [65,68].
— *rapid approach to the critical transition*: if the system is approaching fast the critical threshold, there may not be time for CSD indicators to be detected [66,69].
— *muffling*: if there are multiple thresholds approached (as may well be the case), ecosystem responses may be muffled rendering CSD indicators difficult to detect [70].
— *higher order terms* neglected in linearizations may not damp off as expected and will interfere with CSD [68].
— *fluctuating environments*: periodically fluctuating (e.g. seasonal) patterns either in underlying conditions or external perturbations may mute the fingerprint of CSD on the indicators [67].
— *measuring the wrong variable*: despite the fact that CSD is assumed to affect a system as a whole different ecosystem variables are not all equally sensitive in exhibiting CSD [71–73].
— *non-local bifurcations*: certain kinds of critical transitions that involve non-local bifurcations, such as basin-boundary collisions, will not demonstrate CSD indicators [20,45].
— *non-stationary conditions*: if prior to environmental change, the ecosystem is not in equilibrium, early warning detection

may be challenging unless there is adequate baseline data or a reference for calibration [25].

— *interference with spatial processes*: spatial interactions in the form of disturbance, irregular movement of key species, underlying spatial heterogeneity, or dispersal may influence CSD indicators [23,56].

— *too-infrequent observations or too short a time series*: variance can be estimated more precisely as observations become more frequent, while autocorrelation is estimated more precisely as the time span of the observations increases [36,37,68]. Ecological datasets are usually idiosyncratic, of relatively short length and low resolution, with a lot of discontinuities, while mismatches between the time scale of ecosystem processes and data sampling all hinder the identification of CSD. Datasets of species abundances, like the global population dynamical database (http://www3.imperial.ac.uk/cpb/research/patternsandprocesses/gpdd), or global fisheries catch data RAM (http://ramlegacy.marinebiodiversity.ca/ram-legacy-stock-assessment-database), may not always meet our theoretical expectations on identifying CSD indicators.

8. Prospects

Despite limitations in the application of CSD indicators as early warnings (figure 3), the growing number of successful empirical examples highlights their potential. Nonetheless, we still need to come up with innovative tools, take advantage of multiple sources of information, design novel monitoring programs based on new technologies, and most importantly, understand for which ecosystems or fields of research in general these approaches may prove most promising for application.

(a) Integrating mechanism-based approaches and critical slowing down indicators

Limitations of CSD indicators may sometimes be overcome by interpreting trends with the aid of site-specific ecosystem models. There are cases where appropriate structural models exist or can be determined by fitting models to the data. These approaches have the advantage of statistical inference about the underlying ecosystem dynamics, although they also require good datasets. On the other hand, parametric and non-parametric models with parsimoniously general assumptions have been proposed as possible alternatives [35,54,62,63]. Such model-based approaches combined with the plethora of metric-based CSD-based early warnings for both temporal and spatial data can enable experimentation on multiple approaches for successfully detecting regime shifts [36].

(b) Novel monitoring of data and experimentation

Despite mismatches between theoretical requirements and available data, high-frequency measurements have become routine in recent years offering novel opportunities especially for the marine environment [74]. Remote sensing approaches can provide data on algal groups at high frequency and large spatial scales [75]. Combining such temporal long-term data with spatial information derived from aerial photographs or satellite images can create new opportunities for deriving spatio-temporal signatures of ecosystem dynamics especially in environments that are difficult to sample [60]. Combination of direct ecosystem measurements with other proxies or other potential drivers (e.g. fishing effort) may help develop multivariate indices and navigate away from false positives or unclear signals. Undoubtedly, the most informative way in achieving these goals is experimentation. Enclosures or parallel experiments in lakes [29] pave the way for the development of new monitoring schemes suitable for the detection of CSD indicators in the field.

(c) Identifying best-candidate ecosystems for estimating critical slowing down indicators

The feasibility of detecting CSD will greatly depend on the scale (temporal and spatial), controllability and boundaries of the ecosystem under study. Ecosystems with fast time scales simply offer better possibilities to collect data and tend to be more suitable for manipulation and experimentation. For instance, measuring CSD in perturbation experiments of plankton in a chemostat [27] will yield better results than conducting the same experiments in coral reefs, or in an oceanic community. In addition, the uniqueness of large-scale ecosystems makes the estimation of CSD indicators more difficult compared with ecosystems for which we have many 'replicates' (e.g. lakes, or rock intertidal pools). 'Closed' ecosystems with defined boundaries (e.g. lakes) are better candidates to study than 'open' ecosystems (e.g. oceans). Indeed, the majority of well-documented examples of marine regime shifts are constrained within physical boundaries, like the 'closed' Baltic Sea and Black Sea, or focused on less mobile communities where dispersal processes are less important, like benthic communities (e.g. [5,76]) or communities of the intertidal zone (e.g. [33]). Taking into account such properties can help to apply CSD indicators for the right system and at the right scale.

(d) From anticipating critical transitions to mapping resilience

CSD is not only an ambitious tool for detecting critical transitions in advance. It can be used in hindsight to assess whether past dynamics may be explained by the existence of critical thresholds [77]. Empirical studies are so far restricted to hindsight application with different levels of success, in which cases the *a priori* knowledge of a regime shift may introduce bias towards detecting CSD indicators [78]. Owing to the limited value of CSD indicators as forecasting tools yet, it is perhaps more meaningful to adapt these metrics as indicators of ecosystem resilience (box 1). If we want to compare, for instance, the resilience of two similar clear shallow lakes, differences in recovery rate after small perturbations are likely to be informative [23]. Likewise we can compare changes in the recovery rate at different points in time to assess trends in resilience. These types of metrics can be derived from fish populations or coral reefs given that they share similar features and are situated in the same geographical area. Although such types of comparisons may be challenging, we may still get an approximate estimate of resilience that can help prioritize management. In the end, we may create 'resilience maps' and rather than speculate over the proximity to a potential threshold, we can rank situations at a given moment and place.

Table 2. Open questions towards the practical application of resilience indicators.

- — how can we combine CSD-based early warnings with ecosystem models to enhance the detection of regime shifts?
- — is it possible to use CSD indicators as measures of ecosystem resilience to create resilience maps and identify most vulnerable species, communities, ecosystems?
- — are there ways to go from relative measures to absolute measures of resilience?
- — can we devise indicators of bistability? And if we cannot, does it matter?
- — can we design monitoring protocols targeting at the right scale and at the right variables? For which ecosystems?
- — will integrating CSD-based resilience indicators in decision-making and environmental policy improve ecosystem management?

9. Can we avoid or promote the unexpected?

No doubt 'forewarned is forearmed'. However, knowing the risk of an approaching transition may be a necessary but not sufficient condition for avoiding it. In most cases, the indicators are detected only in retrospect or while the transitions are already unfolding. Even simulation studies have shown that early warnings may not be early enough [69,79]. In some ecosystems, increased variability may occur over a wide range of conditions near a transition, whereas in other ecosystems the range of increased variability may be so narrow as to be useless for practical purposes [23]. Nonetheless, CSD indicators have been demonstrated to effectively detect transitions in well-sampled bistable systems. All these imply that CSD indicators can be part of the solution to the sustainable management of ecosystems at the brink of collapse, but there are still challenges before reaching their practical application (table 2).

CSD indicators can tell us that 'something' important may be about to happen, but they do not tell us what precisely that 'something' may be and when exactly it will happen. Thus, next to the warnings, knowledge of the underlying ecosystem behaviour is important to put the signals in the right context. For this there is no substitute for site-specific knowledge and experiments combined with models. Resilience-building approaches in management [80] must be mindful of the risk of surprises that will appear with no warning even in the best-case scenarios.

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