Predicting catastrophic shifts

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HIGHLIGHTS

- Catastrophic shifts pose a threat to ecology, early warning indicators are needed.
- The tools suggested so far are aimed at predicting the tipping point.
- However in spatial system the transition occurs when alternative state invades.
- We suggest a cluster tracking technique to identify imminent shifts on spatial domains.
- This technique also distinguish between smooth and catastrophic transitions.

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ABSTRACT

Catastrophic shifts are known to pose a serious threat to ecology, and a reliable set of early warning indicators is desperately needed. However, the tools suggested so far have two problems. First, they cannot discriminate between a smooth transition and an imminent irreversible shift. Second, they aimed at predicting the tipping point where a state loses its stability, but in noisy spatial system the actual transition occurs when an alternative state invades. Here we suggest a cluster tracking technique that solves both problems, distinguishing between smooth and catastrophic transitions and to identify an imminent shift in both cases. Our method may allow for the prediction, and thus hopefully the prevention of such transitions, avoiding their destructive outcomes.

1. Introduction

The stability of ecosystems, and in particular the response of populations and communities to external perturbations, is one of the main topics in contemporary science (Müller et al., 2010). As an impact of anthropogenic changes (carbon emission, habitat fragmentation, introduction of non-indigenous species and pathogens) reaches the global scale, worries about their potential outcomes are growing (Dawson et al., 2011). Recently, there is an increasing concern about the scenario known as catastrophic regime shift, where a relatively small change in the environmental conditions leads to a sudden jump from one steady state to another (Scheffer et al., 2001, 2012). This change is often irreversible and accompanied by hysteresis: once the system relaxes to its new state, it will not recover even when the environmental conditions are restored.

One of the main topics considered in the context of catastrophic shifts is the possibility of a sudden extinction of populations as the environment varies (Drake and Griffen, 2010; Takimoto, 2009; Peters et al., 2012). For example, changes in solar radiation owing to variations in the Earth's orbit may have triggered the sudden mid-Holocene (5000 yr ago) desertification of the Sahara (Scheffer et al., 2001). The standard model used to describe this phenomenon involves nonlinear dynamics that supports two alternate steady states with a (backward) fold bifurcation (Scheffer et al., 2001; Rietkerk and Van de Koppel, 1997). This mechanism is illustrated in Fig. 1a, in which the various states of the system are shown for different values of the parameter α that stands for environmental *stress* (e.g. grazing, or
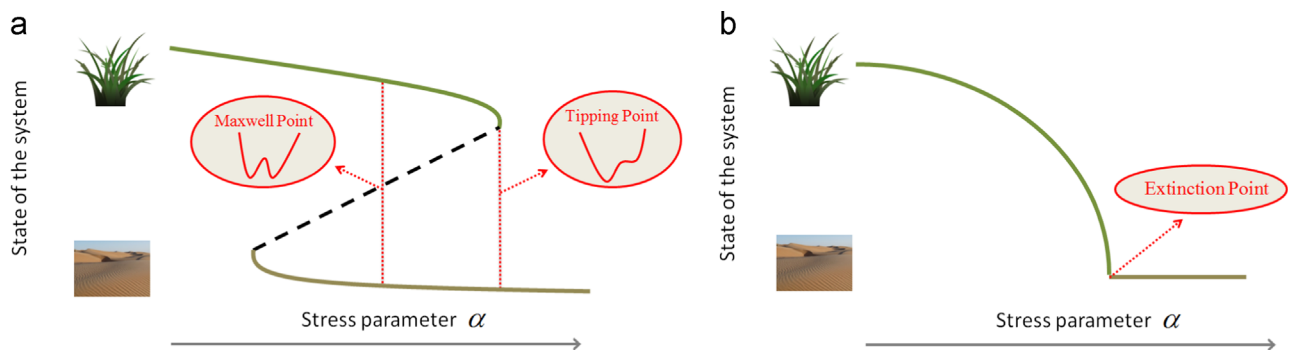
Fig. 1. Catastrophic shift vs. continuous transition. The generic features of a nonlinear system that supports catastrophic shift are illustrated in panel a (left). The two stable state (full lines, here one represents vegetation, the other bare soil) coexist for some region of the stress parameter α. The transition may take place at the tipping point (right dotted line), where the basin of attraction of the vegetation state (corresponding to the right well in the circled cartoon) vanishes, and its attractiveness (the curvature of the well) approaches zero. In spatial systems, on the other hand, large bare-soil clusters will invade vegetation to the right of the Maxwell point (left dotted line), where the stability of both alternate states becomes equal. Under disturbances, the transition takes place at the MP (Bel et al., 2012). A continuous transition scenario is illustrated in panel b (right), where vegetation went extinct as the stress keeps growing. The theory of extinction transitions of this type also suggests diverging spatio-temporal fluctuations at the transition point (Hinrichsen, 2000).

decreased precipitation). For certain values of α the system supports two stable states, one corresponds to vegetation, say, and another to bare soil. This bistability is related to the nonlinearity of the system and reflects a positive feedback mechanism (HilleR-isLambers et al., 2001; Holmgren et al., 1997), such that vegetation grows above some critical density, while below this density the vegetation declines.

For such a system, with positive feedback and alternative steady states, the vegetation collapses from a finite value to zero once α crosses a critical value at the tipping point. Vegetation density by itself provides no indication to the distance of the system from the tipping point, therefore the search for early warning indicators that will allow one to predict an imminent transition has become a major research topic in the last decade.

Most of these efforts were focused on the phenomenon of critical slowing down, i.e., on the diverging sensitivity of the system to external perturbations in the vicinity of a tipping point (Eslami-Andergoli et al., 2014; Scheffer et al., 2009). This feature has, indeed, been demonstrated in recent experiments (e.g. Drake and Griffen, 2010; Dai et al., 2013; Veraart et al., 2012; Carpenter et al., 2011). Basically, the idea is to trace the rates at which the system recovers from spatial or temporal perturbations, and when these rates are becoming slower and slower, this will indicate that the system is approaching catastrophe.

However, a few recent studies cast a severe doubt about the relevance of these indicators to empirical ecological dynamics. First, critical slowing down and its consequences, like fat tailed or skewed patch statistics, do not necessarily indicate a tipping point or a discontinuous transition (Manor and Shnerb, 2008; von Hardenberg et al., 2010; Kéfi et al., 2007, 2010). These features are also a characteristic of continuous transitions, where the system changes its state smoothly and reversibly without any hysteresis (Kéfi et al., 2013; Eslami-Andergoli et al., 2014). A schematic illustration for such a scenario is given in Fig. 1b, where the increase in stress leads to a gradual extinction without bistability. Continuous transitions of this type characterize various generic ecological models, including logistic growth without an Alley effect and the susceptible–infected–susceptible (SIS) model for epidemics. In these cases, and under many other types of dynamics, the transition to extinction as the birth rate decreases is continuous with no sudden jumps, yet the response of the system to external perturbations becomes infinitely slow close to the transition point (see, e.g., Kessler and Shnerb, 2007; Kessler et al., 2008). A few recent studies, showing a non-hysteretic recovery from desertification when the external pressure (grazing, in most

cases) has been removed (Fuhlendorf et al., 2001; Rasmussen et al., 2001; Valone et al., 2002; Zhang et al., 2005; Allington and Valone, 2010), also suggest that the transition is, at least in some cases, continuous and reversible.

Another line of criticism has to do with the effects of systems' spatial structure. When a system admits two stable states, local disturbances and fluctuations often generate patches of an alternate states, like regions of bare soil surrounded by vegetation and vice versa. As pointed out by Durrett and Levin (1994), in a spatial system the Maxwell point (MP, see in Fig. 1a) marks the boundary between two regimes: to the right of the MP, large patches of bare soil invade vegetation, while to the left of the MP vegetation invades bare soil. Accordingly, for the generic case of a spatial system with stochastic dynamics one should expect the transition to take place close to the Maxwell point, not at the tipping point (Bel et al., 2012). At the Maxwell point both states are stable, as seen in Fig. 1a, and there is no critical slowing down. Therefore, the early warning criteria which are based on the slow recovery of the system at the vicinity of the tipping point will fail to predict the crossing of the Maxwell point.

It may be instructive to draw an analogy to the physics of phase transition. A first order transition, like the process of water freezing as the temperature decreases, has also the features illustrated in Fig. 1a: under standard pressure water and ice are two alternative stable states of the system up to the tipping point at $-48.3\,°C$, where the state associated with water loses its stability, and at the vicinity of this critical temperature the healing of fluctuations indeed slows down. But the actual transition in almost any practical situation happens at the melting point (which is the analogous of the Maxwell point) at $T = 0\,°C$, when ice invades water. This happens because the system is spatial, and thermal fluctuations generate microscopic ice droplets that invade water below the melting temperature. In the same manner small bare soil patches will invade the vegetation to the right of the Maxwell point in Fig. 1a, meaning that under inevitable effect of stochastic perturbations (that generate these patches) the transition happens close to the Maxwell point, where indicators like critical slowing down are inefficient.

Here we would like to suggest a new method aimed at identifying the state of the system. Our method both distinguishes between continuous transitions and catastrophic shifts and provides a quantitative measure of the distance from the transition. This method is based on the monitoring of the cluster dynamics, and in particular the probability of a cluster to grow or shrink as a function of its size. It turns out that this technique reveals the
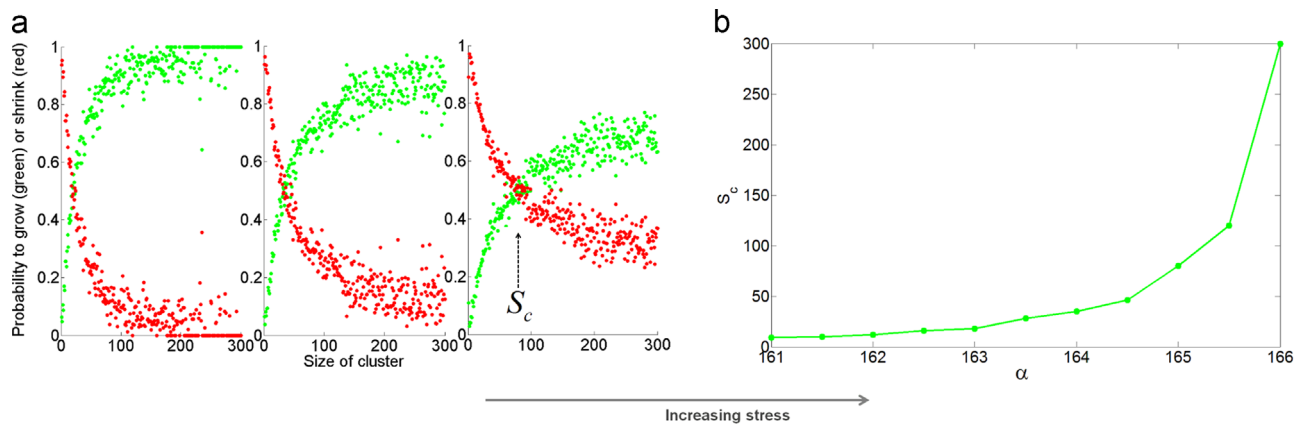
Fig. 2. Cluster dynamics in bistable system. Monitoring the evolution of clusters in a bistable Ginzburg–Landau system with environmental noise (see methods), the chance of a cluster to grow (green) or to shrink (red) is plotted against its size for various values of α: 163 (panel a, left), 164 (middle) and 165 (right) where α corresponds to increased stress. Clearly, the chance of a cluster to grow in size is positively correlated to its area. As the environmental conditions deteriorate the minimal size of a growing cluster is increasing, so the value of S_c grows with α. In panel (b) the S_c is plotted against α, with apparent divergence as α approaches α_{MP}. The parameters for the figures $\zeta = 2$, $D = 6$ and $S = 100 \times 100$. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)
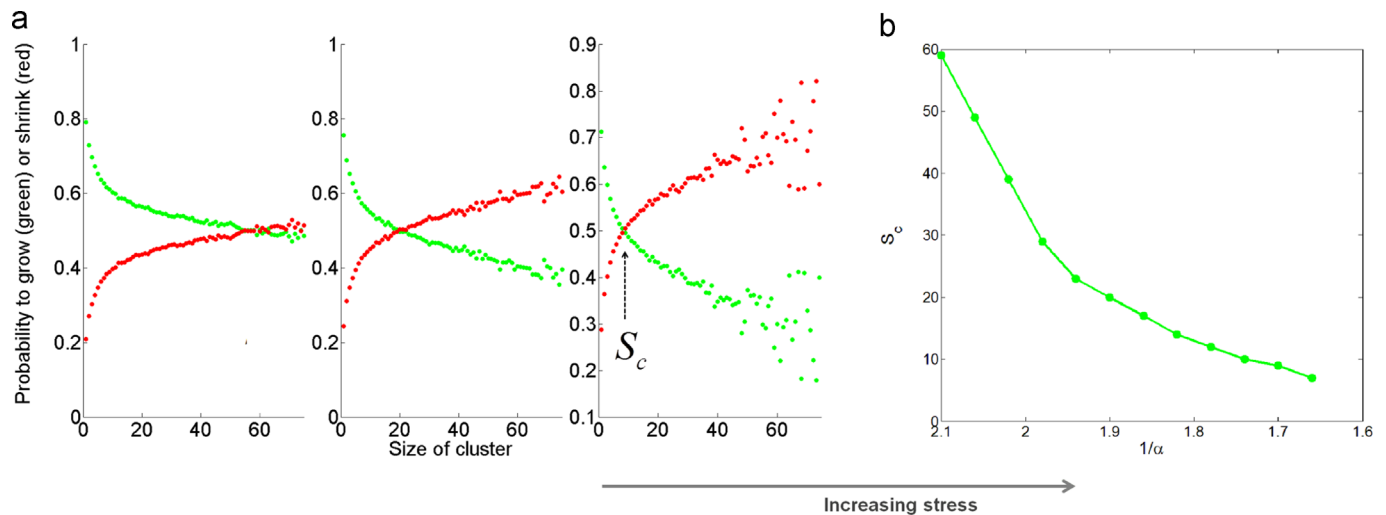

Fig. 3. Cluster dynamics for a system approaching a continuous transition. The time evolution of vegetation clusters described by a contact process (birth–death process with one individual per site, see Methods) was monitored. In contrast with the behavior illustrated in Fig. 2, here the chance of a cluster to grow (green) increases when its size decreases (panel a). The three subplots correspond to those values of α: 0.47 (left), 0.52 (middle) and 0.58 (right). Moreover, as the stress increases, S_c decreases, as only individuals surrounded by bare soil admit positive growth rate (panel b). Results were taken from simulation on a $S = 100 \times 100$ lattice. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

nature of the transition: a catastrophic shift system is characterized by a positive correlation between cluster size and its chance of growing. On the other hand, for a continuous transition the opposite is true, as small clusters tend to grow while large clusters shrink. The distance from the transition, in both cases, is related to the critical cluster size, and we will show that, as the system approaches the transition point, this size diverges for discontinuous transitions and goes to zero for continuous transitions.

This work, as we shall explain below, is based on simple insights gained from nucleation theory (for discontinuous transitions) and the theory of extinction dynamics. To demonstrate its power, we present a numerical study of generic models for continuous and discontinuous transitions. We begin with a comparison between the Ginzburg–Landau model of irreversible transitions and the contact process model for gradual extinction. Then proceed to analyze the same Ginzburg–Landau model, now with different levels of demographic noise. In a recent work (Martín et al., 2015) this model has been shown to have a discontinuous transition when the demographic stochasticity is relatively weak, and a continuous transition when the stochasticity is strong; we show that these features are related to the relative importance of

positive/negative feedback, and that our technique can identify the relevant regime and predict the transition.

All these models are analyzed in the context of desertification, i.e., a transition from an active (vegetation) to an empty (bare-soil) state. However the main lessons acquired are relevant, *mutatis mutandis*, to the analysis of catastrophic and non-catastrophic transitions in general.

2. Methods

Throughout this paper we consider and simulate two generic scenarios, the case of a system with positive feedback that supports a catastrophic shift and irreversible transition, and the case dominated by negative feedback where the transition is continuous and there is no hysteresis. The models and the simulation techniques are presented in this section.

Catastrophic transition: We have implemented the Ginzburg–Landau model, which is the minimal model that describes a discontinuous (first order) transition. In the context of desertification

we are looking at the biomass density, b, that satisfies:

$$\frac{\partial b}{\partial t} = D\nabla^2 b - \alpha b + \beta b^2 - \gamma b^3. \tag{1}$$

Here the β term describes the effect of positive feedback (an increase of the growth rate with density) and the γ term enforces a finite carrying capacity. The diffusion term reflects the spatial spread of the biomass, e.g., plant dispersal. For further details, see Weissmann and Shnerb (2014).

The dynamics described in Eq. (1) supports two alternative stable states: $b=0$ (the bare soil state) and the uniform solution $b = -\alpha/(2\gamma) + \sqrt{\beta^2 - 4\alpha\gamma}/(2\gamma)$ (vegetation). An increase in the control parameter α corresponds to increased stress (less precipitation, more grazing, etc.). Beyond the tipping point at $\alpha_{TP} = \beta^2/(4\gamma)$ the vegetation state no longer exists; as α crosses α_{TP}, a catastrophic shift occurs and the system collapses to the bare soil state. To restore the vegetation state the strength of the environmental pressure has to be reduced until it passes through the other tipping point at $\alpha = 0$.

Environmental stochasticity: Simulations of this model were performed on a 2d, $S = L \times L$ lattice with periodic boundary conditions. The deterministic dynamics was simulated via Euler integration of Eq. (1) with $\Delta t = 0.001$, implementing asynchronous update to avoid artifacts like fictitious bias of the dispersal. To add disturbances to the model, after every ζ elementary timesteps (a "step" is a numerical integration of Eq. (1) over $\Delta t = 0.001$) the biomass at each site was multiplied by $1 + \eta$, where η is a random number taken from a uniform distribution between $-\Delta$ and Δ. The

parameters used for the results presented in Fig. 2 are $\beta = 40$, $\gamma = 1.6$ (hence $\alpha_{MP} = 222.22$ and $\alpha_{TP} = 250$), $L = 100$, $\zeta = 2$, $\Delta = 0.4$.

Demographic stochasticity: Recently, it was shown that the 2d version of Ginzburg–Landau model (see Eq. (1)) supports both continuous and discontinuous transitions, depending on the strength of the demographic noise (Martín et al., 2015). When the noise is relatively weak the transition is first-order-like, with a discontinuous change in the vegetation cover, two tipping points and hysteresis. On the other hand, the very same system under strong noise admits a second order continuous transition that belongs to the directed percolation equivalence class.

To add demographic noise to the dynamics of Eq. (1), we implemented the technique used (and explained in detail) in Weissmann and Shnerb (2014). The deterministic dynamics of (1) is simulated, again, using Euler integration, but the biomass at each site, $b(x,t)$, is replaced by an integer, taken from a Poisson distribution with an average $b(x,t)$, every ζ elementary timesteps. The results for weak noise, presented in Fig. 4, correspond to $\zeta = 50$, while the strong noise results in Fig. 5 were obtained with $\zeta = 2$. The other parameters are the same as above.

Contact process extinction transition (*Lattice SIS*): In a contact process every site is either empty or occupied by one individual (active). An active site dies at a rate one, and is trying to reproduce at rate $1/\alpha$ (again, α is a stress parameter, an increase in α leads to a decrease in the birth rate). When an individual tries to reproduce, it picks at random one of its neighboring sites, and if the chosen site is empty, it becomes active, otherwise, nothing happens. Accordingly, the productivity of a site is inversely proportional to the local density.

The process was simulated using the Gillespie algorithm on a 2D, 100×100 lattice. It is known (Dickman and da Silva, 1998; Hinrichsen, 2000) that in this case the transition is continuous and extinction takes place at $\alpha_c \approx 0.61$.

Cluster tracking: Trying to emulate the results of consecutive censuses of an empirical system, we have "sampled" our system every η generations: a snapshot of the spatial pattern was taken and the dynamics of clusters is obtained by comparison with the

Table 1
Summary of the suggested indicators.

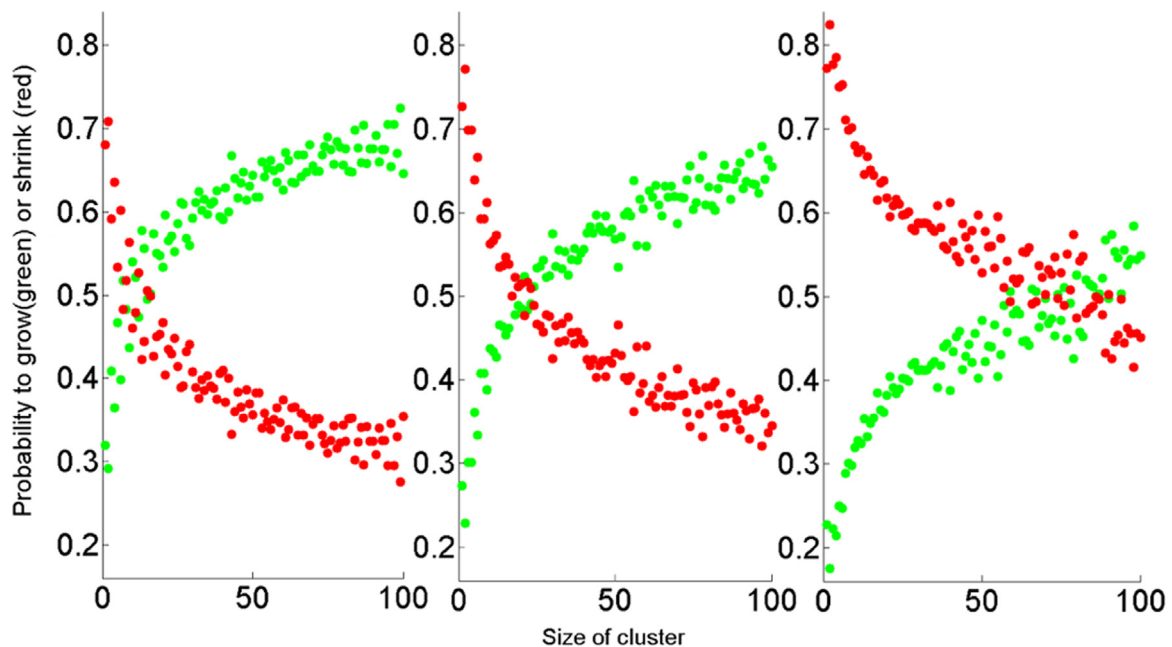| Indicator	Catastrophic regime shift	Continuous transition
Small clusters	Shrink	Grow
Big clusters	Grow	Shrink
Critical cluster	Diverges	Goes to minimal value

Fig. 4. Bistable system with weak demographic noise. Tracking clusters in a bistable Ginzburg–Landau system with *weak* demographic noise (see Methods); the chance of a cluster to grow (green) or to shrink (red) is plotted against its size for various values of α: 193 (panel a, left), 194 (middle) and 195 (right). Clearly, also here the chance of a cluster to grow is positively correlated to its area. The parameters for the figures $\zeta = 50$, $D = 6$ and $S = 100 \times 100$. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

previous snapshot. For the contact process, the definition of a spatial cluster is trivial: it is a collection of active sites in which every pair is connected by a path of nearest neighbor active sites. For the catastrophic shift model every site was classified as "active"/"inactive" depending on whether the biomass $b_{i,j}$ in a given cell of the lattice is above/below a threshold corresponding to the unstable solution of 1. If $b_{i,j}$ is in the basin of attraction of the vegetation state and as "inactive" if this point is attracted to the bare soil state. These clusters were identified and labeled using MATLAB's *bwlabel* subroutine.

To track the evolution of clusters we have implemented a simple motion tracking algorithm (see, e.g., Seri et al., 2012; Falkowski et al., 2006; Hartmann et al., 2014), and then the cluster at one snapshot is compared with the previous one to identify growth or decay.

3. Results

The spatial dynamics of populations is usually modeled (as in Eq. (1)) by some kind of "diffusion" term, representing the random movement (or dispersal) of individuals among neighboring patches. However, the results presented here are independent on the exact form of the spatial movement term. The only crucial feature is that the spatial dynamics prefers "smeared" spatial patterns, i.e., the system is trying to avoid strong spatial gradients of population density.

As mentioned above, the main characteristic of bistable systems that allows for catastrophic transitions is *positive feedback*: in a local patch, small populations go extinct and large populations are self-sustained. However, when the spatial dynamics is taken into account, small patches, for which the area of the surface region is large with respect to their "volume", are under stronger stress from their neighborhood, while the effect of surface stress is vanishingly small for large patches. This phenomenon is analogous to the opposing effects of surface tension and bulk free energy that governs the physics of nucleation in first order transitions (Kelton, 1991). As a result, one expects that, for the same value of the external parameter (say, α), large clusters are more stable, and their tendency to grow (or at least not to shrink) is enhanced with respect to small clusters.

When the system has no, or very weak, positive feedback, there is no bistability. Individuals feel the stress from their neighbors (due to resource competition or any other process that limits the carrying capacity), but they have no (or almost no) benefit from such a proximity, and their fitness increases with the level of spatial isolation. Consequently, there is no bistability and population density goes continuously to zero at some critical value of the external parameter. However, as discussed by many authors (e.g., Bonachela et al., 2012 and references therein), the spatial structure of the system is still very relevant. The fate of a population depends on the ratio between birth and death rates. In spatial systems the local *negative* feedback (meaning that individuals cannot reproduce in, or into, occupied sites), when superimposed on the emergent clustering (since death occurs everywhere but reproduction is local) leads to a decrease of the effective birth rate. As a result, the transition in spatial system takes place when the per capita birth rate is larger than the death rate. Accordingly, for these systems the effect of density is just the opposite: the smaller the cluster, and the larger its interface with empty (or low density) sites, the larger its chance to grow.

To demonstrate the applicability of these qualitative insights, we have analyzed first two generic models. For the case of catastrophic shift, we used, as in Bel et al. (2012) the Ginzburg–Landau model, which is the simplest nonlinear dynamics that provides both positive feedback and finite carrying capacity. To model a

continuous extinction transition we have implemented the contact process, a canonical model of a birth–death process on spatial domains. As suggested by Janssen (1981) and Grassberger (1982), continuous extinction transitions belong generically to the directed percolation equivalence class, for which the contact process is a standard example. In the context of population dynamics, the applicability of this conjecture was demonstrated by Bonachela et al. (2012).

In Fig. 2 the chance of a cluster to grow/shrink is plotted against its size for the Ginzburg–Landau model (see Methods). Clearly, the larger the size of a cluster, the larger is its chance to grow. Just the opposite feature is demonstrated in Fig. 3 for the continuous transition: here the chance of a cluster to grow is negatively correlated with its size. This qualitative feature is quite prominent and may allow one to identify the nature of the system (bistable or not) and to guess the characteristics of an imminent transition (continuous or catastrophic) even with poor-quality data.

A second feature, demonstrated in Figs. 2 and 3, is the appearance of a critical cluster size $S_c(\alpha)$. Clusters of size S_c neither shrink nor grow on average. In catastrophic (positive feedback) systems smaller clusters shrink and larger cluster grow, while the opposite is true when the transition is continuous. As the value of α approaches the Maxwell point (α_{MP}) for a bistable system, $S_c \to \infty$, meaning that no vegetation cluster grows on average above α_{MP}. On the other hand, in a continuous transition S_c takes its minimal value at the extinction point, indicating that even small clusters cannot grow anymore.

Accordingly, our suggested diagnostic procedure has two stages. The first is based on (at least) two snapshots of the spatial system, allowing for a comparison of the chance of a patch to shrink or to grow, thus indicating the type (bistable/catastrophic or monostable/continuous) of the system. Comparing (at least) three snapshots and tracing the value of S_c along time one obtains an early warning indication of an imminent transition if S_c grows (in a catastrophic system) or shrinks (in a continuous system). This procedure is summarized in Table 1.

If a bistable system is in its extinction phase (i.e., $\alpha > \alpha_{MP}$), where a large enough patch of bare soil will invade vegetation, but the disturbance that creates this void has not yet happened) the small patch dynamics still provides an indication as to the state of the system, as the lines representing the chance to grow/shrink (see Fig. 2) will level off and saturate, indicating that $S_c \to \infty$ and that the system is living on a borrowed time.

Clearly, systems with pure positive feedback (like the one considered in Fig. 2) or pure negative feedback (Fig. 3) are just two extremes of a continuum. In general one may expect both positive and negative feedback, with transition characteristics that reflect the weight between these two forces. An interesting opportunity to consider such a complex situation while keeping the model simple was discovered recently by Martín et al. (2015). These authors considered the Ginzburg–Landau model (1) with *demographic* noise, and show that the qualitative features of the transition depend on the strength of this noise. When the noise is weak, the general features of the Ginzburg–Landau model, including positive feedback and bistability, are preserved. The only role of noise is to generate local disturbances that may grow or shrink depending on α, so the transition is still discontinuous and hysteretic. Strong demographic noise implies that the number of individuals per site is small (see the discussion in Kessler and Shnerb, 2012). Accordingly, negative feedback dominates the system (the gain of an individual from its neighbors due to the β term in (1) is weaker than the stress imposed by the same neighbors) and the transition is continuous, contact process like.

We used this system in order to examine the performance of our technique using a model that admits both continuous and discontinuous transition, thus allowing for a fair comparison
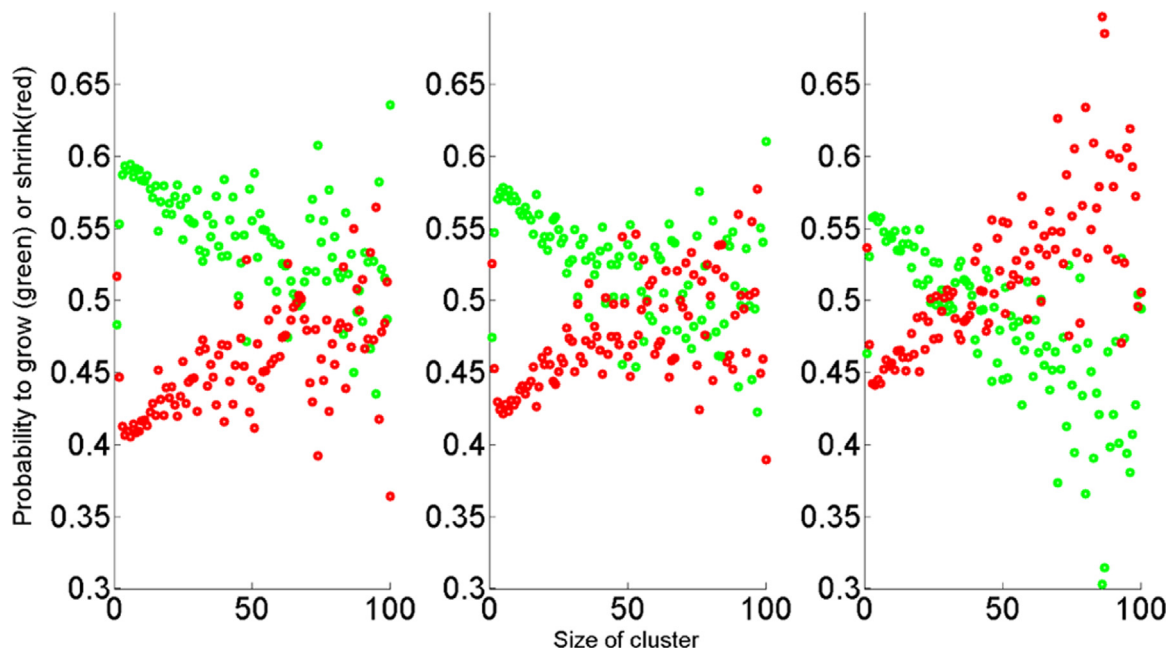
Fig. 5. Bistable system with strong demographic noise. Same as Fig. 4, but the results obtained from a Ginzburg–Landau dynamics with *strong* demographic noise ($\zeta = 2$). The chance of a cluster to grow (green) or to shrink (red) is plotted against its size for various values of α: 174.5 (panel a, left), 174.9 (middle) and 175.3 (right). (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

between the two scenarios. Fig. 4 shows the result for the system considered by Martín et al. (2015) with weak demographic noise; indeed the results are the same as those shown in Fig. 2. By changing only one parameter of the system, increasing the strength of the demographic noise, we obtained the results presented in Fig. 5. Here the effects of negative feedback are pronounced and in general the figure is very similar to Fig. 3, although some reminiscence of the positive feedback still manifest themselves for very small clusters.

Finally, we have checked (see supplementary material) that the results for continuous transitions (negative growth rate for large clusters) are not an artifact of cluster fragmentation by taking into account only changes of clusters' size by 1–3 sites (avoiding events in which one large cluster decomposes into two only because of the "death" of a single patch), and the results were, for all practical purposes, the same. The method may be used even for poor quality data, when one cannot identify an individual unit of vegetation. When we traced the overall vegetation within circles of fixed radius, monitoring the total amount of vegetation within each circle as a function of time, the same results were obtained: for a positive feedback system the per capita growth rate is positively correlated with the density, while for negative feedback systems it is negatively correlated.

4. Discussion

The main insight we have implemented in this paper is the distinction between systems with positive feedback, i.e, positive correlation between the fitness of individuals and the density, and systems with only negative feedback, where an increase in the local density is followed by a decrease of individual's fitness. In the first case one expects an alternate steady state, hysteresis and catastrophic shift, while in the other case the extinction transition is continuous. As explained above, positive feedback leads to an access growth of large clusters, while in systems with negative feedback small clusters are favorable.

Accordingly, we have suggested two diagnostic tools, both are based on comparison between consecutive snapshots taken from the same spatial domain. First, by comparing (at least) two snapshots one may obtain a quantitative assessment of the importance of positive feedback by measuring the correlation between the size of a cluster and its chance to grow or shrink. Using (at least) three snapshots one may get an early indication of an immanent transition, as S_c diverges (in the catastrophic shift scenario) or shrinks to low values (in the continuous transition case). We demonstrated the power of our method in systems with pure negative and pure positive feedback (a contact process and a Ginzburg–Landau model with environmental stochasticity) and in a system where the two feedback interfere with each other and the results depend on their relative weights (Ginzburg–Landau model with demographic stochasticity).

We did not consider here the case in which the effects of positive and negative feedbacks are equal. One should expect such a situation in the model considered in Martín et al. (2015) at the noise level that corresponds exactly to the limit point between continuous and discontinuous transition. We believe that in this point the transition should belong to the voter model equivalence class (Dornic et al., 2001), and the chance of a cluster to grow or shrink is independent of its size (no surface tension).

In summary, we have suggested a general diagnostic tool that may serve any specific study of a potential transition on spatial domain. Tracking cluster dynamics along a certain period reveals the dominant mechanism (positive/negative feedback) that governs the dynamics, the expected character of a transition (smooth/abrupt) and its proximity. We hope that this technique will enhance the predictive ability of relevant studies, assisting the effort to avoid undesirable catastrophic transitions, together with their disastrous consequences.

Appendix A. Supplementary data

Supplementary data associated with this paper can be found in the online version at http://dx.doi.org/10.1016/j.jtbi.2016.02.033.

References

Allington, G., Valone, T., 2010. J. Arid Environ. 74, 973, ISSN 0140-1963.

Bel, G., Hagberg, A., Meron, E., 2012. Theor. Ecol. 5, 591.

Bonachela, J.A., Muñoz, M.A., Levin, S.A., 2012. J. Stat. Phys. 148, 724.

Carpenter, S.R., Cole, J.J., Pace, M.L., Batt, R., Brock, W., Cline, T., Coloso, J., Hodgson, J. R., Kitchell, J.F., Seekell, D.A., et al., 2011. Science 332, 1079.

Dai, L., Korolev, K.S., Gore, J., 2013. Nature 496, 355.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., Mace, G.M., 2011. Science 332, 53.

Dickman, R., da Silva, J.K.L., 1998. Phys. Rev. E 58, 4266.

Dornic, I., Chaté, H., Chave, J., Hinrichsen, H., 2001. Phys. Rev. Lett. 87, 045701.

Drake, J.M., Griffen, B.D., 2010. Nature 467, 456.

Durrett, R., Levin, S., 1994. Theor. Popul. Biol. 46, 363.

Eslami-Andergoli, L., Dale, P., Knight, J., McCallum, H., 2014. Wetl. Ecol. Manag., 1–12.

Falkowski, T., Bartelheimer, J., Spiliopoulou, M., 2006. In: Proceedings of the 2006 IEEE/WIC/ACM International Conference on Web Intelligence, IEEE Computer Society, Washington, DC, USA, pp. 52–58.

Fuhlendorf, S.D., Briske, D.D., Smeins, F.E., 2001. Appl. Veg. Sci. 4, 177.

Grassberger, P., 1982. Z. Phys. B Condens. Matter 47, 365.

Hartmann, T., Kappes, A., Wagner, D., 2014. arXiv:1401.3516.

HilleRisLambers, R., Rietkerk, M., van den Bosch, F., Prins, H.H., de Kroon, H., 2001. Ecology 82, 50.

Hinrichsen, H., 2000. Adv. Phys. 49, 815.

Holmgren, M., Scheffer, M., Huston, M.A., 1997. Ecology 78 (1966).

Janssen, H.-K., 1981. Z. Phys. B Condens. Matter 42, 151.

Kéfi, S., Rietkerk, M., Alados, C.L., Pueyo, Y., Papanastasis, V.P., ElAich, A., de Ruiter, P. C., 2007. Nature 449, 213.

Kéfi, S., Eppinga, M.B., de Ruiter, P.C., Rietkerk, M., 2010. Theor. Ecol. 3, 257.

Kéfi, S., Dakos, V., Scheffer, M., Van Nes, E.H., Rietkerk, M., 2013. Oikos 122, 641.

Kelton, K., 1991. Solid State Phys. 45, 75.

Kessler, D.A., Shnerb, N.M., 2007. Phys. Rev. E 76, 010901.

Kessler, D.A., Shnerb, N.M., 2012. Phys. Rev. E 85, 051138.

Kessler, D.A., et al., 2008. J. Appl. Probab. 45, 757.

Müller, F., Burkhard, B., Kroll, F., 2009. Resilience, integrity and ecosystem dynamics: bridging ecosystem theory and management. In: Landform-Structure, Evolution, Process Control, Springer, Berlin, Heidelberg, pp. 221–242.

Manor, A., Shnerb, N.M., 2008. J. Theor. Biol. 253, 838.

Martín, P.V., Bonachela, J.A., Levin, S.A., Muñoz, M.A., 2015. Proc. Natl. Acad. Sci. U.S. A. 112, E1828.

Peters, D.P., Yao, J., Sala, O.E., Anderson, J.P., 2012. Global Change Biol. 18, 151.

Rasmussen, K., Fog, B., Madsen, J.E., 2001. Global Environ. Change 11, 271.

Rietkerk, M., Van de Koppel, J., 1997. Oikos, 69–76.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Nature 413, 591.

Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., Van Nes, E.H., Rietkerk, M., Sugihara, G., 2009. Nature 461, 53.

Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., Van De Koppel, J., Van De Leemput, I.A., Levin, S.A., Nes, E.H.Van, et al., 2012. Science 338, 344.

Seri, E., Maruvka, Y.E., Shnerb, N.M., 2012. Am. Nat. 180, E161.

Takimoto, G., 2009. Popul. Ecol. 51, 419.

Valone, T.J., Meyer, M., Brown, J.H., Chew, R.M., 2002. Conserv. Biol. 16, 995.

Veraart, A.J., Faassen, E.J., Dakos, V., van Nes, E.H., Lürling, M., Scheffer, M., 2012. Nature 481, 357.

von Hardenberg, J., Kletter, A.Y., Yizhaq, H., Nathan, J., Meron, E., 2010. Periodic versus scale-free patterns in dryland vegetation. Proc. R. Soc. Lond. B: Biol. Sci. rspb20092208.

Weissmann, H., Shnerb, N.M., 2014. Europhys. Lett. 106, 28004.

Zhang, J.Y., Wang, Y., Zhao, X., Xie, G., Zhang, T., 2005. N.Z. J. Agric. Res. 48, 277.