Rising Variability, Not Slowing Down, as a Leading Indicator of a Stochastically Driven Abrupt Transition in a Dryland Ecosystem

Ning Chen,1,* Ciriyam Jayaprakash,2 Kailiang Yu,3 and Vishwesha Guttal4,*

1. School of Life Science, Lanzhou University, No. 222, Tianshui Road, Lanzhou, Gansu 730000, China; and Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, No. 320, Donggang West Road, Lanzhou, Gansu 730000, China; 2. Department of Physics, Ohio State University, Columbus, Ohio 43210; 3. Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia 22904; 4. Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, Karnataka 560012, India

Submitted August 29, 2016; Accepted July 18, 2017; Electronically published November 29, 2017

Online enhancements: appendices, R code. Dryad data: http://dx.doi.org/10.5061/dryad.gg1fk.

Abstract: Complex systems can undergo abrupt state transitions near critical points. Theory and controlled experimental studies suggest that the approach to critical points can be anticipated by critical slowing down (CSD), that is, a characteristic slowdown in the dynamics. The validity of this indicator in field ecosystems, where stochasticity is important in driving transitions, remains unclear. We analyze long-term data from a dryland ecosystem in the Shapotou region of China and show that the ecosystem underwent an abrupt transition from a nearly bare to a moderate grass cover state. Prior to the transition, the system showed no (or weak) signatures of CSD but exhibited expected increasing trends in the variability of the grass cover, quantified by variance and skewness. These surprising results are consistent with the theoretical expectation of stochastically driven abrupt transitions that occur away from critical points; indeed, a driver of vegetation—annual rainfall—showed rising variance prior to the transition. Our study suggests that rising variability can potentially serve as a leading indicator of stochastically driven transitions in real-world ecosystems.

Keywords: early warning signals, critical transitions, stochastic transitions, dryland ecosystems, regime shifts, restoration.

Introduction

Mathematical modeling of complex ecological systems has given rise to the concept of alternative stable states that display contrasting characteristics (May 1977; Strogatz 1994). Alternative states can be maintained by a set of strong positive feedbacks. Models also demonstrate the possibility of abrupt shifts between stable states, often termed catastrophic or critical transitions, even for small changes in a driver value near a threshold or a critical point, where feedbacks maintaining a state are weak (May 1977; Scheffer et al. 2001). Abrupt transitions of ecosystems, such as eutrophication of lakes or desertification of dryland ecosystems, are often accompanied by “hysteresis,” a phenomenon where restoration to a pre-transition state requires substantial reversal in the driver values, far beyond the value at which the transition was precipitated (Knowlton 1992; Blindow et al. 1993; Scheffer et al. 2001; Schröder et al. 2005; Suding and Hobbs 2009; Staver et al. 2011). Due to hysteresis, abrupt ecosystem transitions can be irreversible on human timescales, posing enormous challenges for restoration of degraded ecosystems (Suding et al. 2004; Suding and Hobbs 2009). Therefore, recent studies have focused on developing general tools for measuring resilience (or lack thereof) and forecasting impending transitions even when we may have limited information on the underlying processes driving transitions (Wissel 1984; Ives 1995; Scheffer et al. 2009). Empirical validations of such tools for abrupt transitions in ecosystems in the field remain a challenge because transitions happen over long timescales (e.g., decades), drivers of transitions are poorly understood, and stochastic environmental factors potentially confound analysis (Suding et al. 2004; Scheffer et al. 2009; Suding and Hobbs 2009; Boettiger and Hastings 2012a; Clements et al. 2015).

Tools for measuring the loss of resilience of ecosystems are derived from dynamical systems theories that make the following general prediction: as the system approaches a critical point, perturbations to the system decay slowly. Thus, it takes longer to return to its original or an equilibrium state than when it is far from the critical point, a phenomenon called critical slowing down (CSD; Wissel 1984; Strogatz 1994; Van Nes and Scheffer 2007). Consequently, the state of the system is similar to its earlier state, resulting in increased tem-
poral autocorrelation and an increase in low-frequency fluctuations (called spectral reddening); these measurable properties of the dynamics of the system are considered to be key signatures of CSD (Wissel 1984; Kleinen et al. 2003; Van Nes and Scheffer 2007; Scheffer et al. 2009; Lenton 2013). A system that takes long to return to equilibrium is relatively more vulnerable to external perturbations, resulting in increased variance in the state variable (Carpenter and Brock 2006). Theory also suggests that the variability is skewed in the direction of transition, resulting in increased skewness of the state variable (Guttal and Jayaprakash 2008). These latter two metrics, variance and skewness, do not directly measure dynamics of the slowdown. Rather, they measure consequences of CSD through fluctuations in or variability of the state variables. Hence, we refer to variance and skewness as variability metrics. Put simply, the theory of critical transitions makes a counterintuitive prediction that both autocorrelation and variability of the state variable will increase near a critical transition. This would not be true for an arbitrary stochastic dynamic, and hence the trends in these metrics can be used as leading indicators of abrupt transitions.

Empirical studies of laboratory microcosm populations and controlled experiments in aquatic field systems have shown that critical transitions can be preceded by the theoretically suggested statistical indicators (Drake and Griffen 2010; Carpenter et al. 2011; Dai et al. 2012). These studies offer a promise that CSD-based metrics can act as early warning signals of abrupt critical transitions, with potential for applications in many real-world complex systems. Recent studies have tested the validity of CSD-based metrics using climate and ecological field data (Dakos et al. 2008; Wang et al. 2012; Batt et al. 2013; Helley et al. 2013; Lenton 2013; Burthe et al. 2016; Sommer et al. 2017). However, environmental stochasticity, which often plays a key role in the dynamics of ecosystems, can confound statistical detection of these metrics. Indeed, it is known that environmental stochasticity can drive abrupt transitions (referred to as stochastic transitions) even when the system is away from a critical point (Horsthemke and Lefever 1984; D’Odorico et al. 2005; Guttal and Jayaprakash 2007; Ives et al. 2008; Ditlevsen and Johnsen 2010; Ridolfi et al. 2011; Sharma et al. 2015). There are conflicting views on whether stochastic transitions can be anticipated by early warning signals (Guttal and Jayaprakash 2008; Ditlevsen and Johnsen 2010; Perretti and Munch 2012; Boettiger and Hastings 2013; Drake 2013).

Dryland ecosystems are strongly influenced by seasonal and stochastic factors and are globally threatened as a result of changes in human land-use patterns and increasing variability in weather due to global climate change (Reynolds et al. 2007; IPCC 2014). Dryland ecosystems, for which the vegetated and desert states (with low density of vegetation) are hypothesized to be alternative stable states (Rietkerk et al. 2004; D’Odorico et al. 2007), offer a classic example of abrupt transition. Here, vegetated states rapidly transform to a state with a severe reduction in the density of vegetation and productivity, a process often described as “desertification.” The reversal of desertification to a vegetated state can also be abrupt. Thus, it is important to identify leading indicators of transitions in dryland ecosystems, to assess the imminence of the collapse of a vegetated state, and to assess the efficacy of restoration efforts in pushing the system toward a “reverse transition” (i.e., restoration causing a transition from a degraded to a healthy state). However, empirical validation of leading indicators for ecosystems in which stochasticity plays a key role in general—and for dryland transitions in particular—is lacking because timescales of such state transitions range over several decades (Barbier et al. 2006; Li et al. 2007; Bestelmeyer et al. 2013; Ratajczak et al. 2014).

Here, we examined whether the proposed leading indicators of abrupt transitions exhibited theoretically expected trends in long-term data from a dryland ecosystem in the Shapotou region at the southeastern fringe of the Tengger Desert in China. In this ecosystem, a revegetation project involving shrub planting and metal fencing of borders was conducted in 1956. After more than 3 decades, the system underwent an ecological transition from a nearly bare state to a moderate grass cover state (Li et al. 2007, 2014). Simple mathematical models do not distinguish transitions from a healthy to a degraded state and a reverse transition since either type of transition corresponds to a bifurcation point in mathematical models. Therefore, we hypothesized that key measures of CSD, increasing autocorrelation and increased low-frequency fluctuations, in the temporal dynamics of grass cover could precede this abrupt transition. We also expected that the variability, as quantified by variance in and skewness of the probability distribution of state variables, would increase, as predicted by theory. Surprisingly, our analyses showed that the system exhibited weak or no signatures of CSD; nevertheless, they showed theoretically expected increasing trends in variability metrics. We explain these unexpected results using the framework of stochastic transitions, where large random fluctuations in the driver can induce a transition from one state to another even if the system is not in the vicinity of a critical point. Indeed, our analyses confirmed the presence of increasing fluctuations in one driver of vegetation, annual rainfall. Finally, we discuss the implications of our results for interpreting trends (or lack thereof) of CSD, indicators of stochastic transitions, and how these indicators can be employed to assess changes of state in ecosystems.

Material and Methods

Site Information

Our study site was in the Shapotou area, located at the southeastern fringe of the Tengger Desert (37°28’07”N, 105°00’06”E;
Before 1956, natural vegetation coverage was below 1%, with sandy-soil specialists, known as psammophytes (*Hedysarum scoparium* Fisch. and *Agriophyllum squarrosum* Moq.), as the dominant native species. To protect the Baotou-Lanzhou railway from wind erosion and sand burial in this desert region, a 16-km-long sand-binding vegetation protective system was built along the railway in 1956 by the Chinese Academy of Sciences and the Department of Railways (fig. 1A; Shapotou Desert Research and Experiment Station 1991). Metal fences were built on both borders of the revegetation ecosystem (the gray zone surrounding the railway in fig. 1A). Straw checkerboards of size 1 m × 1 m were established (15–20 cm above the ground) widely over the entire area with wheat or rice straw as mechanical obstacles to reduce wind velocity and further erosion. Within each straw checkerboard, 2-year-old xerophytic shrubs (*Artemisia ordosica* Krasch., *Caragana korshinskii* Kom., and *H. scoparium*) were planted. No further interventions (such as planting, grazing, fire, etc.) were done after these initial manipulations. Straw checkerboards were eventually grown over by vegetation.

After several decades, the ecosystem over the entire revegetation area (i.e., 16 km × 500 m) changed from the bare state to a moderately vegetated desert state in which shrubs, grasses, and biological soil crust covered about 10%, 35%, and 55% of the surface area, respectively (Li et al. 2014). More information about the revegetation project and the ecosystem, including details on the abiotic variables, are available in Shapotou Desert Research and Experiment Station (1991) and Li et al. (2014).

**Grass Cover and Rainfall Data**

The time-series data for the average annual grass cover, consisting of *Eragrostis minor* Host, *Salsola ruthenica*, and *Corispermum declinatum* as dominant species, from 1957 to 2015 (59 data points) were obtained from the Shapotou Station Chinese Ecosystem Research Network database (Chen et al. 2017). To monitor the revegetation of this dryland ecosystem, 10 permanent plots (10 m × 10 m), whose locations were determined randomly in the revegetation belt, were established in 1956 (fig. 1A). Because shrubs were manipulated directly in the initial years of the revegetation project, we selected grass cover as the ecosystem response variable. Within each of the 10 plots, five quadrats (1 m × 1 m) were randomly selected, and multiple investigators estimated grass cover over the monitoring period using consistent methods (Li 2005). For reasons unknown to us, the monitoring of the set of plots described above was discontinued in 2005. The data after 2005 (collected using the same survey method) were from a different set of plots of the same dimensions within the same study area (fig. 1A); all of these new plots were located within 50–200 m of the original plots. We had access only to the average of the grass cover of all replicates (Li 2005; Li et al. 2014), that is, not to individual/quadrat-level data. The time series for annual rainfall was obtained from the Shapotou Meteorological Station (Chen et al. 2017). Missing values in the time series of rainfall data (i.e., years 1962–1964 and 1968–1979) were substituted from a nearby weather data collection center (about 18 km away). Data on the time series of grass cover and annual rainfall are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.gg1fk (Chen et al. 2017).

**Detecting Alternative Stable States and Abrupt Transitions**

We considered grass cover as the state variable in our system. A statistical detection of an abrupt transition is a prerequisite to testing whether leading indicators occurred before the transition (Scheffer et al. 2001; Andersen et al. 2009). Therefore, motivated by mathematical theories (Strogatz 1994; Scheffer and Carpenter 2003), we checked for the following quantitative evidence, all of which are consistent with an abrupt transition: (a) systems exhibiting abrupt transitions are likely to show alternative stable states, which can be quantified by multimodality in the frequency distribution of the specified state variable (Scheffer et al. 2001; Hirota et al. 2011); (b) abrupt transitions lead to a sudden change in the dynamics of the state variable (Seddon et al. 2014); and (c) a state variable can take multiple values, corresponding to different stable states, for the same value of the driver. Hence, the relationship between the driver and the state variable exhibits no clear patterns if we do not account for abrupt transitions. However, we expect the relationship between the driver and the state variable to change in a threshold fashion, reflecting an abrupt transition (Scheffer and Carpenter 2003; Ratajczak et al. 2014).

First, to check whether the system exhibited a single stable state or alternative stable states, we tested whether the frequency distribution of grass cover was unimodal or multimodal. We used a hierarchical clustering method, using the package mclust in R (R Core Team 2015), to fit models with one, two, or three modes. We calculated the Bayesian information criterion (BIC), the Akaike information criterion (AIC), and the integrated completed likelihood (ICL) criterion to find the best-fit model. As a test of the robustness of these results, we employed a latent class analysis (Hirota et al. 2011), which is a generic method to test whether the data follow a mixture of regression models, including a mixture of multiple non-Gaussian modes in data. Here too we used the AIC, the BIC, and the ICL criterion to find the best-fit model.

Second, to check whether the system showed evidence for an abrupt transition from a low to a higher grass cover state, we tested whether the growth rate of grass cover (state variable) suddenly increased. A sudden increase in growth rate implies an accelerated growth of grass cover, thus capturing
threshold effects associated with abrupt transitions. We quantified the growth rate by the slope of the moving-window average of the grass cover; the average was computed over a 10-year window weighted by a Gaussian kernel. When the slope exceeds a baseline range of slopes, we consider that to be a quantitative measure of sudden change, potentially indicating a transition. We set the baseline range to be equal to the mean plus 1 standard deviation of the moving-window slopes over the entire time series.

Third, we tested the relationship between a driver (annual rainfall) and the state variable (grass cover) in this ecosystem. Previous studies suggest that key drivers of vegetation in dry-
land ecosystems include rainfall, fire, grazing, and so on (Schaefer et al. 2001; Hirota et al. 2011; Staver et al. 2011; D’Odorico et al. 2012; Bestelmeyer et al. 2013; Ratajczak et al. 2014; Chen and Wang 2016). After the initial manipulation event, the ecosystem under study was shielded from grazing, fire, and other anthropogenic influences (Shapotou Desert Research and Experiment Station 1991). Consequently, we chose one potential driver of vegetation, annual rainfall, a limiting resource in arid ecosystems and an important driver of vegetation cover across various vegetation biomes (Rietkerk et al. 2002; Hirota et al. 2011; Staver et al. 2011). We considered the following class of models to test the rainfall–grass cover relationship: a simple linear model (using the gls function in the stats package in R ver. 3.2.3) that includes the possibility of no relationship (i.e., a null model), a generalized additive model (GAMM) that accounts for nonlinearities (we used the gamm function in the mgcv package since gamm allows us to account for autocorrelations in data), and a threshold generalized additive model (TGAMM) that accounts for a threshold relationship (Ciannelli et al. 2004; R Core Team 2015). We used the default options of gamm with spline smoothing and temporal autocorrelation at lag 1 for the correlation structure. A TGAMM is built as a superposition of two plain GAMMs, one of which is a best-fit GAMM for the time window from year 1 to year $T$ and the other is a best-fit GAMM for the window from $T + 1$ to the last year in which data are available; the year $T$ is called the threshold year. We also constructed a linear model in which the relationship between rainfall and grass cover changes in a threshold fashion after year $T$ (see app. A and R code; apps. A–E and R code are available online) for further details of implementation.1 To compare goodness of fit between the linear models (i.e., with or without a threshold behavior), GAMM, and TGAMM, we employed genuine cross validation (gCV). If a TGAMM is the best fit among these models for our data, it suggests that the rainfall–grass cover relationship changes in a threshold-like fashion, exhibiting qualitatively different dynamics as a function of time, analogous to a regime shift (Czepluch and Carpenter 2003; Bestelmeyer et al. 2011; Vasilakopoulos and Marshall 2015).

On the basis of the analyses described above, we obtained the location of the “onset of the transition” in grass cover using two methods: (1) the year in which the growth rate or slope of a moving-window average of the grass cover changed suddenly and (2) the threshold year in the TGAMM of the driver–response relationship (Ratajczak et al. 2014; Seddon et al. 2014; Vasilakopoulos and Marshall 2015). Methods 1 and 2 offer independent criteria to determine the thresholds of abrupt transitions in the grass cover dynamics. To reduce the possibility of false detections, we required a simultaneous detection of thresholds in both of these metrics and use the threshold to be the year of the onset of the grassland transition. Further details on detecting sudden changes are presented in appendix A.

**Leading Indicators of Abrupt Transitions**

We computed the following four leading indicators of critical transitions (Scheffer et al. 2009): autocorrelation function at lag 1 (ACF), spectral density ratio (SDR), standard deviation (SD), and skewness (SK). For autocorrelation, we chose a 1-year lag since statistical significance typically declines at higher lags. SDR is a measure of the spectral properties of the state variable: models show that CSD causes the spectral function of the state variable to exhibit a pronounced increase near low frequencies, termed spectral reddening (Carpen
ter and Brock 2006; Gutal and Jayaprakash 2008). It can be shown mathematically that spectral reddening is equivalent to increasing autocorrelation. In real data, however, the structure of noise, sampling frequency, and errors ensure that spectral properties may sometimes offer better statistical signatures of regime shifts (Kleinen et al. 2003; Biggs et al. 2009), despite their mathematical equivalence. Therefore, we measure both ACF and SDR for grass cover data and call them signatures or measures of CSD. As described in the introduction, the variability metrics SD and SK, although derived from CSD for critical transitions, are not measures of dynamical slowing down. A few empirical studies have employed the coefficient of variation (CV), defined as the ratio of the SD to the mean, as a leading indicator of transitions (Drake and Griffen 2010; Dai et al. 2012). Although the SD is expected to increase prior to critical transitions, the mean of the state variable can increase or decrease depending on the system. Thus, there is no general theoretical expectation for trends in the CV prior to a critical transition. Hence, we did not use the CV as an indicator for our analysis.

Methods and procedures used to calculate the leading indicators were adopted from Dakos et al. (2012). We first chose a rolling window of size 13 years (for exploration of wider range of values, see “Sensitivity Analysis”). Grass cover data were detrended with Gaussian filtering (bandwidth, 10 years) within a rolling window before computing indicators. Three of these indicators—ACF, SD, and SK—were computed using the R package earlywarnings (Dakos et al. 2012; R Core Team 2015). SDR was calculated as the ratio of the average spectral density at low frequencies (0–0.125 per time window) to that at high frequencies (0.375–0.5 per time window); spectral density was computed as the absolute value of the Fourier transform of the rolling window, using the functions abs and fft in R software, respectively. We then moved the rolling window by 1 year, detrended the data, and computed all four indicators again until we reached the onset of the grassland tran-

---

1. Code that appears in The American Naturalist is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.
sition, as described in "Detecting Alternative Stable States and Abrupt Transitions."

Trends in the Leading Indicators of Abrupt Transitions

According to theoretical predictions, the signatures of critical transitions should be found in the years immediately preceding the transition. Theory makes no predictions about how these indicators behave after the transition because the ecosystem would have reached a different stable state that is stabilized by an entirely different set of mechanisms and positive feedbacks. Moreover, our aim is to test whether these metrics offered signals indicative of a transition before the transition occurred. Therefore, we restricted our analysis of trends in indicators to the years preceding the transition; the onset of the transition was determined by the analysis in "Detecting Alternative Stable States and Abrupt Transitions."

We measured the strength of trends in each of the indicators in the rolling window prior to the grassland transition. To quantify the strength, we chose the nonparametric Kendall's $\tau$ correlation coefficient, which measures the degree of similarity in the rankings of different variables. A positive (negative) Kendall's $\tau$ value indicates an increasing (decreasing) trend in that indicator. To test the statistical significance of these trends, we compared the trends obtained in the real data with the trends in indicators from two different null models, described below, in which observed trends in indicators are due to chance alone; therefore, they serve as baselines for trends in indicators (Boettiger and Hastings 2012b; Dakos et al. 2012).

The first null model is obtained by fitting the grass cover time series prior to the grassland transition to a linear autoregressive moving average (ARMA) model (Dakos et al. 2012); this model assumes a stationary data set with no impending transition, and therefore the trends in indicators in this null model will be due to chance alone. We simulated the fitted model to generate 1,000 synthetic time series, each of which had the same length as the grass cover data. We estimated all indicators and the corresponding Kendall's $\tau$ for each of the synthetic data sets. We obtained a $P$ value for each indicator, denoted $P_{\text{sim}}$, defined as the number of synthetic data sets whose positive (negative) Kendall's $\tau$ was equal to or smaller (larger) than that of the simulated data sets. A small $P$ value indicates that the ARMA-based null model is unlikely to produce trends in indicators observed in the real data. We set a threshold of .05 for $P$ values to conclude that the trends in indicators were statistically significant, whereas $P$ values in the range of [0.05–0.1] were considered marginally significant.

Our second null model was derived from bootstrapping, in which we generate synthetic data sets by drawing data from the grass cover time series prior to the grassland transition in random order but with replacement; this method uses data points from the original time series but destroys any temporal pattern in them. Therefore, we expect that the trends in indicators of such time series arise due to chance alone. We generated 1,000 bootstrap data sets and computed trends in each indicator for each of the data sets. We quantified and interpreted $P$ values, denoted $P_{\text{boot}}$ as in the previous null model method.

Finally, we compared the joint strengths of signatures of CSD (ACF and SDR) with the joint strength of variability-based metrics (SD and SK; Conover and Iman 1981; Clarke 1993). To do so, we employed structural equation modeling using the package lavaan in R. We rank transformed the indicator data and created a latent variable to capture the joint response of CSD (or variability) by integrating ACF and SDR (SD and SK). Using the sem function, we extracted the regression coefficient and AIC values of both joint CSD and joint variability metrics. We selected the latent variable with the larger regression coefficient as showing stronger trends and the one with a lower AIC to be the better model fit. See appendix B for more details.

Mathematical Model of Catastrophic Transitions with Noise

We employed a simple model of catastrophic transitions with noise to contrast leading indicators of (i) critical transitions that occur near critical points and (ii) stochastic transitions that occur away from critical points. The prototypical model of catastrophic transitions is given by Strogatz (1994):

$$\frac{dx}{dt} = rx - x^3 + h + \sigma \eta(t),$$

where $x$ is a state variable driven by the external variable $h$, $r$ represents the growth rate of the state at low densities, and the term $\eta(t)$ captures stochasticity in the driver $h$. We model $\eta(t)$ as a Gaussian white-noise process with mean 0 and SD unity (i.e., $\langle \eta(t)\eta(t') \rangle = \delta(t - t')$), whereas the coefficient $\sigma$ represents the strength of the noise. For $r > 0$, the deterministic model exhibits a region of bistability; that is, a system can be in two alternative states depending on the initial conditions. For analyzing transitions, we turn on the noise term in the model. For critical transitions, we start in the lower stable branch and increase $h$ deterministically toward the bifurcation point. For a stochastic transition induced by a large but constant noise, we assume a large value of $\sigma$ and wait for a transition from the lower to the upper branch. For a stochastic transition induced by increasing noise, we deterministically increase $\sigma$ from low to high values. See appendix C for further details.

Analysis of Variability in Rainfall

To investigate the possibility that increasing variability in a driver may be one of the causes of the abrupt transition
in grass cover, we computed the trends in SD in the time series of rainfall in the years preceding the transition. We used the same parameter values of the rolling window and bandwidth for detrending the data as we did for grass cover analysis. To measure the strength of the trends over time and their statistical significance, we computed the nonparametric Kendall’s τ correlation coefficient and used the two null models described in “Leading Indicators of Abrupt Transitions.” A statistically significant and increasing trend for the SD in precipitation prior to transition would support the hypothesis that increasing variability in rainfall may be one of the causes of the abrupt transition from a low to a high grass cover state.

**Sensitivity Analysis**

To test the sensitivity of our results to changes in the location of quadrats in the year 2006, we redid all of the above-described analyses for years 1–49, thus considering only the initial set of quadrats. To test the sensitivity of leading indicators to the size of the rolling window and filtering bandwidths, we reestimated the strength of trends in all four indicators under various combinations of rolling window sizes and filtering bandwidths (both ranging from 5 to 20 years with an increment of 1 year). To account for the uncertainty in the location of the onset of the transition, we redid the analysis of leading indicators assuming the year of transition to be ±2 years of the threshold year detected in “Detecting Alternative Stable States and Abrupt Transitions.”

**Results**

**Multimodality and an Abrupt Transition in Grass Cover Dynamics**

Quantitative analysis of the frequency distribution of grass cover suggested that low and moderate grass cover states are alternative stable states in this dryland ecosystem. Specifically, we found that grass cover exhibited a bimodal frequency distribution (fig. 1C), with two modes at covers of 11.5% and 40.9% based on the hierarchical mixture model. The latent class analysis also suggested a model with two clusters (see table A1; tables A1–A3, B1, B2, D1–D3 are available online).

Our analysis supports the hypothesis that the system underwent an abrupt transition from a low to a moderate grass cover state: grass cover began to increase rapidly in year 38, as quantified by the sudden increase in the growth rate (or slope of temporal dynamics) of grass cover above baseline levels from the year 38 after revegetation (fig. A1; figs. A1, A2, D1–D5, E1 are available online). This phase of increased growth rate lasted from year 38 to year 44. The growth rate returned to baseline levels by year 47, by which time the grass cover had reached around 40%. We color-coded frequency bars in the histogram (fig. 1C) on the basis of the distinction of pretransition years (red; up to year 37) and later years (blue; beyond year 37). This graph suggests a “temporal partitioning” of modes; that is, the low grass cover state occurs in pretransition years, whereas the moderate grass cover state occurs mostly in later years, consistent with an abrupt state transition.

Analysis of the relationship between annual rainfall and grass cover suggested a threshold behavior, with the best-fit model being a TGAMM (fig. 1D), providing further evidence for the occurrence of a regime shift in our data (the gCV of the TGAMM was lower than that of both the GAMM and the linear model; see tables A2, A3). The best-fit TGAMM predicted the threshold year (the year during which the relationship between rainfall and grass cover underwent a sudden change) to be either 38 or 43. On the basis of the criterion of simultaneous detection of sudden change from the analysis of growth rate and TGAMM, we identified year 38 as the onset of the abrupt transition (figs. 1B, A2), referred to as “grassland transition” in the rest of the article.

These results largely hold true even if we consider data only up to 2005 (see figs. D1–D3; tables D1, D2), the year in which the original plots were discontinued and new sets of plots were added to the study.

**Lack of CSD with Rising Variability prior to Grassland Transition**

We found a lack of statistically significant trends in the ACF and SDR prior to the onset of the grassland transition (i.e., up to year 37). Specifically, the ACF of the residual data exhibited a weakly visible increasing trend (fig. 2A; Kendall’s τ = 0.55), but it was not statistically significant (P_{arma} = .15, P_{boot} = .11). Similarly, the SDR exhibited a weak increasing trend (fig. 2B; Kendall’s τ = 0.32), but this too was not statistically significant (both P_{arma} and P_{boot} = .11; table D3).

In contrast to the dynamical indicators (CSD) of abrupt transitions, the variability metrics SD and SK displayed statistically significant increasing trends with the impending onset of the grassland transition. Specifically, the SD showed strong increasing trends (fig. 2C; Kendall’s τ = 0.95), and this trend was statistically significant (P_{arma} = .003, P_{boot} = .001). The trend in SK was also strong (fig. 2D; Kendall’s τ = 0.76) and was statistically significant (P_{arma} = .01, P_{boot} = .02). The joint response of the variability metrics SD and SK (regression coefficient = 0.992, P < .001; AIC = 270) was also substantially higher than that of the signatures of CSD (ACF and SDR; regression coefficient = 0.651, P < .210; AIC = 338.5; table B2).

Sensitivity analyses revealed that the conclusions described above about the lack of (or weak) signatures of CSD and clear trends in rising variance and skewness were largely robust to changes in rolling window size and the bandwidth of detrending (fig. D4). Kendall’s τ for trends in variance and skewness was largely positive and skewed toward higher val-
ues across parameter scans, supporting the conclusion that these indicators showed increasing trends. Kendall’s $\tau$ for ACF and SDR were relatively broadly spread out, ranging from negative to positive values but with a visually observable bias toward positive values, suggesting that there was either no or rather weak evidence for signatures of CSD.

Finally, we found that the results presented above were not sensitive to the uncertainty in the location of the onset of the transition (table D3).

**Stochastic Origin for the Abrupt Transition Suggested by Theory**

To interpret the results described above, we analyzed a prototypical model of catastrophic transitions (Strogatz 1994) with stochasticity (see “Material and Methods”). Consistent with previous studies, our results showed, as expected, that all four standard indicators exhibit characteristic increasing trends prior to critical transitions (see the left column of fig. 3 and app. B for analytical formulas). If the abrupt transition was driven by a large but constant strength of stochastic fluctuation (Horsthemke and Lefever 1984; Scheffer et al. 2001; Guttal and Jayaprakash 2007; Scheffer et al. 2009; Ditløven and Johnsen 2010; Ashwin et al. 2012), we do not expect any leading indicators of abrupt transition (fig. 3, middle column; Boettiger and Hastings 2013; Guttal et al. 2016). If, however, we drive the model with stochastic noise and increase the strength of the noise, we observe a stochastically driven abrupt transition (fig. 3, right column; Ditløven and Johnsen 2010; Guttal et al. 2016). In this case, as the variability in the external driver gradually increases with time, the temporal dynamics of the state variable exhibits increased variance and skewness, with no trends in autocorrelation and spectral reddening (fig. 3, right column). This last scenario is exactly as we have found in our empirical analysis of grass cover (fig. 2). Therefore, we hypothesized that increasing
stochasticity in an underlying driver of grassland state could have been one of the causes of the grassland transition.

Increasing Fluctuations in Rainfall prior to Grassland Transition

On the basis of the data analyses and model investigations described above, we expected that rainfall, one of the drivers of grass cover, should have exhibited increased SD prior to the onset of the grassland transition that was detected in year 37. Indeed, our analysis of the time series of rainfall (fig. 4A) showed relatively strong trends toward increasing variability (Kendall’s $\tau = 0.74$) prior to the grassland transition (fig. 4B). The trend was statistically significant, with a $P$ value generated by the bootstrap method of .045. A sensitivity analysis showed that Kendall’s $\tau$ was positive for a wide range of...
Dashed line denotes the average value for annual rainfall during the growing and the bandwidth of detrending. Trends to changes in the choice of parameter values of the rolling windows from earlier years. See figure D5 for the robustness of these trends to changes in the choice of parameter values of the rolling window and the bandwidth of detrending.

rolling windows and bandwidth of detrending (fig. D5). Thus, we conclude that there is plausible evidence for an increasing trend toward variability in rainfall prior to the onset of the grassland transition.

Discussion

Our analysis of a long-term data set from a dryland ecosystem demonstrated an abrupt “reverse” transition from a poorly vegetated state to a state with moderate grass cover. We found the surprising result that there was no (or weak) evidence for CSD, an empirically tested key signature of critical transitions. However, we found clear trends toward rising variability, as quantified by increasing values of variance and skewness, in the temporal dynamics of grass cover prior to the transition. We argue that the observed shift in grass cover is consistent with a stochastic transition driven by increasing fluctuations in the annual rainfall even though the system is not in the vicinity of a critical point. This study is in contrast to previous studies that focused on critical transitions that occur near a deterministic critical point with little stochasticity. Our study suggests that measures of rising variability, not dynamical slowing down, serve as leading indicators of certain types of stochastically driven abrupt transitions in real ecosystems.

Leading Indicators and Stochastic Transitions in Ecosystems

A major challenge associated with observing state transitions in field systems, such as dryland ecosystems, is that the timescales of transitions can be long (e.g., decades to centuries; Scheffer et al. 2001; Li et al. 2007; Bestelmeyer et al. 2011), thus posing difficulties in testing predictions of mathematical theories (Clements et al. 2015). Our analysis of a 59-year data set from the Shapotou region, on the basis of which previous studies had suggested that the system had undergone a “regime shift” to a moderately vegetated desert state, offered an excellent opportunity to investigate a reverse ecological state transition. We argue that the ecological management of this ecosystem in the initial years of the study (see “Material and Methods”) does not affect our interpretation of the occurrence of abrupt transitions or of its leading indicators for the following reasons. First, the system was left with no anthropogenic disturbances for more than 5 decades after the initial one-time event of manipulation (see Li et al. 2014). Second, the grass cover itself did not change dramatically after the manipulation. Rather, the onset of the transition in grass cover occurred 3 decades after the initial experimental manipulation. Furthermore, our interpretations of the abrupt transition and leading indicators are based on the dynamics of grass cover and rainfall over 3–5 decades. Hence, it is unlikely that the transition and the leading indicators are a consequence of the sudden initial change in external conditions alone (fig. E1; also see app. A). Instead, it is likely that driver (rainfall) stochasticity and internal feedback mechanisms have both played a role in the dynamics of abrupt transitions (see also “Rainfall Stochasticity and Mechanisms of Grassland Restoration” below).

Various studies have argued that CSD could be used as a generic indicator of impending regime shifts (Wissel 1984; Van Nes and Scheffer 2007; Dakos et al. 2008; Scheffer et al. 2009; Dai et al. 2012). Much of the focus of research on abrupt shifts has been on critical transitions in which systems at a tipping or critical point abruptly switch from one state to another, even for small changes in the drivers. However, it is known that large stochasticity in environmental factors can cause abrupt shifts, known as stochastic transitions, even when the system is far away from a critical point (Horsthemke and Lefever 1984; Guttal and Jayaprakash 2007; Scheffer et al. 2009; Ditlevsen and Johnsen 2010; Ashwin et al. 2012). Our conclusions on indicators of stochastic transitions are con-

Figure 4: Increasing fluctuations in annual rainfall prior to the onset of the grassland transition. A, Time series of annual rainfall. The dashed line denotes the average value for annual rainfall during the period 1957–2015. B, Trends in the standard deviation (SD) in rainfall. The red arrow indicates the size of the rolling window (13 years) used in the calculation of trends; $P_0$ is a $P$ value based on comparison to trends in a synthetic time series generated by bootstrap iterations (5,000). For both A and B, data points comprising the black solid line, determined by the size of the rolling window, are used to quantify the trend (Kendall’s $\tau$) of SD in rainfall; the gray solid line shows data points from earlier years. See figure D5 for the robustness of these trends to changes in the choice of parameter values of the rolling window and the bandwidth of detrending.
sistent with recent results in widely different systems (Ditlev- sen and Johnsen 2010; Wang et al. 2012; Benedetti-Cecchi et al. 2015; Guttal et al. 2016). For instance, an experimental study demonstrated that variance, rather than autocorrelation (CSD), was a better indicator of microbial populations undergoing regime shifts driven by stochasticity (Benedetti-Cecchi et al. 2015). Variability-based indicators have also been shown to perform well as early warning signals when systems flicker between alternative states before undergoing a regime shift (Wang et al. 2012). Another study argues that financial markets do not show CSD either but exhibit clear trends toward rising variability prior to crashes (Guttal et al. 2016). Stochastic transitions, which have received less attention in the literature, may occur frequently in complex real systems. Our study alerts us to the possibility that even if CSD indicators do not show a trend, evidence of increased variability may possibly indicate an impending transition in the ecological state if a concomitant analysis of the driver time series also shows rising variability.

Boettiger and Hastings (2012b) argue that post hoc analyses of real-world data, testing for the occurrence of a specific pattern, are prone to increased rates of false positives due to a statistical bias called the prosecutor’s fallacy (Thompson and Schumann 1987). Translated into our case, it emphasizes exercising care in distinguishing the probability of finding a stochastic transition (equivalent of guilty in a legal scenario) given the results of our time series (i.e., the evidence) from the probability that the transition is not stochastic (innocent) given our results (the evidence). Although the former probability is expected to be small, the latter, which is equivalent to the rate of false alarms, can be relatively large; this can result in wrong categorization of a nonstochastic transition as a stochastic transition. In other words, is the evidence we found (i.e., a lack of CSD with increasing variability) sufficient to conclude that this system exhibited stochastic, but not critical, transition? The answer to this question depends on the rate of false negatives of indicators in true critical transitions and the rate of false positives in stochastic transitions. In addition to this issue, time-series field data are beset with the usual difficulties of reduced statistical significance due to a lack of resolution of sampling, errors in sampling, and limited data, which can all potentially confound our inferences (Bestelmeyer et al. 2011; Boettiger and Hastings 2012a, 2012b; Perretti and Munch 2012; Clements et al. 2015). Although conducting controlled studies with multiple replicates can help resolve such statistical issues, ecosystem managers often need to assess risks of transitions for a specific ecosystem based on single-sample and short-duration data, similar to what we have analyzed. In our study, to minimize statistical biases and to enhance the robustness of our results, we used a preset criterion for signaling indicators based on whether such signals can arise by chance alone (Dakos et al. 2008, 2012) and conducted thorough sensitivity analysis of parameter values. On the basis of these, we found the trends toward rising variability and the lack of (or weak) trends in CSD prior to the grassland transition to be consistent with a stochastically driven regime shift.

Rainfall Stochasticity and Mechanisms of Grassland Restoration

Previous studies in our dryland ecosystem of the Shapotou region have shown that the initial manipulation involving shrub planting reduced the erosion of soil by winds and water and thus played an important role in the process of restoration (Shapotou Desert Research and Experiment Station 1991; Li et al. 2007, 2014). Shrubs provide conditions for formation of biological crusts, which may increase rainfall infiltration depending on the type of crust and soil (Kidron et al. 2012; Kidron 2015). Shrubs may cause enhanced seed trapping, whereas biocrust can facilitate interactions between grasses and soil microbes by providing increased nitrogen to plants (Chung and Rudgers 2016). Hence, shrubs can set up a positive feedback between vegetation and soil properties, acting as islands of fertility (Rachal et al. 2015). Therefore, the initial restoration effort together with various positive feedback mechanisms were likely crucial in creating conditions necessary for initiating a transition to an alternative state dominated by grasses (Li et al. 2007, 2014). Our analysis does not preclude roles for any of these mechanisms of grassland restoration. Rather, it offers a complementary perspective that rainfall stochasticity has played a role in restoration.

Restoration of degraded ecosystems exhibiting alternative stable states is challenging because the system may show little response to management until it reaches the threshold point of shift (Suding et al. 2004; Palmer et al. 2014). Our work points to an interesting implication for restoration of ecosystems. Stochastic fluctuations, which are inescapable features of ecosystems and, in particular, semiarid ecosystems, can sometimes accelerate such restoration measures by inducing a shift even before a threshold point is reached. This possibility can be tested in real data by analyzing the stochastic variability of putative drivers and correlating them with the dynamics of the leading indicators. Clearly, stochasticity does not always enhance restoration protocols, since it can potentially wipe out small patches of vegetation that are present or introduced in the restoration process. We hasten to add that stochasticity is neither a sufficient nor a necessary condition for a restoration process. Rather, we suggest that rainfall stochasticity may have aided, or even sped up, the restoration in this dryland ecosystem.

Summary and Future Directions

In summary, our analyses of a long-term temporal data set around a regime shift in a dryland ecosystem have offered
insights into the role of stochasticity leading to abrupt transitions in complex systems. We elucidated differences between leading indicators of abrupt transitions arising due to proximity to a critical point and those induced by stochastic fluctuations away from a critical point. Despite the promise offered by early warning signals in a few empirical systems, more work is needed to examine the role of confounding factors and in interpreting trends in indicators of ecological transitions, especially from field systems. Studies show that early warning signals based on spatial metrics can sometimes overcome limitations associated with time-series data analysis, such as the requirement of long-term and finely resolved data (e.g., Rietkerk et al. 2004; Ké et al. 2007; Guttal and Jayaprakash 2009; Ké et al. 2014; Eby et al. 2017). Future research could employ series of spatial patterns over time, which are becoming increasingly available through satellite and aerial imagery, to assess both drivers and resilience of ecosystem states.

Acknowledgments

We thank Hari Sridhar, Krishnapriya Tamma, Vasilis Dakos, Xin Yin, and Zak Ratajczak for helpful comments on the manuscript. We are also grateful to two anonymous reviewers for improving the manuscript. N.C. is supported by the National Natural Science Foundation of China (31700373, 31600332) and the Chinese Academy of Sciences (CAS) “Light of West China” Program. V.G. is supported by the Indian Space Research Organisation (ISRO)–Indian Institute of Science (IISc) Space Technology Cell, the Department of Biotechnology (DBT)–IISc Partnership Program, and the Ministry of Environment, Forest, and Climate Change (MoEF-CC), government of India. K.Y. is supported by Environmental Resilience and Sustainability Fellowships. Author contributions: N.C., V.G., C.J., and K.Y. designed the research; N.C. analyzed the data; V.G. and C.J. analyzed the mathematical model; and N.C. and V.G. wrote the manuscript. All authors contributed to discussions and revisions of the manuscript.

Literature Cited


Shapotou Desert Research and Experiment Station. 1991. Principles and measures for Baotou-Lanzhou railway sand-fixing at Shapotou section. People Press, Yinchuan, Ningxia. [In Chinese.]

References Cited Only in the Online Appendixes

Associate Editor: Tom E. X. Miller
Editor: Judith L. Bronstein