REVIEWS

Early-warning signals for critical transitions

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Complex dynamical systems, ranging from ecosystems to financial markets and the climate, can have tipping points at which a sudden shift to a contrasting dynamical regime may occur. Although predicting such critical points before they are reached is extremely difficult, work in different scientific fields is now suggesting the existence of generic early-warning signals that may indicate for a wide class of systems if a critical threshold is approaching.

t is becoming increasingly clear that many complex systems have critical thresholds—so-called tipping points—at which the system shifts abruptly from one state to another. In medicine, we have spontaneous systemic failures such as asthma attacks[1] or epileptic seizures[2,3]; in global finance, there is concern about systemic market crashes[4,5]; in the Earth system, abrupt shifts in ocean circulation or climate may occur[6]; and catastrophic shifts in rangelands, fish populations or wildlife populations may threaten ecosystem services[7,8].

It is notably hard to predict such critical transitions, because the state of the system may show little change before the tipping point is reached. Also, models of complex systems are usually not accurate enough to predict reliably where critical thresholds may occur. Interestingly, though, it now appears that certain generic symptoms may occur in a wide class of systems as they approach a critical point. At first sight, it may seem surprising that disparate phenomena such as the collapse of an overharvested population and ancient climatic transitions could be indicated by similar signals. However, as we will explain here, the dynamics of systems near a critical point have generic properties, regardless of differences in the details of each system[9]. Therefore, sharp transitions in a range of complex systems are in fact related. In models, critical thresholds for such transitions correspond to bifurcations[10]. Particularly relevant are 'catastrophic bifurcations' (see Box 1 for an example), where, once a threshold is exceeded, a positive feedback propels the system through a phase of directional change towards a contrasting state. Another important class of bifurcations are those that mark the transition from a stable equilibrium to a cyclic or chaotic attractor. Fundamental shifts that occur in systems when they pass bifurcations are collectively referred to as critical transitions[11].

We will first highlight the theoretical background of leading indicators that may occur in non-equilibrium dynamics before critical transitions, and illustrate how such indicators can perform in model generated time-series. Subsequently, we will review emerging empirical work on different systems and discuss prospects and challenges.

Theory

Critical slowing down and its symptoms. The most important clues that have been suggested as indicators of whether a system is getting close to a critical threshold are related to a phenomenon known in dynamical systems theory as 'critical slowing down'[12]. Although critical slowing down occurs for a range of bifurcations, we will focus on the fold catastrophe (Box 1) as a starting point. Inappropriate use of this classical model caused some controversy in the past[13], but it is now

considered to capture the essence of shifts at tipping points in a wide range of natural systems ranging from cell signalling pathways[14] to ecosystems[7,15] and the climate[6]. At fold bifurcation points (F_1 and F_2, Box 1), the dominant eigenvalue characterizing the rates of change around the equilibrium becomes zero. This implies that as the system approaches such critical points, it becomes increasingly slow in recovering from small perturbations (Fig. 1). It can be proven that this phenomenon will occur in any continuous model approaching a fold bifurcation[12]. Moreover, analysis of various models shows that such slowing down typically starts far from the bifurcation point, and that recovery rates decrease smoothly to zero as the critical point is approached[16]. Box 2 describes a simple example illustrating this.

The most straightforward implication of critical slowing down is that the recovery rate after small experimental perturbation can be used as an indicator of how close a system is to a bifurcation point[16]. Because it is the rate of change close to the equilibrium that matters, such perturbations may be very small, posing no risk of driving the system over the threshold. Also, models indicate that in spatially extensive systems at risk of systemic collapse, small-scale experimental probing may suffice to test the vicinity of the threshold for such a large-scale transition. For instance, it has been shown that recovery times after local perturbation increase in models of fragmented populations approaching a threshold for global extinction[17].

For most natural systems, it would be impractical or impossible to monitor them by systematically testing recovery rates. However, almost all real systems are permanently subject to natural perturbations. It can be shown that as a bifurcation is approached in such a system, certain characteristic changes in the pattern of fluctuations are expected to occur. One important prediction is that the slowing down should lead to an increase in autocorrelation in the resulting pattern of fluctuations[18] (Fig. 1). This can be shown mathematically (Box 3), but it is also intuitively simple to understand. Because slowing down causes the intrinsic rates of change in the system to decrease, the state of the system at any given moment becomes more and more like its past state. The resulting increase in 'memory' of the system can be measured in a variety of ways from the frequency spectrum of the system[19,20]. The simplest approach is to look at lag-1 autocorrelation[21,22], which can be directly interpreted as slowness of recovery in such natural perturbation regimes[16,18]. Analyses of simulation models exposed to stochastic forcing confirm that if the system is driven gradually closer to a catastrophic bifurcation, there is a marked increase in autocorrelation that builds up long before the

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Box 1 | Critical transitions in the fold catastrophe model

The equilibrium state of a system can respond in different ways to changes in conditions such as exploitation pressure or temperature rise (Box 1 Figure a, b, c). If the equilibrium curve is folded backwards (Box 1 Figure c, d), three equilibria can exist for a given condition. The grey dotted arrows in the plots indicate the direction in which the system moves if it is not in equilibrium (that is, not on the curve). It can be seen from these arrows that all curves represent stable equilibria, except for the dashed middle section in Box 1 Figure c, d. If the system is driven slightly away from this part of the curve, it will move further away instead of returning. Hence, equilibria on this part of the curve are unstable and represent the border between the basins of attraction of the two alternative stable states on the upper and lower branches. If the system is very close to a fold bifurcation point (for example point F_1 or point F_2), a tiny change in the condition may cause a large shift in the lower branch (Box 1 Figure c). Also, close to such a bifurcation a small perturbation can drive the system across the boundary between the attraction basins (Box 1 Figure d). Thus, those bifurcation points are tipping points at which a tiny perturbation can produce a large transition. Small perturbations can also cause large changes in the absence of true bifurcations, provided that the system is very sensitive in a certain range of conditions (Box 1 Figure b). Finally, a shift in system state may simply be caused by a sudden large external force (Box 1 Figure a). Early-warning signals tend to arise as systems approach a bifurcation point such as in Box 1 Figure c, d, and also if systems approach a non-catastrophic threshold such as the one shown in Box 1 Figure b.
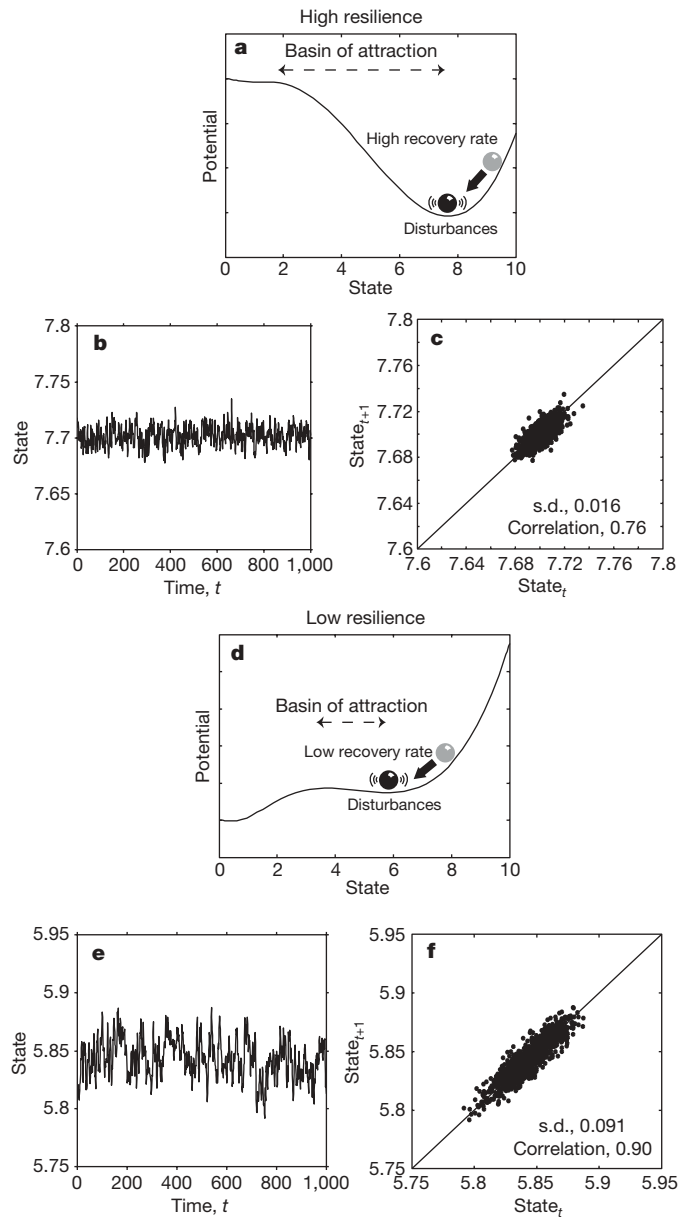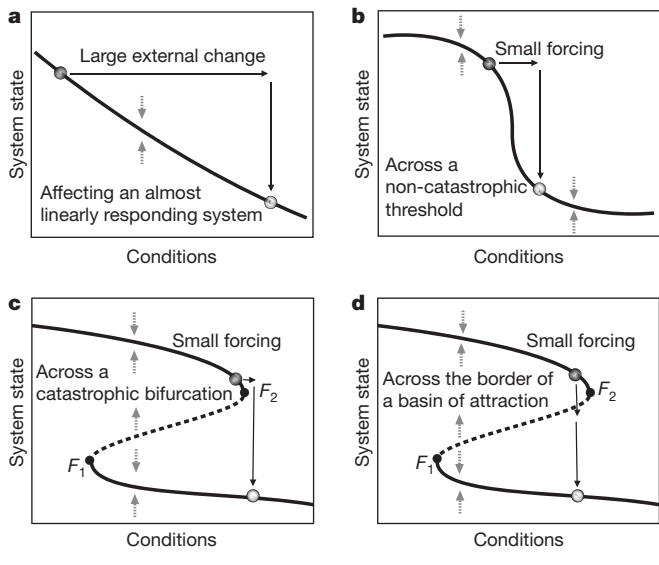

Figure 1 | Some characteristic changes in non-equilibrium dynamics as a system approaches a catastrophic bifurcation (such as F_1 or F_2, Box 1). **a, b, c,** Far from the bifurcation point (**a**), resilience is large in two respects: the basin of attraction is large and the rate of recovery from perturbations is relatively high. If such a system is stochastically forced, the resulting dynamics are characterized by low correlation between the states at subsequent time intervals (**b, c**). **d–f,** When the system is closer to the transition point (**d**), resilience decreases in two senses: the basin of attraction shrinks and the rate of recovery from small perturbations is lower. As a consequence of this slowing down, the system has a longer memory for perturbations, and its dynamics in a stochastic environment are characterized by a larger s.d. and a stronger correlation between subsequent states (**e, f**). Plots produced from a stochastically forced differential equation[15] representing a harvested population: $dX/dt = X(1 − X/K) − c(X^2/(X^2 + 1))$, where X is population density, K is the carrying capacity (set to 10) and c is the maximum harvest rate (set to 1 for high resilience and 2.6 for low resilience).

critical transition occurs (Fig. 2d). This is true not only for simple models[22], but also for highly elaborate and relatively realistic models of spatially complex systems[23].

Increased variance in the pattern of fluctuations is another possible consequence of critical slowing down as a critical transition is approached[24] (Fig. 1). Again, this can be formally shown[25] (Box 3), as well as intuitively understood: as the eigenvalue approaches zero, the impacts of shocks do not decay, and their accumulating effect increases the variance of the state variable. In principle, critical slowing down could reduce the ability of the system to track the fluctuations, and thereby produce an opposite effect on the variance[26,27]. However, analyses of models show that an increase in the variance usually arises and may be detected well before a critical transition occurs[24] (Fig. 2).

In summary, the phenomenon of critical slowing down leads to three possible early-warning signals in the dynamics of a system approaching a bifurcation: slower recovery from perturbations, increased autocorrelation and increased variance.

Skewness and flickering before transitions. In addition to autocorrelation and variance, the asymmetry of fluctuations may increase

before a catastrophic bifurcation[28]. This does not result from critical slowing down. Instead, the explanation is that in catastrophic bifurcations such as fold bifurcations (Box 1), an unstable equilibrium that marks the border of the basin of attraction approaches the attractor from one side (Box 1). In the vicinity of this unstable point, rates of change are lower (reflected in a less steep slope in the stability landscapes). As a result, the system will tend to stay in the vicinity of

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Box 2 | Critical slowing down: an example

To see why the rate of recovery rate after a small perturbation will be reduced, and will approach zero when a system moves towards a catastrophic bifurcation point, consider the following simple dynamical system, where γ is a positive scaling factor and a and b are parameters:

$$\frac{dx}{dt} = \gamma(x-a)(x-b) \qquad (1)$$

It can easily be seen that this model has two equilibria, $\bar{x}_1 = a$ and $\bar{x}_2 = b$, of which one is stable and the other is unstable. If the value of parameter a equals that of b, the equilibria collide and exchange stability (in a transcritical bifurcation). Assuming that $\bar{x}_1$ is the stable equilibrium, we can now study what happens if the state of the equilibrium is perturbed slightly ($x = \bar{x}_1 + \varepsilon$):

$$\frac{d(\bar{x}_1 + \varepsilon)}{dt} = f(\bar{x}_1 + \varepsilon)$$

Here $f(x)$ is the right hand side of equation (1). Linearizing this equation using a first-order Taylor expansion yields

$$\frac{d(\bar{x}_1 + \varepsilon)}{dt} = f(\bar{x}_1 + \varepsilon) \approx f(\bar{x}_1) + \left.\frac{\partial f}{\partial x}\right|_{\bar{x}_1} \varepsilon$$

which simplifies to

$$f(\bar{x}_1) + \frac{d\varepsilon}{dt} = f(\bar{x}_1) + \left.\frac{\partial f}{\partial x}\right|_{\bar{x}_1} \varepsilon \Rightarrow \frac{d\varepsilon}{dt} = \lambda_1 \varepsilon \qquad (2)$$

With eigenvalues λ_1 and λ_2 in this case, we have

$$\lambda_1 = \left.\frac{\partial f}{\partial x}\right|_a = -\gamma(b-a) \qquad (3)$$

and, for the other equilibrium

$$\lambda_2 = \left.\frac{\partial f}{\partial x}\right|_b = \gamma(b-a) \qquad (4)$$

If $b > a$ then the first equilibrium has a negative eigenvalue, λ_1, and is thus stable (as the perturbation goes exponentially to zero; see equation (2)). It is easy to see from equations (3) and (4) that at the bifurcation ($b = a$) the recovery rates λ_1 and λ_2 are both zero and perturbations will not recover. Farther away from the bifurcation, the recovery rate in this model is linearly dependent on the size of the basin of attraction ($b - a$). For more realistic models, this is not necessarily true but the relation is still monotonic and is often nearly linear[16].

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Box 3 | The relation between critical slowing down, increased autocorrelation and increased variance

Critical slowing down will tend to lead to an increase in the autocorrelation and variance of the fluctuations in a stochastically forced system approaching a bifurcation at a threshold value of a control parameter. The example described here illustrates why this is so. We assume that there is a repeated disturbance of the state variable after each period Δt (that is, additive noise). Between disturbances, the return to equilibrium is approximately exponential with a certain recovery speed, λ. In a simple autoregressive model this can be described as follows:

$$x_{n+1} - \bar{x} = e^{\lambda \Delta t}(x_n - \bar{x}) + \sigma \varepsilon_n$$

$$y_{n+1} = e^{\lambda \Delta t} y_n + \sigma \varepsilon_n$$

Here y_n is the deviation of the state variable x from the equilibrium, ε_n is a random number from a standard normal distribution and σ is the standard deviation.

If λ and Δt are independent of y_n, this model can also be written as a first-order autoregressive (AR(1)) process:

$$y_{n+1} = \alpha y_n + \sigma \varepsilon_n$$

The autocorrelation $\alpha \equiv e^{\lambda \Delta t}$ is zero for white noise and close to one for red (autocorrelated) noise. The expectation of an AR(1) process $y_{n+1} = c + \alpha y_n + \sigma \varepsilon_n$ is[18]

$$E(y_{n+1}) = E(c) + \alpha E(y_n) + E(\sigma \varepsilon_n) \Rightarrow \mu = c + \alpha\mu + 0 \Rightarrow \mu = \frac{c}{1-\alpha}$$

For $c = 0$, the mean equals zero and the variance is found to be

$$\mathrm{Var}(y_{n+1}) = E(y_n^2) - \mu^2 = \frac{\sigma^2}{1-\alpha^2}$$

Close to the critical point, the return speed to equilibrium decreases, implying that λ approaches zero and the autocorrelation α tends to one. Thus, the variance tends to infinity. These early-warning signals are the result of critical slowing down near the threshold value of the control parameter.
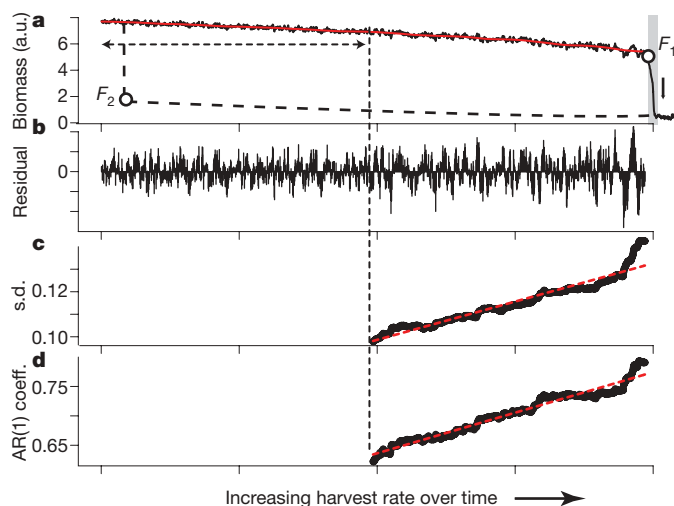
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the unstable point relatively longer than it would on the opposite side of the stable equilibrium. The skewness of the distribution of states is expected to increase not only if the system approaches a catastrophic bifurcation, but also if the system is driven closer to the basin boundary by an increasing amplitude of perturbation[28].

Another phenomenon that can be seen in the vicinity of a catastrophic bifurcation point is flickering. This happens if stochastic forcing is strong enough to move the system back and forth between the basins of attraction of two alternative attractors as the system enters the bistable region before the bifurcation[26,29]. Such behaviour is also considered an early warning, because the system may shift permanently to the alternative state if the underlying slow change in conditions persists, moving it eventually to a situation with only one stable state. Flickering has been shown in models of lake eutrophication[24] and trophic cascades[30], for instance. Also, as discussed below, data suggest that certain climatic shifts and epileptic seizures may be presaged by flickering. Statistically, flickering can be observed in the frequency distribution of states as increased variance and skewness as well as bimodality (reflecting the two alternative regimes)[24].

Indicators in cyclic and chaotic systems. The principles discussed so far apply to systems that may be stochastically forced but have an underlying attractor that corresponds to a stable point (for example the classic fold catastrophe illustrated in Box 1). Critical transitions in cyclic and chaotic systems are less well studied from the point of view

Figure 2 | Early warning signals for a critical transition in a time series generated by a model of a harvested population[77] driven slowly across a bifurcation. a, Biomass time series. **b, c, d**, Analysis of the filtered time series (**b**) shows that the catastrophic transition is preceded by an increase both in the amplitude of fluctuation, expressed as s.d. (**c**), and in slowness, estimated as the lag-1 autoregression (AR(1)) coefficient (**d**), as predicted from theory. The grey band in **a** identifies the transition phase. The horizontal dashed arrow shows the width of the moving window used to compute the indicators shown in **c** and **d**, and the red line is the trend used for filtering (see ref. 22 for the methods used). The dashed curve and the points F_1 and F_2 represent the equilibrium curve and bifurcation points as in Box 1 Figure c, d. a.u., arbitrary units.

of early-warning signals. Such transitions are associated with different classes of bifurcation[10]. First, there are the bifurcations that mark the transitions between stable, cyclic and chaotic regimes. An example is the Hopf bifurcation, which marks the transition from a stable system to an oscillatory system[31]. Like the fold bifurcation, this bifurcation is signalled by critical slowing down[32]: close to the bifurcation, perturbations lead to long transient oscillations before the system settles to the stable state.

Another class of bifurcations are the non-local bifurcations[10] that occur if intrinsic oscillations bring the system to the border of the basin of attraction of an alternative attractor. Such basin-boundary collisions[33] are not associated with particular properties of stable or unstable points that can be analytically defined. We know of no explicit work on early-warning signals for such transitions. Nonetheless, the dynamics may be expected to change in a characteristic way before basin-boundary collisions occur. For instance, oscillations may become 'stretched', as the system dwells longer in the vicinity of the basin boundary, where rates of change are slower[34], implying increased autocorrelation. Finally, there is the phenomenon of phase locking between coupled oscillators. Again, alternative attractors are often involved[35] and the corresponding bifurcations are associated with critical slowing down[36], suggesting the existence of early-warning signals. Indeed, rising variance and flickering occur before an epileptic seizure, a phenomenon associated to the phase locking of firing in neural cells (see below).

Spatial patterns as early-warning signals. In addition to early-warning signals in time series, there are particular spatial patterns that can arise before a critical transition. Many systems can be seen as consisting of numerous coupled units each of which tends to take a state similar to that of the units to which it is connected. For instance, it is well known that financial markets affect each other. Also, the attitudes of individuals towards certain issues is affected by the attitudes of their peers[37,38], and the persistence of species in habitat patches in a fragmented landscape depends on the presence of the same species in neighbouring patches from which recolonization can happen[39,40]. In such systems, phase transitions may occur[9,41] much as in ferromagnetic materials, where individual particles affect each others' spin. As gradual change in an external forcing factor (for example a magnetic field) drives the system closer to a transition, the distribution of the states of the units in such systems may change in characteristic ways. For instance, scale-invariant distributions of patch sizes occur close to a systemic transition, and there is a general tendency towards increased spatial coherence, measured as increased cross-correlation (or in oscillating units, resonance) among units before a critical event[9,41].

Certain classes of spatial system deviate from this general pattern and can have other, more specific, indicators of imminent transitions. For instance, in systems governed by local disturbance (for example grazers foraging locally on vegetation patches), scale-invariant power-law structures that are found for a large parameter range vanish as a critical transition is approached[42]. In systems that have self-organized regular patterns[43], critical transitions may be signalled by particular spatial configurations. For instance, models of desert vegetation show that as a critical transition to a barren state is neared, the vegetation becomes characterized by regular patterns because of a symmetry-breaking instability. These patterns change in a predictable way as the critical transition to the barren state is approached (Fig. 3), implying that this may be interpreted as early-warning signal for a catastrophic bifurcation[44].

In conclusion, when it comes to interpreting spatial patterns it is important to know which class of system is involved. Although broad classes have similar early-warning signals, there is no 'one-size-fits-all' spatial pattern announcing critical transitions.

Precursors of transitions in real systems

Most of the work on early-warning signals for critical transitions has so far been done using simple models, and empirical proof that critical slowing down occurs at bifurcations has been provided by controlled
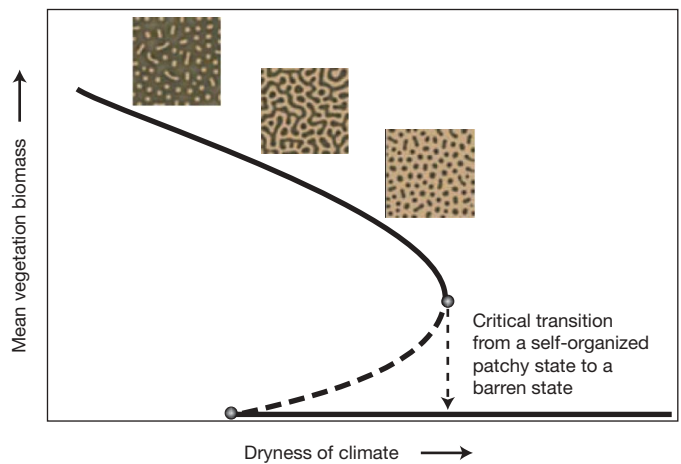

Figure 3 | Ecosystems may undergo a predictable sequence of self-organized spatial patterns as they approach a critical transition. We show the modelled response of semi-arid vegetation to increasing dryness of the climate. Solid lines represent mean equilibrium densities of vegetation. The insets are maps of the pattern: the dark colour represents vegetation and the light colour represents empty soil. As the bifurcation point for a critical transition into a barren state is approached, the nature of pattern changes from maze-like to spots. Modified from ref. 44. Reprinted with permission from AAAS.

experiments with lasers[45] and neurons[46]. The question therefore remains of whether highly complex real systems such as the climate or ecosystems will show the theoretically expected early-warning signals. Results from elaborate and relatively realistic climate models including spatial dynamics and chaotic elements[23] suggest that some signals might be robust in the sense that they arise despite high complexity and noisiness. Nonetheless, it is clearly more challenging to pick up early-warning signals in complex natural systems than in models. We now review some emerging results on the climate and ecosystems. Also, we highlight empirical successes in finding early-warning signals of transitions in systems for which we have a relatively poor understanding of the mechanisms that drive the dynamics, such as the human brain and financial markets.

Climate. Interest in the possibility of critical transitions in the Earth system has been sparked by records of past climate dynamics revealing occasional sharp transitions from one regime to another[47]. For instance, about 34 Myr ago the Earth changed suddenly from the tropical state in which it had been for many millions of years to a colder state in which Antarctica was glaciated, a shift known as the greenhouse–icehouse transition[48–50] (Fig. 4). Also, glacial cycles tend to end with an abrupt warming[51,52].

Uncertainty in reconstructing such dynamics remains considerable, and it is even more difficult to unveil the underlying mechanisms. Nonetheless, the sharpness of the shifts and the existence of positive feedbacks that, if strong enough, could cause self-propelling change have led to the suggestion that these and other examples of rapid climate change could be explained as critical transitions[6,47,53]. Therefore, the reconstructed climate dynamics before such transitions are an obvious place to look for early-warning signals. In a recent analysis, a significant increase in autocorrelation was found in each of eight examples of abrupt climate change analysed[22] (Fig. 4).

Another recent study suggests that flickering preceded the abrupt end of the Younger Dryas cold period[54]. Although the first part of this cold episode was quite stable, rapid alternations between a cold mode and a warm mode characterized the later part, and the episode eventually ending in a sharp shift to the relatively warm and stable conditions of the Holocene epoch[55]. After examination of longer timescales, it has been suggested that the increasing Pleistocene climate variability may be interpreted as a signal that the near geological future might bring a transition from glacial–interglacial oscillations to a stable state characterized by permanent mid-latitude Northern Hemisphere glaciation[56].
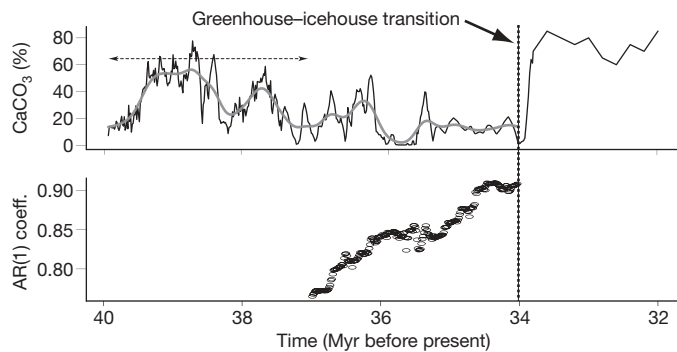
Figure 4 | Critical slowing down indicated by an increase in lag-1 autocorrelation in climate dynamics. We show the period preceding the transition from a greenhouse state to an icehouse state on the Earth 34 Myr ago. The trends in the $CaCO_3$ concentration time series removed by filtering before computing autocorrelation (AR(1) coefficient) are represented by the grey line. The horizontal dashed arrow shows the width of the moving window used to compute the autocorrelation. Modified from ref. 22.

Ecosystems. In ecology, critical transitions have become a major focus of research. The existence of alternative attractors has been demonstrated experimentally in lakes[57], and a large body of work now suggests that alternative stable states separated by critical thresholds also occur in ecosystems ranging from rangelands to marine systems[7,58]. Work on early-warning signals in this field is just emerging. As mentioned earlier, in dry regions self-organization can lead to particular spatial patterns under some conditions. Here the complete loss of vegetation is an important transition, as recovery from the barren state may require more rain than is needed to preserve the last patches. There is good evidence to support the idea that a regular pattern characterized by spots of vegetation signals the proximity of a threshold to such catastrophic desertification[44]. Other studies show how, in line with model predictions, vegetation-patch size distributions lose their scale-free structures and become characterized by truncated power laws as a transition to a barren state is approached[42].

Early-warning signals are also being found for destabilization of exploited fish stocks. It has been shown that harvesting tends to lead to increased fluctuations in fish populations[59]. This increase in variance is most likely due to increased intrinsic growth rates in the resulting populations, as older age classes are preferentially harvested and the younger fish have higher overall intrinsic rates of change[60]. Such higher growth rates lead to increased nonlinearity as they drive populations towards the critical transition from a stable to a cyclic or chaotic regime, as mentioned earlier.

Asthma attacks and epileptic seizures. Abrupt transitions in physiology include epileptic seizures and asthma attacks. In the case of asthma, it has been shown that human lungs can display a self-organized pattern of bronchoconstriction that might be the prelude to dangerous respiratory failure, and which resembles the pattern formation in collapsing desert vegetation[1].

Epileptic seizures happen when neighbouring neural cells all start firing in synchrony. Predicting such seizures far in advance remains very difficult[61]. However, before the seizure becomes noticeable several characteristic changes in neural activity can occur. For instance, minutes before an epileptic seizure, variance in the electrical signal recorded by electroencephalography may increase[3] (Fig. 5). More subtle changes (reduced dimensionality of the signal) occur up to 25 min before epileptic seizures, reflecting a continuous increase in the degree of synchronicity (and thus correlation) between neural cells[62]. Also, hours before the seizure, mild energy bursts can occur in the brain followed by frequent symptomless seizures too small for the patients to notice[2]. This resembles patterns of flickering in which smaller transient excursions to the vicinity of an alternative state precede the upcoming major shift.

Finance. The prediction of shifts in financial markets is a heavily researched area. In this field, the discovery of predictability quickly
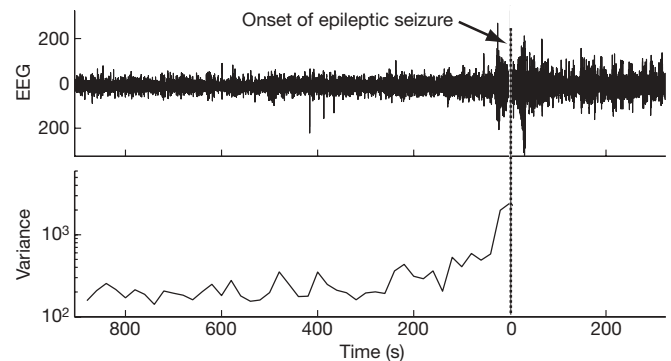

Figure 5 | Subtle changes in brain activity before an epileptic seizure may be used as an early warning signal. The epileptic seizure clinically detected at time 0 is announced minutes earlier in an electroencephalography (EEG) time series by an increase in variance. Adapted by permission from Macmillan Publishers Ltd: Nature Medicine (ref. 3), copyright 2003.

leads to its elimination, as profit can be made from it, thereby annihilating the pattern. As a result, although there is always some predictability that can be exploited by specialists[63,64], overall financial markets are notoriously difficult to predict[65]. Nonetheless, many papers in the financial literature show that market dynamics may contain information presaging major events[66–68]. For instance, some events are preceded by measures of increased trade volatility (for example the spread between the value of put options and the value of call options[66,67]), but a 'volatility calm' before the abrupt change can also happen[66,69]. A prominent volatility-based early-warning signal in financial markets is the VIX, or 'fear' index[70,71]. There is also evidence of systematic relationships in variance and first-order autocorrelation[72], although lead–lag relationships tend to be erratic. Finally, increased spatial coherence may be an early warning of major transitions. There is evidence that correlation increases across returns to different stocks in a falling market and patterns embodied in options prices may serve as a type of early-warning indicator[73].

Outlook

As our overview shows, similar early-warning signals can appear in widely different systems: flickering may occur before epileptic seizures, the end of a glacial period and in lakes before they shift to a turbid state; self-organized patterns can signal an imminent transition in desert vegetation and in asthma; increased autocorrelation may indicate critical slowing down before all kinds of climatic transitions and in ecosystems; and increased variance of fluctuation may be a leading indicator of an epileptic seizure or instability in an exploited fish stock. Some of these complex systems are better understood than others. However, turning the reasoning around, it could be argued that the generic character of some early-warning signals suggests that these transitions may be somehow related to bifurcations, where universal laws of dynamical systems govern the pattern.

The theoretical basis of the work on early-warning signals in simple models is quite strong, and the first results from more elaborate models suggest that similar signals may arise in highly complex systems[23]. Nonetheless, more work is needed to find out how robust these signals are in situations in which spatial complexity, chaos and stochastic perturbations govern the dynamics. Also, detection of the patterns in real data is challenging and may lead to false positive results as well as false negatives. False negatives are situations in which a sudden transition occurred but no early-warning signals could be detected in the behaviour before the shift. This can happen for different reasons. One possibility is that the sudden shift in the system was not preceded by a gradual approach to a threshold. For instance, it may have remained at the same distance from the bifurcation point, but been driven to another stable state by a rare extreme event. Also, a shift that is simply due to a fast and permanent change of external conditions (Box 1 Figure a) cannot be detected from early-warning signals. A

second class of false negatives may arise from the statistical difficulty of picking up the early-warning signal. For instance, the detection of increased autocorrelation may require long time series[74]. A third difficulty arises if the external regime of perturbations changes over time. This may distort or counteract the expected signals. False positives occur if a supposed early-warning signal is not the result of approaching a bifurcation. This may happen by chance or may result from a confounding trend within the system or in the external regime of perturbations.

Importantly, most of the indicators we have identified signal a wide class of impending transitions in complex systems. The same signals may even occur, albeit in a less pronounced way, as the system approaches a threshold that is not related to catastrophic bifurcations (Box 1 Figure b)[27]. This has been shown for critical slowing down[16], and may also be true for autocorrelation and variance. Nonetheless, such non-catastrophic thresholds are related to the more spectacular catastrophic ones (Box 1), and systems may in fact move from one type of threshold to another. In conclusion, most early-warning signals are indicators of proximity to a broad class of thresholds, where small forces can cause major changes in the state of a complex system.

The idea that critical transitions across a range of systems may be related in the sense that they can be described by similar equations, implying similar possible bifurcations and early-warning signals, implies an exciting opportunity for connecting work across disciplines. However, there are many challenges to be overcome. For instance, filtering techniques for time series[75] are necessary to increase the sensitivity of indicators while preventing false positives[22], but results depend on parameter choices in filtering[22,23]. Therefore, it would be useful to build a set of reliable statistical procedures to test whether an increase in autocorrelation, for example, is significant. We note also that most of the signals we have discussed should still be interpreted in a relative sense. For instance, although autocorrelation is predicted to approach unity at a fold bifurcation, measurement noise will tend to reduce correlations. Also, perturbations will often trigger a transition well before a bifurcation point is reached. Thus, although a trend in the indicators may serve as a warning, the actual moment of a transition remains difficult to predict. A key issue when it comes to practical application is the question of whether a signal can be detected sufficiently early for action to be taken to prevent a transition or to prepare for one[25]. Understanding spatial early-warning signals better might be particularly useful in this respect, as a spatial pattern contains much more information than does a single point in a time series, in principle allowing shorter lead times[76].

In any case, generic early-warning signals will remain only one of the tools we have for predicting critical transitions. In systems in which we can observe transitions repeatedly, such as lakes, rangelands or fields such as physiology, we may empirically discover where the thresholds are. Nonetheless, some extremely important systems, such as the climate or ocean circulation, are singular and afford us limited opportunity to learn by studying many similar transitions. Also, we are far from being able to develop accurate models to predict thresholds in most complex systems, ranging from cells to organisms, ecosystems or the climate. We simply do not understand all the relevant mechanisms and feedbacks sufficiently well in most cases. The generic character of the early-warning signals we have discussed here is reason for optimism, as they occur largely independently of the precise mechanism involved. Thus, if we have reasons to suspect the possibility of a critical transition, early-warning signals may be a significant step forwards when it comes to judging whether the probability of such an event is increasing.

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