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Anticipating Critical Transitions

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Tipping points in complex systems may imply risks of unwanted collapse, but also opportunities for positive change. Our capacity to navigate such risks and opportunities can be boosted by combining emerging insights from two unconnected fields of research. One line of work is revealing fundamental architectural features that may cause ecological networks, financial markets, and other complex systems to have tipping points. Another field of research is uncovering generic empirical indicators of the proximity to such critical thresholds. Although sudden shifts in complex systems will inevitably continue to surprise us, work at the crossroads of these emerging fields offers new approaches for anticipating critical transitions.

About 12,000 years ago, the Earth suddenly shifted from a long, harsh glacial episode into the benign and stable Holocene climate that allowed human civilization to develop. On smaller and faster scales, ecosystems occasionally flip to contrasting states. Unlike gradual trends, such sharp shifts are largely unpredictable (1–3). Nonetheless, science is now carving into this realm of unpredictability in fundamental ways. Although the complexity of systems such as societies and ecological networks prohibits accurate mechanistic modeling, certain features turn out to be generic markers of the fragility that may typically precede a large class of abrupt changes. Two distinct approaches have led to these insights. On the one hand, analyses across networks and other systems with many components have revealed that particular aspects of their structure determine whether they are likely to have critical thresholds where they may change abruptly; on the other hand, recent findings suggest that certain generic indicators may be used to detect if a system is close to such a “tipping point.” We highlight key findings but also challenges in these

emerging research areas and discuss how exciting opportunities arise from the combination of these so far disconnected fields of work.

The Architecture of Fragility

Sharp regime shifts that punctuate the usual fluctuations around trends in ecosystems or societies may often be simply the result of an unpredictable external shock. However, another possibility is that such a shift represents a so-called critical transition (3, 4). The likelihood of such transitions may gradually increase as a system approaches a “tipping point” [i.e., a catastrophic bifurcation (5)], where a minor trigger can invoke a self-propagating shift to a contrasting state. One of the big questions in complex systems science is what causes some systems to have such tipping

points. The basic ingredient for a tipping point is a positive feedback that, once a critical point is passed, propels change toward an alternative state (6). Although this principle is well understood for simple isolated systems, it is more challenging to fathom how heterogeneous structurally complex systems such as networks of species, habitats, or societal structures might respond to changing conditions and perturbations. A broad range of studies suggests that two major features are crucial for the overall response of such systems (7): (i) the heterogeneity of the components and (ii) their connectivity (Fig. 1). How these properties affect the stability depends on the nature of the interactions in the network.

Domino effects. One broad class of networks includes those where units (or “nodes”) can flip between alternative stable states and where the probability of being in one state is promoted by having neighbors in that state. One may think, for instance, of networks of populations (extinct or not), or ecosystems (with alternative stable states), or banks (solvent or not). In such networks, heterogeneity in the response of individual nodes and a low level of connectivity may cause the network as a whole to change gradually—rather than abruptly—in response to environmental change. This is because the relatively isolated and different nodes will each shift at another level of an environmental driver (8). By contrast, homogeneity (nodes being more similar) and a highly connected network may provide resistance to change until a threshold for a systemic critical transition is reached where all nodes shift in synchrony (8, 9).

This situation implies a trade-off between local and systemic resilience. Strong connectivity

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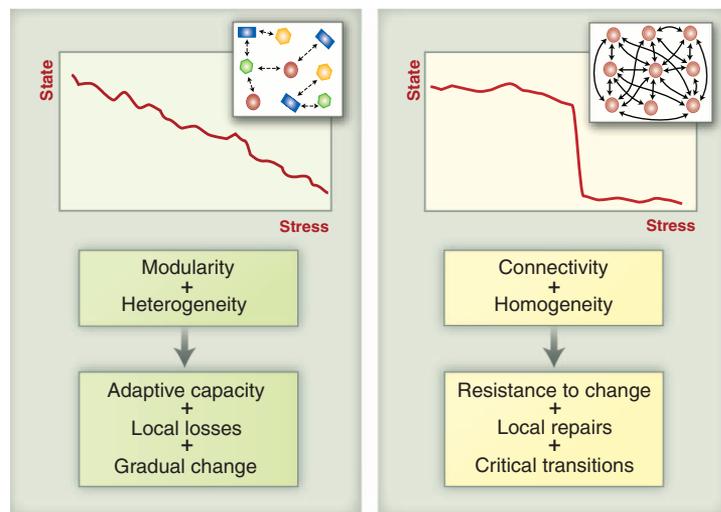


Fig. 1. The connectivity and homogeneity of the units affect the way in which distributed systems with local alternative states respond to changing conditions. Networks in which the components differ (are heterogeneous) and where incomplete connectivity causes modularity tend to have adaptive capacity in that they adjust gradually to change. By contrast, in highly connected networks, local losses tend to be “repaired” by subsidiary inputs from linked units until at a critical stress level the system collapses. The particular structure of connections also has important consequences for the robustness of networks, depending on the kind of interactions between the nodes of the network.

promotes local resilience, because effects of local perturbations are eliminated quickly through subsidiary inputs from the broader system. For instance, local damage to a coral reef may be repaired by “mobile link organisms” from nearby reefs, and individual banks may be saved by subsidiary inputs from the larger financial system (10). However, as conditions change, highly connected systems may reach a tipping point where a local perturbation can cause a domino effect cascading into a systemic transition (8). Notably, in such connected systems, the repeated recovery from small-scale perturbations can give a false impression of resilience, masking the fact that the system may actually be approaching a tipping point for a systemic shift. For example, before the sudden large-scale collapse of Caribbean coral systems in the 1980s evoked by a sea urchin disease outbreak, the reefs were considered highly resilient systems, as they recovered time and time again from devastating tropical storms and other local perturbations (11). In summary, the same prerequisites that allow recovery from local damage may set a system up for large-scale collapse.

Robustness in different kinds of networks. In addition to the work on systems where units can switch between alternative states in a contagious way, there has been an increasing interest in understanding robustness of webs of other kinds of interactions. For instance, species in ecosystems can be linked through mutualistic (+/+) interactions such as in pollinators and plants, or by competition (-/-) or predation (+/-). Rather than asking what causes the overall systems response to be catastrophic or gradual, most of these studies have focused on what topology of interaction structures makes the overall system less likely to fall apart when components are randomly removed. The answer turns out to depend on the kind of interactions between the units. Overall, networks with antagonistic interactions (e.g., competition) are predicted to be more robust if interactions are compartmentalized into loosely connected modules, whereas networks with strong mutualistic interactions (e.g., pollination) are more robust if they have nested structures where specialists are preferentially linked in their mutualism to generalists that act as hubs of connectivity (12, 13). Empirical studies in ecology suggest that the structures predicted to be more robust are also found most in nature (13–15), but this is an active field of research where new insights are still emerging (16) and much remains to be explored.

The challenge of designing robust systems. Work on ecological networks has led to the idea that we might apply our insights in the functioning of natural systems when it comes to designing structures that are less vulnerable to collapse. For instance, about half a year before the collapse of global financial markets in 2008, it was pointed out (17) that it could be helpful to analyze the financial system for the generic structural features that were found by ecologists to affect the risk

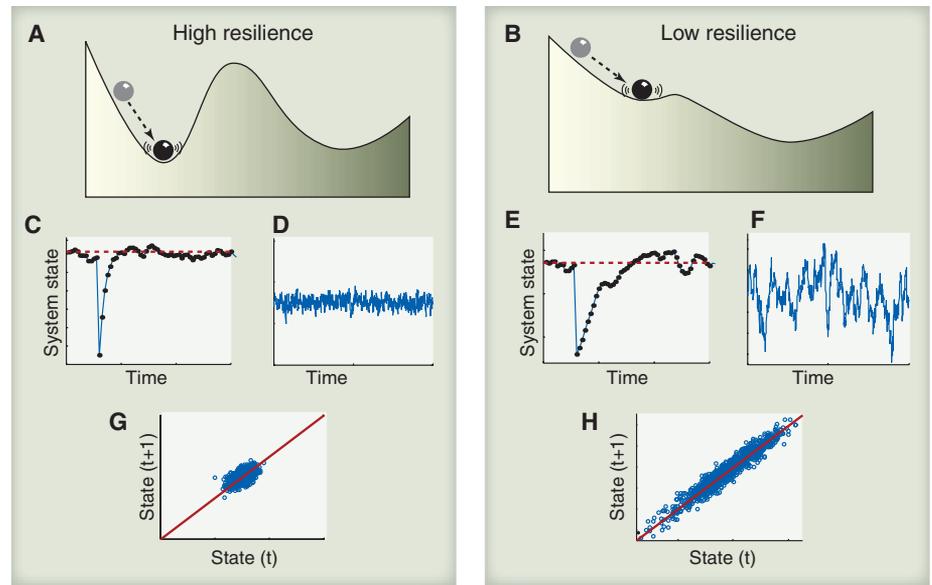


Fig. 2. Critical slowing down as an indicator that the system has lost resilience and may therefore be tipped more easily into an alternative state. Recovery rates upon small perturbations (C and E) are slower if the basin of attraction is small (B) than when the attraction basin is larger (A). The effect of this slowing down may be measured in stochastically induced fluctuations in the state of the system (D and F) as increased variance and “memory” as reflected by lag-1 autocorrelation (G and H).

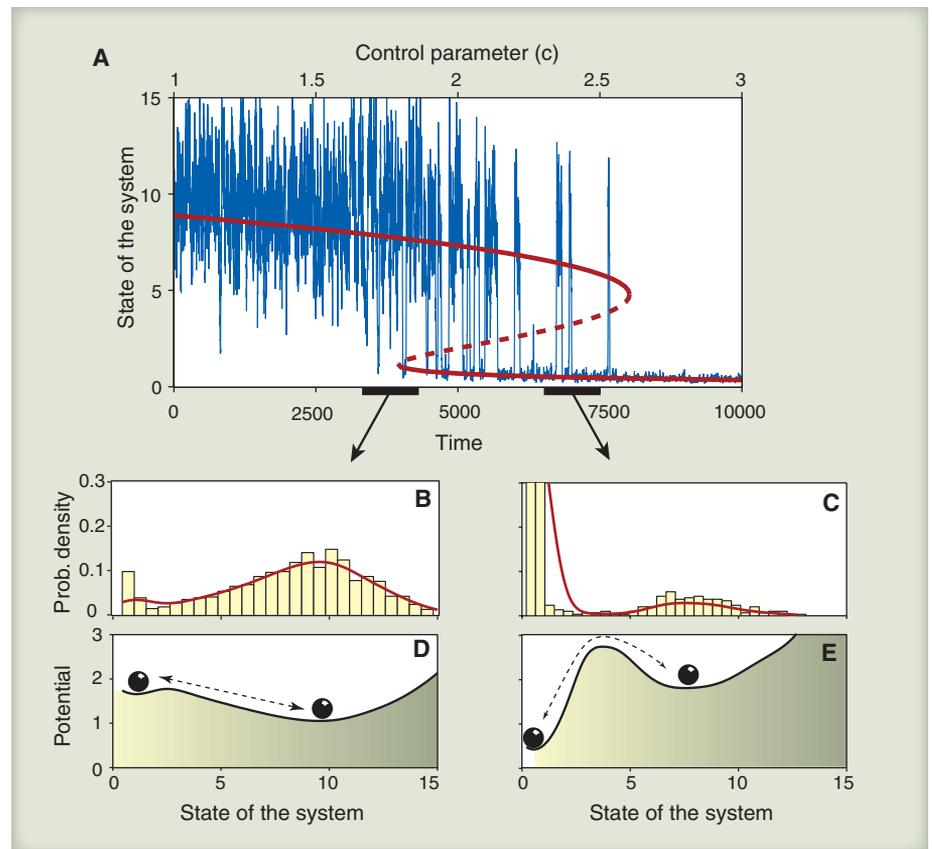


Fig. 3. (A) Flickering to an alternative state as a warning signal in highly stochastic systems. In such situations, the frequency distribution of states (B and C) can be used to approximate the shape of the basins of attraction of the alternative states (D and E). The data in this example are generated with a model of overexploitation (38): $\frac{dx}{dt} = x(1 - \frac{x}{K}) - \frac{cx}{1+x}$ with different additive and multiplicative stochastic terms (30) (we used $K = 11$).

of systemic failure. Building on such parallels between the architecture of ecological and financial systems, Haldane and May (18) have made specific recommendations to encourage modularity and diversity in the financial sectors as a way to decrease systemic risk. There are still obvious challenges in bridging from ecosystems and conceptual models to societal structures, and much will be beyond our reach when it comes to “design.” For instance, the extremely fast global spread of information is an important feature of current social systems, and the worldwide connection of social-ecological systems through markets implies a daunting level of complexity (19). Nonetheless, this line of thinking about features that affect robustness across systems clearly offers fresh perspectives

on the question of how we can make the complex networks on which we depend more robust.

Early-Warning Signals for Critical Transitions

Although such insight into structural determinants of robustness and fragility can guide the design of systems that are less likely to go through sharp transitions, there are so far no ways in which these features can be used to measure how close any particular system really is to a critical transition. A new field of research is now emerging that focuses on precisely that (20).

Critical slowing down near tipping points. One line of work is based on the generic phenomenon that in the vicinity of many kinds of tipping points, the rate at which a system recovers from small perturbations becomes very slow, a

phenomenon known as “critical slowing down” (Fig. 2). This happens, for instance, at the classical fold bifurcation, often associated with the term “tipping point,” as well as more broadly in situations where a system becomes sensitive so that a tiny nudge can cause a large change (20). The increasing sluggishness of a system can be detected as a reduced rate of recovery from (experimental) perturbations (21, 22). However, the slowness can also be inferred indirectly from rising “memory” in small fluctuations in the state of a system (Fig. 2), as reflected, for instance, in a higher lag-1 autocorrelation (23, 24), increased variance (25), or other indicators (26, 27).

Not all abrupt transitions will be preceded by slowing down. For instance, sharp change may simply result from a sudden big external impact. Also, slowing down of rates can have causes other than approaching a tipping point (e.g., a drop in temperature). Therefore, slowing down is neither a universal warning signal for shifts nor specific to an approaching tipping point. Instead, slowing down should be seen as a “broad spectrum” indicator of potential fundamental change in the current regime. Further diagnosis of what might be coming up requires additional information.

Changing stability landscapes in stochastic systems. In highly stochastic systems, transitions will typically happen far from local bifurcation points. This makes it unlikely that in such stochastic situations slowing down is a useful characteristic to measure. Nevertheless, the behavior of systems exposed to strong perturbation regimes can hint at features of the underlying stability landscape. When an alternative basin of attraction begins to emerge, one may expect that in stochastic environments, systems will occasionally flip to that state, a phenomenon referred to as “flickering” (20). Rising variance can reflect such a change. Moreover, under certain assumptions, the probability density distribution of the state of a system can even be used to estimate how the potential landscape reflecting the stability properties of the system changes over time (28) or is affected by important drivers (29) (Fig. 3). The idea behind this approach is that even if stochasticity is large, systems will more often be found close to attractors than far away from them. The scope of this approach is different from that implied in work on critical slowing down. Slowing down suggests an increased probability of a sudden transition to a new unknown state. By contrast, the information extracted from more wildly fluctuating systems suggests a contrasting regime to which a system may shift if conditions change. Just as in the detection of critical slowing down, patterns in the data should be interpreted with caution. For instance, multimodality of the frequency distribution of states over a parameter range may be caused by nonlinear responses to other, unobserved drivers or from a multimodality of the distribution of such drivers. Also, the character of the perturbation regime may have a large effect.

Table 1. Studies of early-warning indicators for critical transitions in different complex systems. (+) Cases in which early warning signals were detected by indicators; (0) cases in which transitions were not preceded by indicators; (–) cases of unknown or opposite effect.

Field	Phenomenon	Indicator	Signal	References
Chemistry	Critical slowing down	Recovery rate/ return time	+	(39)
Physics	Critical slowing down	Return time/ dominant eigenvalue	+	(40)
		Rate of change of amplitude	+	(41)
Engineering	Critical slowing down	Autocorrelation at lag 1	+	(42)
Tectonics	Not specified	Autocorrelation/ spatial correlation	+	(43)
Climate	Critical slowing down	Autocorrelation at lag 1	+	(23, 44, 45)
			0	(44, 46)
		Detrended fluctuation analysis	+	(27, 44)
			-	(44)
	Increasing variability	Variance	+	(44)
		0	(44, 46)	
	Skewed responses	Skewness	0	(47)
Ecology	Critical slowing down	Return time/dominant eigenvalue	+	(22, 48–50)
		Autocorrelation at lag 1	+	(22)
		Spectral reddening	0	(48)
	Increasing variability	Spatial correlation	+	(48, 49, 51, 52)
		Variance	+	(48, 49, 52, 53)
		0	(22, 54)	
		Spatial variance	+	(48, 49, 55, 56)
	Skewed responses	Skewness	+	(48, 49)
Microbiology	Critical slowing down	Autocorrelation at lag 1	+	(57)
		Variance	+	(57)
		Return time	+	(57)
		Skewness	0	(57)
Physiology	Critical slowing down	Recovery rate/ return time	+	(58)
Epilepsy	Critical slowing down	Correlation	+	(59, 60)
	Increasing variability	Variance	+	(61)
Behavior	Critical slowing down	Recovery rate/ return time	+	(62, 63)
Sociology	Critical slowing down	Autocorrelation at lag 1	+/0	(64)
		Variance	+/0	(64, 65)
		Fisher information	+	(66)
Finance	Not specified	Correlation	+	(60)
	Not specified	Shannon index	+	(67)
	Not specified	Variance	+	(68)

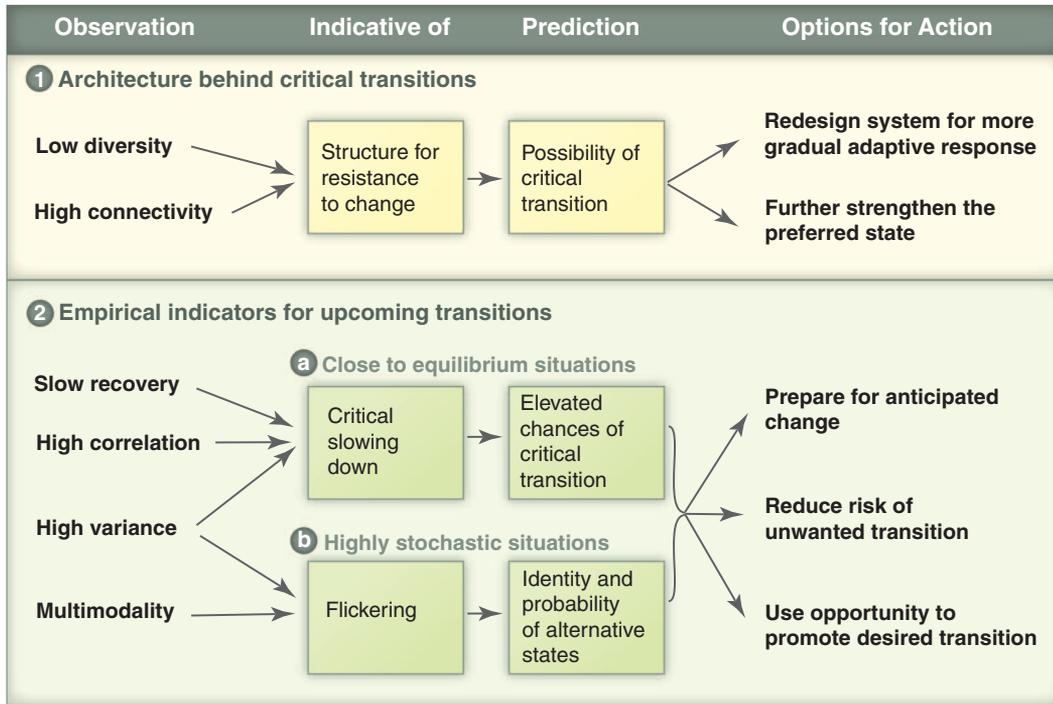


Fig. 4. Different classes of generic observations that can be used to indicate the potential for critical transitions in a complex system.

Prospects, challenges, and limitations. Although research on empirical indicators of robustness and resilience is just beginning, there is already a fast-growing body of modeling as well as empirical work (Table 1). Nonetheless, major challenges remain in developing robust procedures for assessment. One problem is that methods for detection of incipient transitions from time series tend to require long, high-resolution data (23, 30). As a picture of a spatial pattern can carry much more information than a single point in a time series, the interpretation of spatial patterns is a potentially powerful option. Like increased memory in time series, correlation between neighboring units can reflect slowing down (31). Similarly, spatial data can be used to infer how resilience of alternative states depends on key drivers (29). Various aspects of spatial patterns may also change in specific ways near a critical point (31–36), but these patterns and their interpretation differ across systems in ways that are not yet entirely understood.

A fundamental limitation is that the indicators cannot be used to predict transitions, as stochastic shocks will always play an important role in triggering transitions before a bifurcation point is reached. Also, interpreting absolute values of indicators as signaling particular levels of fragility so far remains beyond reach. Thus, indicators should be used to rank situations on a relative scale from fragile to resilient. Detecting early-warning signals in monitoring time series may seem an obvious application. However, this requires the rare situation of having high-resolution data for a system that moves toward a tipping

point gradually (37). In addition to such challenges in detection, there are still gaps in our understanding of how indicators will behave in more complex situations. Given these limitations, there is no “silver bullet” approach. Instead, a diverse collection of complementary indicators and methods of applying them is emerging. A state-of-the-art overview linked to a Web site with open-source software for data analysis is published elsewhere (30) (www.early-warning-signals.org).

Toward an Integrative Approach for Anticipating Critical Transitions

So far, research on network robustness and work on empirical indicators of resilience have been largely segregated. However, connecting these fields opens up obvious new perspectives. First, there is complementarity in the existing approaches. The structural features that create tipping points and the different empirical indicators for their proximity offer alternative angles for diagnosis and potential action (Fig. 4). A smart combination of approaches in a unified framework may therefore greatly enhance our capacity to anticipate critical transitions.

At the same time, linking these two vital fields may generate exciting new directions for research. For instance, an intriguing question is how early-warning signals for loss of resilience may best be detected in a complex network (e.g., of species, persons, or markets). Will particular nodes in the network reveal critical slowing down or other early-warning indicators more than others? Can we know a priori which nodes

would carry such a clear signal? Or would some integrative indicator over the entire network be best? Clearly, this is an open area of research, and much may be gained by developing the different lines of work into an integrative science for understanding and predicting fragility and transitions in complex systems. Occasional radical transitions will continue to surprise us. However, the emerging field of research that we have sketched may reduce the realm of surprise in transitions related to tipping points.

Perhaps the most exciting aspect of this work is that it is uncovering generic features that should in principle hold for any complex system. This implies that we may use these approaches even if we do not understand all details of the underlying mechanisms that drive any particular system. This is the rule rather than the exception, as we are far from being able to construct accurate predictive mechanistic

models for most, if not all, complex systems. So far, most work on generic indicators of resilience has been carried out in ecology and climate science (Table 1). However, social sciences and medicine might well be particularly rich fields for exploration.

Developing sound predictive systems based on these generic properties poses major challenges. However, the potential gains are formidable. Empirically detecting opportunities where positive transitions in social or ecological systems can be invoked with minimal effort may be of great value. On the risk side, guidelines for designing financial systems that are less prone to systemic failure, or ways to foresee critical transitions ranging from epileptic seizures to the collapse of fish stocks or tipping elements of the Earth climate system, rank high in their importance to humanity.

References and Notes

1. A. D. Barnosky et al., *Nature* **486**, 52 (2012).
2. C. Folke et al., *Annu. Rev. Ecol. Evol. Syst.* **35**, 557 (2004).
3. M. Scheffer, *Critical Transitions in Nature and Society* (Princeton Univ. Press, Princeton and Oxford, 2009).
4. C. Kuehn, *Physica D* **240**, 1020 (2011).
5. Y. A. Kuznetsov, *Elements of Applied Bifurcation Theory* (Springer, New York, 1995).
6. D. Angeli, J. E. Ferrell Jr., E. D. Sontag, *Proc. Natl. Acad. Sci. U.S.A.* **101**, 1822 (2004).
7. S. A. Levin, *Fragile Dominion: Complexity and the Commons* (Perseus Publishing, Cambridge, MA, 2000).
8. E. H. van Nes, M. Scheffer, *Ecology* **86**, 1797 (2005).
9. J. A. Dunne, R. J. Williams, N. D. Martinez, *Ecol. Lett.* **5**, 558 (2002).
10. J. Lundberg, F. Moberg, *Ecosystems (N.Y.)* **6**, 87 (2003).

11. D. R. Bellwood, T. P. Hughes, C. Folke, M. Nyström, *Nature* **429**, 827 (2004).
12. M. Pascual, J. A. Dunne, *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Santa Fe Institute Studies on the Sciences of Complexity (Oxford Univ. Press, New York, 2006).
13. E. Thébault, C. Fontaine, *Science* **329**, 853 (2010).
14. J. Bascompte, P. Jordano, C. J. Melián, J. M. Olesen, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 9383 (2003).
15. S. B. Otto, B. C. Rall, U. Brose, *Nature* **450**, 1226 (2007).
16. S. Allesina, M. Pascual, *Ecol. Lett.* **12**, 652 (2009).
17. R. M. May, S. A. Levin, G. Sugihara, *Nature* **451**, 893 (2008).
18. A. G. Haldane, R. M. May, *Nature* **469**, 351 (2011).
19. W. N. Adger, H. Eakin, A. Winkels, *Front. Ecol. Environ* **7**, 150 (2009).
20. M. Scheffer *et al.*, *Nature* **461**, 53 (2009).
21. E. H. van Nes, M. Scheffer, *Am. Nat.* **169**, 738 (2007).
22. A. J. Veraart *et al.*, *Nature* **481**, 357 (2012).
23. V. Dakos *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 14308 (2008).
24. A. R. Ives, *Ecol. Monogr.* **65**, 217 (1995).
25. S. R. Carpenter, W. A. Brock, *Ecol. Lett.* **9**, 311 (2006).
26. T. Kleinen, H. Held, G. Petschel-Held, *Ocean Dyn.* **53**, 53 (2003).
27. V. N. Livina, T. M. Lenton, *Geophys. Res. Lett.* **34**, L03712 (2007).
28. V. N. Livina, F. Kwasiak, T. M. Lenton, *Climate of the Past* **6**, 77 (2010).
29. M. Hirota, M. Holmgren, E. H. van Nes, M. Scheffer, *Science* **334**, 232 (2011).
30. V. Dakos *et al.*, *PLoS ONE* **7**, e41010 (2012).
31. V. Dakos, E. H. van Nes, R. Donangelo, H. Fort, M. Scheffer, *Theor. Ecol.* **3**, 163 (2010).
32. S. Kéfi *et al.*, *Nature* **449**, 213 (2007).
33. M. Pascual, F. Guichard, *Trends Ecol. Evol.* **20**, 88 (2005).
34. R. V. Solé, S. C. Manrubia, B. Luque, J. Delgado, J. Bascompte, *Complexity* **1**, 13 (1996).
35. M. Rietkerk, S. C. Dekker, P. C. de Ruiter, J. van de Koppel, *Science* **305**, 1926 (2004).
36. C. S. Holling, *Ecosystems (N.Y.)* **4**, 390 (2001).
37. R. Biggs, S. R. Carpenter, W. A. Brock, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 826 (2009).
38. R. M. May, *Nature* **269**, 471 (1977).
39. J. Kramer, J. Ross, *J. Chem. Phys.* **83**, 6234 (1985).
40. J. R. Treddic *et al.*, *Am. J. Phys.* **72**, 799 (2004).
41. J. Lim, B. I. Epaneau, *Phys. Rev. E Stat. Nonlin. Soft Matter Phys.* **83**, 016203 (2011).
42. P. Hines, E. Cotilla-Sanchez, S. Blumsack, in *Proceedings of the Annual Hawaii International Conference on System Sciences* (2011).
43. O. Ramos, *Tectonophysics* **485**, 321 (2010).
44. T. M. Lenton, V. N. Livina, V. Dakos, E. H. van Nes, M. Scheffer, *IMA J. Appl. Math.* **76**, 27 (2011).
45. P. D. Ditlevsen, S. J. Johnsen, *Geophys. Res. Lett.* **37**, L19703 (2010).
46. V. Guttal, C. Jayaprakash, *Ecol. Lett.* **11**, 450 (2008).
47. S. R. Carpenter *et al.*, *Science* **332**, 1079 (2011).
48. J. M. Drake, B. D. Griffen, *Nature* **467**, 456 (2010).
49. C. Wissel, *Oecologia* **65**, 101 (1984).
50. G. Beaugrand, M. Edwards, K. Brander, C. Luczak, F. Ibanez, *Ecol. Lett.* **11**, 1157 (2008).
51. C. H. Hsieh *et al.*, *Nature* **443**, 859 (2006).
52. B. deYoung *et al.*, *Trends Ecol. Evol.* **23**, 402 (2008).
53. B. T. Bestelmeyer *et al.*, *Ecosphere* **2**, art129 (2011).
54. J. E. Hewitt, S. F. Thrush, *Mar. Ecol. Prog. Ser.* **413**, 267 (2010).
55. M. A. Litzow, J. D. Urban, B. J. Laurel, *Ecol. Appl.* **18**, 1331 (2008).
56. L. Dai, D. Vorsele, K. S. Korolev, J. Gore, *Science* **336**, 1175 (2012).
57. G. Matsumoto, T. Kunisawa, *J. Phys. Soc. Jpn.* **44**, 1047 (1978).
58. C. Meisel, C. Kuehn, *PLoS ONE* **7**, e30371 (2012).
59. A. N. Gorban, E. V. Smirnova, T. A. Tyukina, *Physica A* **389**, 3193 (2010).
60. P. E. McSharry, L. A. Smith, L. Tarassenko, *Nat. Med.* **9**, 241 (2003).
61. J. A. S. Kelso, J. P. Scholz, G. Schöner, *Phys. Lett. A* **118**, 279 (1986).
62. J. P. Scholz, J. A. S. Kelso, G. Schöner, *Phys. Lett. A* **123**, 390 (1987).
63. Y. Neuman, O. Nave, E. Dolev, *Complexity* **16**, 58 (2011).
64. S. Saavedra, J. Duch, B. Uzzi, *PLoS ONE* **6**, e26705 (2011).
65. A. L. Mayer *et al.*, in *Exploratory Data Analysis Using Fisher Information*, B. R. Frieden, R. A. Gatenby, Eds. (Springer London, London, 2007), pp. 217–244.
66. J. G. Brida, L. F. Punzo, *Struct. Change Econ. Dyn.* **14**, 159 (2003).
67. D. Sornette, R. Woodard, in *Econophysics Approaches to Large-Scale Business Data and Financial Crises*, M. Takayasu, T. Watanabe, H. Takayasu, Eds. (Springer Japan, Tokyo, 2010), pp. 101–148.

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