Generic Indicators for Loss of Resilience Before a Tipping Point Leading to Population Collapse
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Science **336**, 1175 (2012)

Recommended with a commentary by Mehran Kardar, MIT

As dramatic manifestations of collective behavior, phase transitions have been central to the development of novel tools and concepts in statistical and condensed matter physics. The study of phase transitions have since expanded to include out of equilibrium phenomena, and changes in the ground states of quantum mechanical systems. Tipping points or bifurcations, as phase transitions are often called outside physics, also play a major role in many complex systems. Examples include climate, ecosystems, and infrastructure [1]. In these systems, positive feedbacks lead to alternative stable states such as an operational or non-operational power grid, warm climate or glaciation, a productive ecosystem or a dead zone. Transitions between these states are often catastrophic, and tools to avert or at least forecast tipping points are desirable.

One approach to predict a transition is to develop a detailed model of the system. Unfortunately, this is often not feasible for a complicated system like climate, or a large ecosystem due to the complexity of the interactions and the number of model parameters. Another approach is to look for generic or universal indicators of phase transitions that are shared among many systems. For example, second order phase transitions are often preceded by a divergence of the correlation length, susceptibility, and heat capacity. Similarly, many tipping points are preceded by the phenomenon of *critical slowing down* [1]. Consider a one-dimensional dynamical system that can be represented by a potential function with two minima. When the conditions or control parameters slowly change, the barrier between the states may gradually disappear, resulting in a single stable state [1]. As this transition is approached, the disappearing minimum becomes more shallow leading to weaker restoring forces, longer times to recover from perturbations, larger fluctuations, and stronger autocorrelations between the consecutive states of the system. These signatures of critical slowing down can then be used to forecast an impending transition.

The above *Science* article reports observations of critical slowing down in a laboratory yeast population. The authors grew yeast in liquid medium with sucrose as the main food source, and, at the end of each growth cycle, transfered a fraction of the population to a fresh medium. At moderate transfer fractions, these populations exhibited two alternative stable states: high population size and extinction. Extinction was a stable state because yeast cells break down sucrose cooperatively outside the cell, thus, requiring a large population density for effective digestion of this sugar. At low transfer fractions, cells did not grow sufficiently fast and population declined with each transfer; therefore, extinction was the only stable state. The authors measured stable and unstable fixed points of population dynamics at various transfer fractions, thus, mapping out the bifurcation diagram. They also

[1] This is an example of a fold bifurcation. The closest analogy in condensed matter physics is crossing the spinodal curve of a metastable phase.

measured fluctuations in population density around the high density stable state, and the probability of the system to recover from a large perturbation. In agreement with theoretical predictions, several signatures of critical slowing down were observed, including larger and more correlated fluctuations near the tipping point. Thus, they could in principle anticipate impending population collapse at lower transfer fractions.

Compared to natural ecosystems, experimental microbial populations could be a useful testing ground for early warning signals of tipping points. Microbes reproduce fast and, therefore, high quality time series data could be obtained in short periods of time. More importantly, many replicate populations can be studied at once providing a measurement of variation in the quality of indicators between different realizations. Nevertheless, experimental populations avoid many of the complications present in systems of interest, such as fluctuating environment or coupling to a large number of other species, and more empirical and theoretical work would be required to faithfully forecast future catastrophes.

References

[1] Marten Scheffer, et al., Nature **461**, 53 (2009).