COMMENTARY

Predicting tipping points in complex environmental systems

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Ecologists have long recognized that ecosystems can exist and function in one state within predictable bounds for extended periods of time and then abruptly shift to an alternate state (1–5). Desertification of grasslands, shrub expansion in the Arctic, the eutrophication of lakes, ocean acidification, the formation of marine dead zones, and the degradation of coral reefs represent real and potential ecological regime shifts marked by a tipping point or threshold in one or more external drivers or controlling variables within the system that when breached causes a major change in the system's structure, function, or dynamics (6–9). Large or incremental alterations in climate, land use, biodiversity (invasive species or the overexploitation of species), and biogeochemical cycles represent external and internal drivers that when pushed too far cross thresholds that can could lead to regime shifts (Fig. 1). Seeing the tipping point after the fact and ascribing mechanisms to the change is one thing; predicting them using empirical data has been a challenge. The difficulty in predicting tipping points stems from the large number of species and interactions (high dimensionality) within ecological systems, the stochastic nature of the systems and their drivers, and the uncertainty and importance of initial conditions that the nonlinear nature of the systems introduce to outcomes. In PNAS, Jiang et al. (10) confront these issues using a dimension-reduction framework that uses empirical data from 59 complex multidimensional plant–pollinator mutualistic networks, some of which contain scores of species and interactions, to develop simpler 2D models for studying and predicting tipping points.

General system theory is replete with examples of tipping points and regime shifts and approaches that have been developed to study them. Ecologists have used these ideas to identify and predict tipping points and explain the mechanisms behind them in real-world situations using a combination of models and observations from long-term datasets or short-term experiments (11–13). Time-series data may reveal an abrupt change or shift system. Simplified models of the system that include the essential components, interactions, and drivers and an element of stochasticity are constructed. The initial conditions of the models are informed by first principles and the empirical

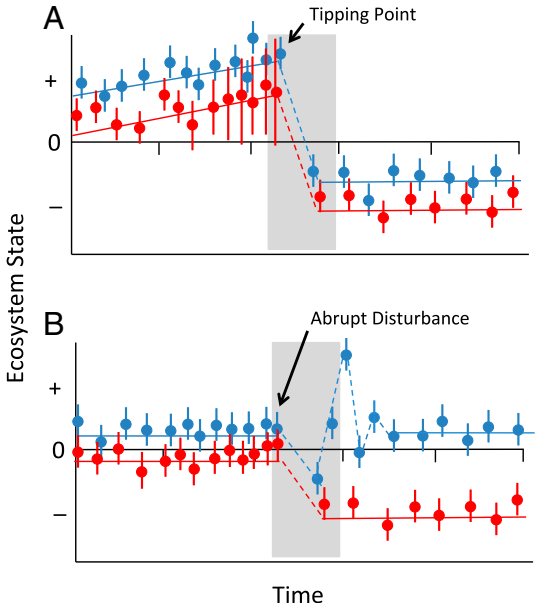

Fig. 1. Tipping points and ecological regime shifts are difficult to predict. *A* and *B* represent hypothetical time series of the trajectories of the mean and variation about the mean of variables of interest or the states of different ecosystem (blue and red), while the shaded gray area represents the transition region. (*A*) An external driver is incrementally changing and altering the state of the each ecosystem until a threshold is breached, representing tipping point after which the ecosystems transition to new states. The blue and red ecosystems both exhibit a change in state that tracks the incremental change in driver, but the blue ecosystem provides no early warning of approaching the tipping points, while the red exhibits an early warning in the form of increased variation about its mean state. (*B*) Both ecosystems possess relatively stable states until an abrupt disturbance occurs which initially alters their states. The blue ecosystem recovers from the disturbance and returns to its original state, while the red ecosystem is pushed beyond a tipping point and transitions to an alternate state.

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data, the drivers are incrementally or dramatically altered, and the ensuing changes to the system are recorded. This approach has shown conflicting outcomes. For certain types of ecological systems an analysis of the model and real-world time series reveals that there are indeed leading indicators of regime shifts in the form of increases in the variance of populations or process variables (e.g., decomposition and mineralization) or changes in the underlying dynamics of the system. Other types of models, particularly those that have multiple attractors or the potential for chaos, exhibit abrupt changes with no advanced warning in the time series.

Jiang et al. (10) studied tipping points with an approach that utilizes first principles and empirical data to describe the dynamics of 59 complex plant–pollinator networks (real networks) that vary in the number of species (plants and pollinators) and interactions and then used the information to construct a simple 2D analog (2D reduced network) containing only a plant and pollinator. For each of the 59 real networks the population dynamics of each of the plants and pollinators within the network were described by a set of first-order, nonlinear (ODEs). The ODEs included intrinsic growth rates for plants and pollinators, terms for intraspecific and interspecific competition among the plants and among the pollinators, a function for mutualistic interactions that saturate as both partners increase in abundance (akin to a Holling type II functional response in a predator–prey system), a specific death rate of the pollinator, and immigration terms for plants and pollinators. For the 2D reduced networks the empirical data are used to reduce the complexity of the system to two dimensions in the form of a set of two nonlinear ODEs describing the dynamics of the pollinators and the plants that were based on averages of the population sizes and parameter values used to construct the real networks.

To study tipping points, two resilience functions—one based on the fraction of removed pollinators and the interactions that they engaged in and one based on the decay rate of individual species—were calculated to account for the disappearance of pollinators and concomitant mutualistic interactions they engage in and the increase in species loss in a deteriorating environment, respectively. Remarkably, the 2D reduced models accurately reflected the average population densities and responses of plants and pollinators captured in the 59 real networks. In cases where incremental increases in the resilience functions with and without stochastic disturbances did and did not generate tipping points in the 59 real networks the 2D reduced networks followed suit. In all cases the 2D model accurately predicted the tipping point, although its accuracy was dependent on the method of averaging that was used for the parameters describing the mutualistic interaction strengths of the plants and pollinators.

Jiang et al. (10) then argue that these results indicate that the low dimension and tractable 2D reduced network models captured the dynamics of the high dimension and not tractable 59 real network models with both slow and abrupt changes in environmental conditions sufficiently to study the emergence of tipping points. Eigenvalue-based stability analyses of parameter regimes that did not possess tipping points generated steady-state population estimates consistent with the simulations. A closer examination of the parameter regimes that did generate tipping points could tie the thresholds to changes in specific parameters. When the resilience function was incrementally increased to reflect the removal of pollinators from the system and the intrinsic rates of growth for plants and pollinators were low the system exhibited a tipping point with dynamic behavior without hysteresis behavior. When the resilience function based on the decay rate (death rate) of the pollinators was increased, the tipping point exhibited hysteresis behavior.

The approach presented by Jiang et al. (10) provides a framework to study tipping points not limited to plant–pollinator systems but across a variety of complex systems. There are a couple of important implications. First, simple models have been criticized for lacking sufficient information (read complexity) to capture the complexity and nuances of the contexts of individual systems to address challenges. However, the insights that simple models can provide when informed by and used in conjunction with more complex empirically based models as shown here can be invaluable. Their work should not be interpreted to say that all systems can be reduced to two dimensions but rather should challenge us to discern the utilities of simple versus complicated models of complex systems. Second, this approach could be very useful in understanding the thresholds that precipitate regime shifts in environmental systems and their connections to human well-being (2). For example, Rockström et al. (14) applied the concept of ecological thresholds when proposing nine planetary boundaries based on the key Earth system process of climate change, ocean acidification, stratospheric ozone depletion, freshwater use, land-system change, atmospheric aerosol loading, alteration of biogeochemical (N and P) cycles, and the rate of biodiversity loss as concomitant control variables and thresholds. They argued that transgressing one or more "may be deleterious or even catastrophic due to the risk of crossing thresholds that will trigger non-linear, abrupt environmental change [read ecological regime shift] within continental- to planetary-scale systems." However, for many boundaries, the positioning of the boundary is unclear. The dimension-reduction approach advanced by Jiang et al. (10) provides a means of establishing and studying these boundaries.

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