

## IDEA AND PERSPECTIVE

### Robust scaling in ecosystems and the meltdown of patch size distributions before extinction

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#### Abstract

Robust critical systems are characterized by power laws which occur over a broad range of conditions. Their robust behaviour has been explained by local interactions. While such systems could be widespread in nature, their properties are not well understood. Here, we study three robust critical ecosystem models and a null model that lacks spatial interactions. In all these models, individuals aggregate in patches whose size distributions follow power laws which melt down under increasing external stress. We propose that this power-law decay associated with the connectivity of the system can be used to evaluate the level of stress exerted on the ecosystem. We identify several indicators along the transition to extinction. These indicators give us a relative measure of the distance to extinction, and have therefore potential application to conservation biology, especially for ecosystems with self-organization and critical transitions.

#### Keywords

Deviations from power laws, indicators of transitions, local interactions, patch size distribution, power law, power law with an exponential cutoff, robust criticality, scaling, spatial patterns, truncated power law.

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#### INTRODUCTION

The idea that spatial patterns could provide important indicators of the level of degradation of spatially organized ecosystems is gaining increased attention (Rietkerk *et al.* 2004; Oborny *et al.* 2005; Manor & Shnerb 2008; Guttal & Jayaprakash 2009; Scheffer *et al.* 2009). Many ecosystems show spatial organization, where patches of different shapes, sizes and species compositions coexist. A well-known example is the patchiness of the vegetation cover in drylands. The fact that this spatial organization changes in response to external stress led to the idea that observing the spatial structure of an ecosystem could provide information about the level of stress exerted on the ecosystem and about its level of degradation (von Hardenberg *et al.* 2001; Rietkerk *et al.* 2004; Kéfi *et al.* 2007b).

The patch size distributions of vegetation in arid ecosystems have been found to follow approximate power laws over a wide range of environmental conditions (e.g. mean annual rainfall; Scanlon *et al.* 2007). In these ecosystems, the number of vegetation patches appears as a straight line when plotted as a function of their size on logarithmic scales. These ecosystems exhibit many small patches and progressively rarer large ones, and they show no characteristic patch size. However, arid ecosystems that experienced high grazing pressures show a deficiency in large patches compared with power laws (Kéfi *et al.* 2007b). Therefore, it has been proposed that deviations from pure power laws towards fewer large patches could serve as indicators of the proximity to a desertification threshold (Kéfi *et al.* 2007b). Despite the potential practical relevance of patch size distributions for the management and preservation of spatially organized ecosystems, the ecological mechanisms underlying the wide emergence of power laws and their deviations are not yet fully understood.

Power laws have been observed in a wide range of physical and biological systems (e.g. Bak *et al.* 1988; Brown *et al.* 2002; Solé & Bascompte 2006). The number of links in mutualistic and metabolic networks, the size of the clusters of ant nests, the size of vegetation patches, the population of cities, the intensities of earthquakes, the size of fires, the number of connections of internet routers, for example, are quantities whose distributions tend to be power laws (Stauffer & Aharony 1985; Jordano *et al.* 2003; Goldstein *et al.* 2004; Newman 2005; Vandermeer *et al.* 2008; White *et al.* 2008; Bascompte 2009; Clauset *et al.* 2009). The ubiquitous occurrence of power laws in both natural and man-made phenomena has long raised questions about their dynamical origin (Newman 2005).

In physics, power laws are known to emerge in the proximity of continuous phase transitions (also called second-order phase transitions) in closed systems (Stauffer & Aharony 1985; Solé & Bascompte 2006). Examples of such transitions are ferromagnetic and percolation transitions. At the critical point, i.e. the point at which the phase transition occurs, power laws appear, leaving the system with no characteristic scale (Newman 2005). The parameters of the system have to be finely

tuned to produce these scale-free patterns because the power laws occur only at (or very close to) the percolation point. Because these power-law patterns are so dependent on precise parameter values, such phase transitions are an unlikely explanation for the widespread presence of power laws in real systems.

As an alternative explanation for the ubiquity of these patterns, Bak *et al.* (1988) proposed that some open systems spontaneously evolve to the critical point at which power laws emerge regardless of their parameter values. This phenomenon is referred to as self-organized criticality. A classical and well-known example is the forest fire model of Drossel & Schwabl (1992). Through time, the forest fire model self-organizes to a state in which the distribution of sizes of fires follows a power law (in other terms the systems leads itself to the critical point). Self-organized criticality requires the active propagation of a disturbance, such as a fire, and the clear separation between the temporal scales of disturbance and recovery (Pascual & Guichard 2005). Thus, this concept is potentially relevant to other biological systems with local birth and death processes, including infectious diseases with intermittent epidemics (Rhodes & Anderson 1996), but not to all of them.

Another explanation for the widespread observation of power laws in ecological systems, and the focus of this article, was proposed by Pascual and colleagues (Pascual *et al.* 2002; Roy *et al.* 2003). They showed that, in stochastic spatial systems with local interactions, distributions resembling power laws can arise over a range of environmental conditions without the typical separation of time scales of self-organized criticality (Wootton 2001; Pascual *et al.* 2002). More specifically, in these systems power laws arise at a percolation point, where the typical size and connectedness of the system change drastically. However, an important distinction between these systems and classical critical systems is that when the system moves away from that percolation point towards extinction, deviations from power law occur less rapidly than expected for classical percolation because of the presence of the local interactions (Roy *et al.* 2003). This phenomenon of slower decay, also influenced by the finite size of the systems, is referred to as 'robustness' here and would make the observation of patterns that resemble power laws more likely in nature. This type of behaviour may apply to a variety of ecosystems recently described in the ecological literature (e.g. Pascual *et al.* 2002; Kéfi *et al.* 2007b; Scanlon *et al.* 2007; Solé 2007; Vandermeer *et al.* 2008). However, the properties of these systems, referred to as 'robust critical systems', are still poorly studied.

We should note that many processes, including the Yule process, coherent noise mechanisms and stochastic processes such as stochastic multiplicative processes (Levy & Solomon 1996; Sornette 1998; Manor & Shnerb 2009) have been proposed as possible mechanisms capable of generating power-law distributions in nature (see Mitzenmacher 2003; Newman 2005 for reviews). However, we are specifically interested here in stochastic spatial systems with local interactions that are able to generate power-law like patterns in the size distribution of patches. Among all the

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possible processes, robust criticality appears especially relevant because it is able to generate robust power-law like patterns, likely to be observed in nature, also for systems with no clear separation of time scales (Guichard *et al.* 2003; Kéfi *et al.* 2007b; Scanlon *et al.* 2007; Solé 2007).

This paper specifically addresses the complete trajectory of spatial patterns in the transition between the percolation point, where power laws emerge, and extinction in various robust critical systems. We ask: how do spatial patterns in these systems vary as a function of external conditions? More specifically, do they all show the same behaviour in their deviation from power laws towards extinction as observed in arid ecosystems?

We address the above questions by comparing simulation results from three ecological models: a vegetation model of arid ecosystems which includes local facilitation, a mussel bed model which includes both local facilitation and disturbance and a predator–prey model with local antagonistic interactions. All three models exhibit spatial self-organization, with clusters that continually form and disappear, and the size distributions of these clusters exhibit power law (Pascual *et al.* 2002). We further consider a null model that lacks any sort of local interaction (i.e. in which no underlying dynamical process governs the spatial organization of the system) for comparison.

We describe the full range of patterns that emerge in these models when a ‘stress-factor’ becomes progressively stronger. Our study is motivated by the identification of indicators of proximity to extinction based on these distributions. Moreover, we compare this pathway to extinction to that of the null model to determine the role of local interactions in the existence of such indicators.

## METHODS

All the models are asynchronous, stochastic cellular automata (also called interacting particle systems; Durrett & Levin 1994). Space in these systems consists of a grid of cells each of which, at any given time, can be in one of different possible states. At each time step, the status of each cell can change with a rate that determines the probability per unit time of the different events (or dynamical rules). Except for the null model, these dynamical rules depend on the state of the neighbourhood, defined as the four nearest neighbours. We briefly review here the dynamical rules of the four models. See Appendix S1; Pascual *et al.* (2002), Guichard *et al.* (2003) and Kéfi *et al.* (2007c) for detailed descriptions of the parameters of the three models with local interactions.

### Null model

In the null model, the cells can be in one of two states, occupied or empty. A fraction of the lattice is initially filled randomly with occupied cells. At each time step, an empty cell is recolonized at a rate  $r$  (probability per unit of time), and an occupied cell becomes empty at rate  $m$ . Both processes occur independent of the states of the neighbouring cells. In the mean field picture, the dynamics of this system would be described by:

$$\frac{dp}{dt} = r - (m+r)p,$$

where  $p$  is the fraction of occupied cells. At steady state, the fraction of occupied cells is determined by the ratio  $\bar{p} = \frac{r}{1+(m/r)}$ . This system cannot exhibit other transition than the percolation one. As the percolation threshold in a 2D system (four neighbours) is  $p_c = 0.59$  (Stauffer & Aharony 1985), the  $r$  value at which percolation takes place in our null model is:  $r_c = \frac{mp_c}{(1-p_c)}$ . For example, for  $m = 0.25$ ,  $r_c = 0.36$ .

This model is ‘null’ in the sense that there is no process governing the spatial distribution of occupied cells. The null model is introduced to check how local interactions affect the spatial organization of the occupied cells compared with the null case for a given fractional cover. The ratio  $m/r$  was therefore adjusted (by keeping  $m$  fixed and changing  $r$ ) so that the cover of occupied cells (i.e. the fraction of occupied cells in the lattice) matches those of the other models (for comparison).

### Arid ecosystem model

In the arid ecosystem model (Kéfi *et al.* 2007c), the cells can be in three possible states: vegetated, empty or degraded. The first one designates patches that are occupied by plants. The second state designates empty patches whose soil is still fertile. The third one refers to degraded soil that is unsuitable for colonization by plants.

Vegetation reproduces by spreading seeds in the lattice. A fraction of the seeds is dispersed locally in the neighbourhood of the mother plant; the rest is dispersed globally throughout the whole lattice. A seed that ends up on an empty cell can germinate. After vegetation dies, vegetated cells revert to empty. A cell that is empty for too long can become degraded (in reality, e.g. by processes like erosion). The regeneration rate of degraded cells into fertile empty cells (that can later be recolonized by seedling) increases with the proportion of neighbours that are occupied by vegetation. With this local positive effect, plants increase the recruitment of new individuals in the system (in their nearest neighbourhood).

### Mussel bed model

In the mussel bed model (Guichard *et al.* 2003), the cells can be in three states: disturbed, empty or occupied by mussels.

An empty cell can be colonized by mussels if at least one of its neighbours is occupied by a mussel. An occupied cell may become disturbed (in reality, e.g. when wave disturbance destroys the byssal thread attachment of the mussels to their neighbours and substratum). Mussels that are in sites adjacent to disturbed cells have a higher chance of becoming disturbed themselves: thus, the disturbance spreads locally. A disturbed cell eventually becomes empty. Mussels die at a density-independent rate.

### Predator–prey model

In the predator–prey model (Durrett & Levin 1994; Pascual *et al.* 2002), the cells can either be occupied by a prey, occupied by a predator or be empty (a cell cannot contain both predators and prey).

A prey samples its neighbourhood at random and, if the chosen site is empty, gives birth at a given rate and the empty site then becomes occupied by a new prey. A predator that has at least one prey in its surrounding chooses one prey site at random and eats it, moving to the prey site. This predator that has just eaten reproduces at a certain rate and the offspring occupies the original site of the predator. Predators who failed to find a prey die at a given rate. Note that in the original model of Pascual *et al.* (2002), there was also local dispersal by which random neighbouring pairs of cells exchanged their state at a slow rate. This local dispersal was not implemented here.

## Analysis

A ‘patch’ is a connected set of cells of the same type (this definition assesses connectivity based on the same neighbourhood than the one used for the range of local interactions, i.e. the four nearest neighbours). We considered patches of occupied cells (null model), vegetation cells (arid ecosystem model), mussel cells (mussel bed model) and prey cells (predator–prey model). We sampled the patch size distribution after a stationary state was reached in  $100 \times 100$  lattices (Kéfi *et al.* 2007a).

In Fig. 1 and Fig. 3 (the latter in Appendix S2), the percolation probability was estimated using  $500 \times 500$  lattices. The system is considered to be percolated when it has at least one patch that spans from one edge of the system to the opposite edge. The location of the percolation point is defined as the parameter value at which the percolation probability is 0.5 (see the Results for further details about the percolation point).

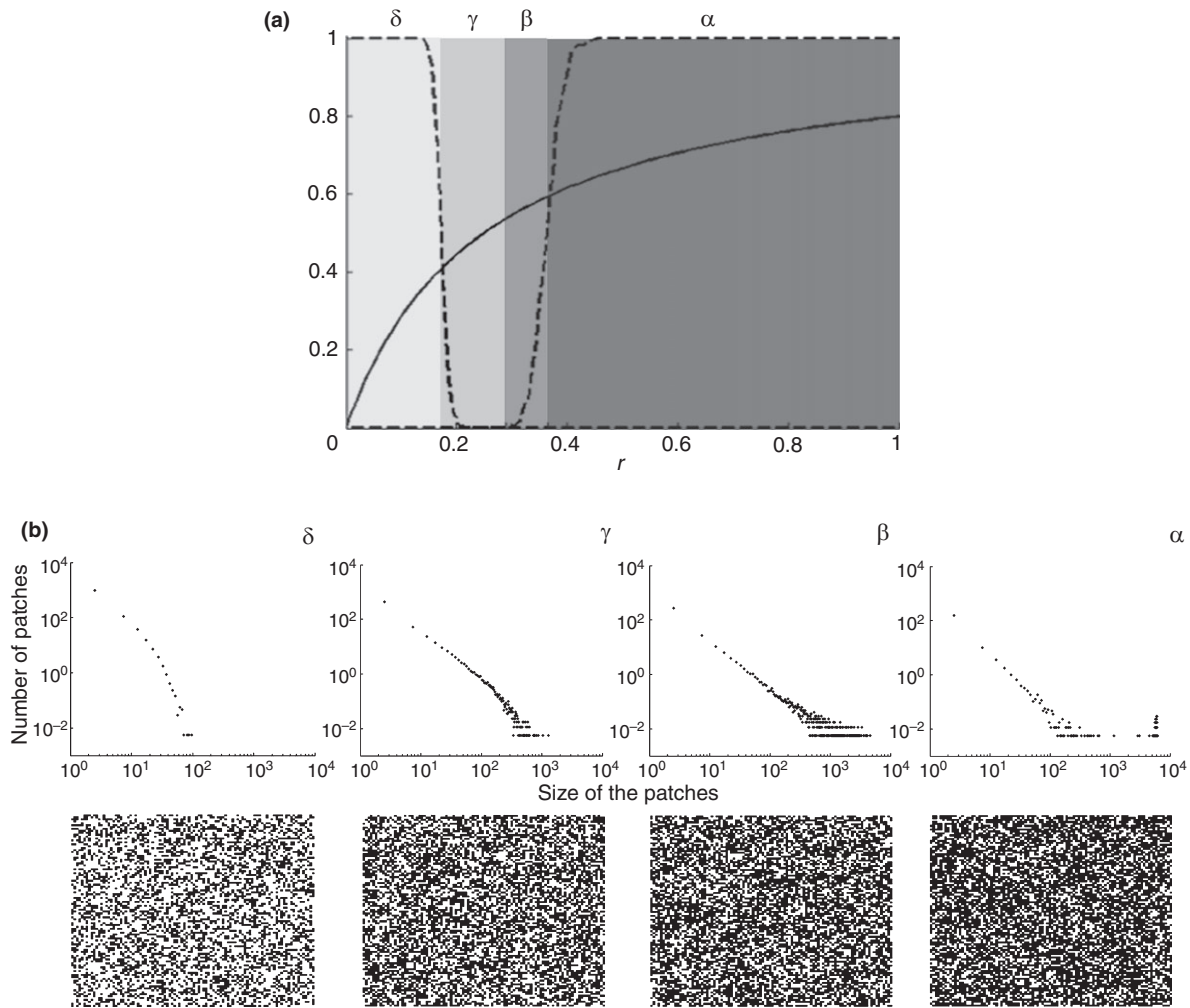
The patch size distributions were obtained as follows. Simulations were run for 10 000 time units. The first 3000 transient time steps were discarded. Thereafter, patch size data were recorded every 40 snapshots, to minimize any temporal correlation among successive snapshots. Data from 175 such snapshots were used to plot the patch size distribution.

We plotted the non-cumulative patch size distribution using bins of five cells. The distributions were fitted to three different functional forms: power law, power law with an exponential cutoff and exponential. We used least squares regressions on the binned log–log data and determined which model fitted the data best with the Akaike Information Criterion (Akaike 1974).

This method of binning of the data followed by least squares regression has been shown to produce bias and large variance in the estimation of the scaling exponent of the power law (Newman 2005; White *et al.* 2008; Clauset *et al.* 2009). White *et al.* (2008) showed that maximum likelihood estimates (MLE) give the most accurate and less variable estimates of the scaling exponents. Here, we are interested in the shape of the distribution and not in the exact value of the scaling exponent. However, binning can also lead to differences in the determination of which distribution best fits the data. MLE are currently available for power laws and exponential distributions, but not for power laws with an exponential cutoffs. We tried to fit the patch size distributions with other distributions for which MLE exist, but we could not find one able to reproduce the bending of the distribution adequately. The same problem arises when using the cumulative distribution function. For this reason, although we are aware of the limitations of the method, we decided to illustrate our idea here using binning and least squares regression.

We ran the three models with local interactions for different stress levels and plotted the corresponding patch size distributions at the stationary state. What we call ‘stress’ differs among the different models: aridity for the facilitation model, wave disturbance for the mussel bed model and predation pressure in the predator–prey model (in this simple system, the predation pressure can be modulated by varying the predator mortality rate, which affects the density of predators in the system; when the predator mortality rate is higher, there are less predators in this system and the predation pressure on the prey is lower; note, however, that this link between predator mortality and their population size is not always that simple; see, e.g. Gamarra & Solé 2002). There is no stress in the null model. In this case, what we vary is the fractional expected cover of occupied cells determined by the ratio  $1/[1 + (m/r)]$ .

We then compared the patch size distributions generated by the three models with local interactions with those generated by the null model for the same fractional cover.



**Figure 1** Succession of patch size distributions in the null model for different recolonization rates ( $r$  increases to the right). (a) Each of the grey areas corresponds to a different region. Full line: fraction of occupied cells in the lattice at steady state for different  $r$  values. Dashed left line: percolation probability of empty cells. Dashed right line: percolation probability of occupied cells. (b) Patch size distributions of occupied cells at steady state on a log–log scale, and the corresponding snapshots of the system at the end of the simulations for each of the four regions shown in (a). Black: occupied cell. White: empty cell. Parameter values  $m = 0.25$ ; from left to right: exponential,  $r = 0.15$ , cover = 0.37; power law with an exponential cutoff,  $r = 0.28$ , cover = 0.53; power law,  $r = 0.35$ , cover = 0.58; spanning clusters,  $r = 0.45$ , cover = 0.64. Percolation point of empty cells:  $r = 0.170 \pm 0.005$ ; truncation point:  $r = 0.290 \pm 0.005$ ; percolation point of occupied cells:  $r = 0.365 \pm 0.005$ .

We call ‘extinction point’ the level of stress above which the system cannot maintain itself anymore, e.g. the aridity level above which there is no vegetation in the system, the wave disturbance above which there is no mussel or the predation rate above which there is no prey. ‘Extinction’ in the three spatial models is similar to a phase transition to an absorbing state which belongs generically to Directed Percolation in time discrete systems or to Contact Processes in time continuous systems (Marro & Dickman 1999). Our three spatial models exhibit two phase transitions: the emergence of a giant cluster (critical percolation point) and transition to an absorbing state (here, extinction). We are interested here in showing that the path between these transitions runs through generic trajectories in the geometrical patterns.

**RESULTS**

**The sequence of patch size distributions towards extinction in the null model**

We first follow the changes in the size distribution of patches of occupied cells when the cover (i.e. the fraction of occupied cells) decreases in the null model (Fig. 1). For high cover, the patch size distribution is characterized by the presence of very large patches of the size of the system itself (so-called spanning clusters). As the cover decreases, spanning clusters of occupied cells first disappear at a point that is referred to as the percolation point of occupied cells. Interestingly, at this point there is a drastic change in system-wide connectivity, as the probability that a spanning patch appears in the system changes dramatically, but other ecological variables of interest, such as the fraction of occupied cells, vary smoothly with no apparent shift (Fig. 1a). As well-known in physics, the power laws are born at this point (Stauffer & Aharony 1985;

Solé & Bascompte 2006). From the percolation point of occupied cells towards lower covers, the large patches are progressively lost, leading to deviations from power laws. These deviations become stronger as the system approaches extinction, and the tail of the distribution exhibits increasingly fewer large patches than at the percolation point. Simultaneously, as the cover keeps decreasing, the probability that spanning clusters of empty cells appear in the system increases (Fig. 1a).

We propose that the sequence of patch size distributions with decreasing cover can be characterized by four distinct patterns (Fig. 1):

$\alpha$ : Two widely separated scales of patch sizes, corresponding to large patches of the order of the system size and remnant small patches;

$\beta$ : A power-law behaviour extending from small to large patches, where the patch distribution can be described by:

$$N(S) = CS^{-\lambda}, \tag{1}$$

with  $N(S)$ , the number of patches of sizes  $S$ ,  $\lambda(>0)$ , the estimated scaling exponent and  $C$ , a constant.

$\gamma$ : A deviation from a power law towards fewer large patches, which we describe as a power law with an exponential cutoff; the patch size distribution is given by:

$$N(S) = CS^{-\lambda}e^{-\frac{S}{S_x}}, \tag{2}$$

with  $S_x$  the cut-off above which patch size  $N(S)$  decreases faster than in a power law ( $S_x > 0$ ). At the percolation point,  $S_x$  goes to infinity and expression (2) reduces to a

power-law distribution such as in (1). Away from this point,  $S_x$  begins to decrease and this function combines a power-law behaviour with an exponential decay for larger patches. In the extreme case, when  $\lambda$  tends to zero, the patch size distribution falls as an exponential law over the entire range of patch sizes [i.e.  $N(S) = Ce^{-\lambda S}$ ]. Distributions characterized by eqn 2 are also referred to as 'truncated power laws' (Roy *et al.* 2003; Solé & Bascompte 2006; Kéfi *et al.* 2007b). However, here we prefer the expression 'power law with an exponential cutoff' which we find more explicit. This case where the patch size distribution deviates from a power law as described by eqn 2 can be subdivided in two parts depending on whether there are spanning clusters of empty cells or not in the system. Region  $\gamma$  corresponds to systems in which there are no spanning clusters of empty cells.

$\delta$ : A deviation from a power law as described by eqn 2 with spanning clusters of empty cells.

After the percolation point of occupied cells is passed, the change from a power law to a power law with an exponential cutoff (and then to an exponential law) reflects the gradual loss of the largest patches along the transition towards extinction, and thus a stronger deviation from a power law. The precise formulation of the mathematical functions describing the different zones along transitions is of course subjective. However, the functions we chose appear to describe very well the increasing deviation from a power law when the system goes away from the percolation point of occupied cells. Moreover, the functions are embedded within each other (the power law with an exponential cutoff contains the pure power law and the exponential law) and this provides a continuous representation of the gradual losses of patches along the transitions.

In an infinite system, we would expect the null model to exhibit a pure power law (i.e. a distribution described by eqn 1) only at the percolation point. Here, because of the finite size of the system (a norm in nature) and the statistical characterization of the patterns (a logistical necessity), we consider a region, and not a point, for which the deviations from power laws are not apparent (i.e. not statistically detectable).

We define ranges of conditions under which the patch size distribution is statistically indistinguishable from a given distribution as follows: for a system without a spanning cluster of occupied cells, statistical tests can be used to check which of the two functions (a power law or a power law with an exponential cutoff) best describes the patch size distribution of the system (Kéfi *et al.* 2007a,b). In systems best described by power laws with an exponential cutoff, the presence of spanning clusters of empty sites can be assessed. For practical purposes, we can thus define 'regions' as the range of environmental conditions under which the patch size distribution of the system is best described by a given function combined with the presence or absence of spanning clusters (of both occupied and empty cells). We define 'indicators' as the points which sets the limit of these regions. We call the point at which significant deviations from power laws, towards fewer large patches, become empirically detectable, the 'truncation point'. It is noteworthy that this indicator is quite different than the percolation and the extinction points. Indeed the truncation point is statistically defined and thus its absolute location depends on the statistical test and its accuracy. On the contrary, the locations of the percolation and the extinction points can be computed numerically using very large grids.

### How general is this phenomenon? Adding the ecological mechanisms

Interestingly, in the three models with local interactions, the same sequence of patch size distribution occurs in the same order towards extinction (Fig. 2a–c), showing an increasing deviation from a power law towards distributions that have fewer large patches than at the percolation point. Furthermore, this happens both when the transition to extinction is continuous (i.e. when the population density gradually decreases until extinction), and when it is discontinuous (i.e. when the population suddenly drops to zero once a stress level is reached) (Fig. 3 in Appendix S2).

By considering the patch size distribution and sequential changes in the spatial patterns from region  $\alpha$ , to  $\beta$ ,  $\gamma$  and  $\delta$ , one can infer that the system is moving towards less favourable conditions. As these sequential changes always occur in the same order (Fig. 4 in Appendix S3), the shape of the patch size distribution associated with the presence or absence of spanning clusters provides a relative distance to the extinction point.

Local interactions do not affect the sequence of patch size distributions, but they affect the shape of the patch size distribution that emerges for a given fractional cover (Fig. 2), as well as the width of the regions (Fig. 4 in Appendix S3). The role of local interactions can now be assessed more specifically by comparing the patch size distributions generated by the null model (Fig. 2d) and models including local interactions with the same fractional cover (Fig. 2a–c; Appendix S3). Given a certain cover, the patch size distributions of the null model show a deficiency of large patches compared with those in the local interaction models (Fig. 2a–c). In other words, in the local interaction models more large patches occur than expected on the basis of the null model. Indeed, in the three models with local interactions, the local interactions favour the formation of patches (i.e. local dispersal of the prey in the predator–prey model, local recruitment of the mussels in the mussel bed model and local facilitation in the local facilitation model).

This finding is in agreement with Scanlon *et al.* (2007), who found that power laws produced by a null model showed a deficiency of scales compared with patch size

distributions produced by cellular automaton taking local positive interactions into account.

This is also in agreement with Roy *et al.* (2003), who showed in the case of the predator–prey model that the size distribution of prey clusters resembles a power law for a broad range of parameter values. They also showed that, as the system moves away from the percolation point, the departure from power laws occurs more slowly than for classical percolation because of the presence of local interactions (see also Fig. 5 in Appendix S3). This robustness of the power-law behaviour is not merely the result of the system size (Roy *et al.* 2003; Pascual & Guichard 2005). More technically, the exponent characterizing how quickly the correlation length of the system decays is independent from system's size (Roy *et al.* 2003).

## DISCUSSION

### The succession of patch size distributions in robust critical systems

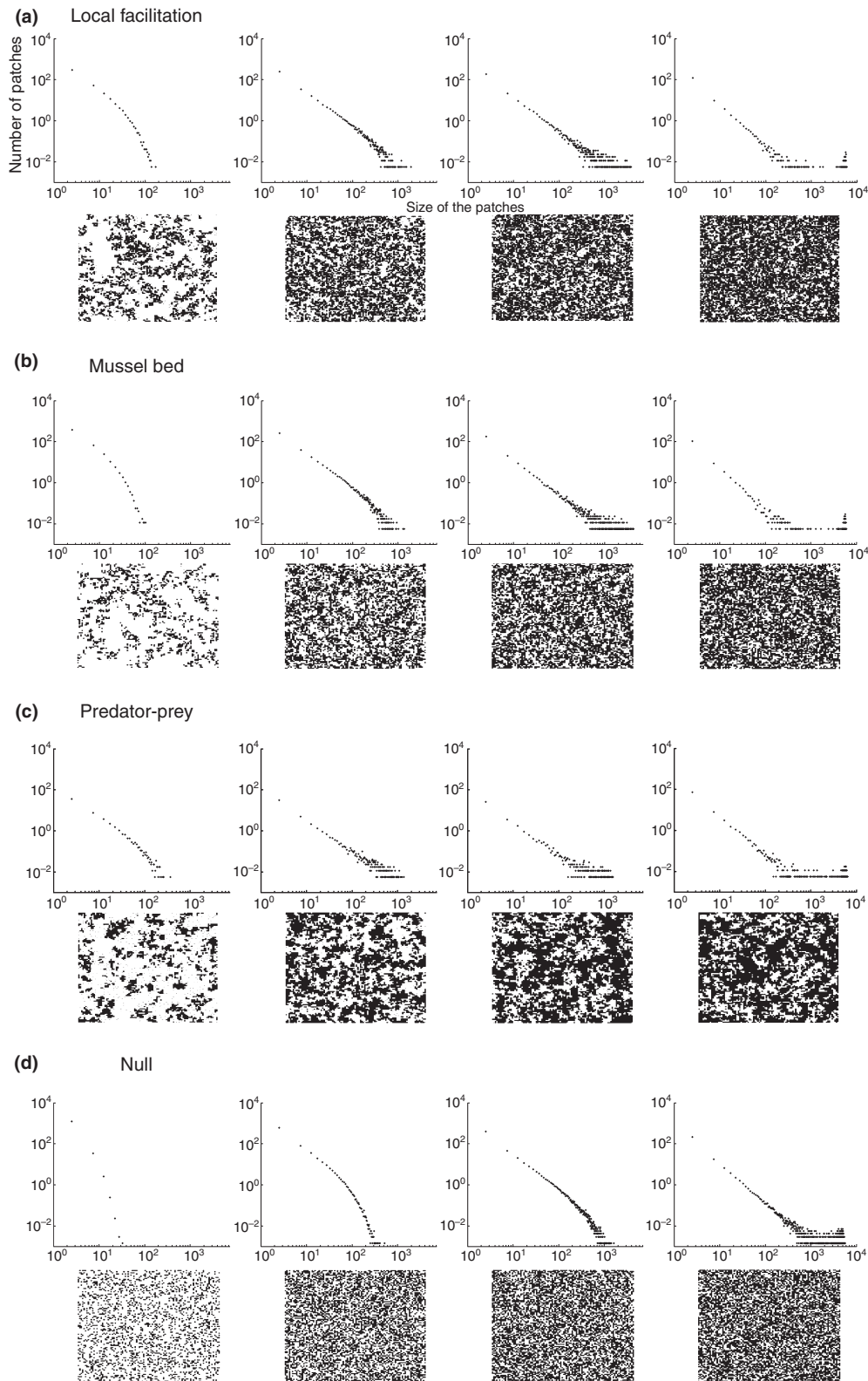
We studied three stochastic spatial systems with local interactions (robust critical models) and a null model. We investigated the changes in their spatial patterns under increasing stress. Our results suggest that tracking changes in patch size distributions associated with knowledge on the connectedness of the system (and more specifically on the presence or absence of spanning clusters) might provide qualitative information regarding the level of stress exerted on the ecosystem.

The four models analysed here all present the same succession of patch size distributions with decreasing cover (i.e. increasing stress level in the three spatial models), revealing a gradual meltdown of the distribution due to the disappearance of the large patches. Starting from favourable environmental conditions and increasing the stress level exerted on the system, the connectedness of the system suddenly drops at the percolation point of occupied cells. This point is the origin of the power-law behaviour in the patch size distribution (Stauffer & Aharony 1985; Solé & Bascompte 2006). At this point, there is a drastic change in the system-wide connectivity of the system, as well as in the average patch size, but not in the fractional cover of occupied cells. The presence of power-law behaviour, associated with the high connectedness of occupied cells reflects a state of the system away from extinction. The observation of an increasing deviation from power-law behaviour and an increasing connectedness of empty (or degraded) cells indicate a movement of the system towards extinction. A deviation from a power law towards fewer large patches associated with a high connectedness of empty (or degraded) cells is the last state of the system that occurs before extinction.

The patch size distribution is a more complicated measure than the cover, which is traditionally used as an indicator of ecosystem degradation (Maestre & Escudero 2009; Kéfi *et al.* 2010). However, there are cases where looking at the cover only might not be sufficient. For ecosystems that can potentially undergo discontinuous transitions, the cover will not be a good indicator of potential shifts because the ecosystem might shift at an unknown cover. In that case, other indicators must be used, in addition to cover, to be able to detect the proximity to a transition, and spatial patterns could be such additional indicators. Moreover, there is not always a straightforward link between cover and spatial patterns as observed in the field (Bautista *et al.* 2007; Lin *et al.* 2010). Bautista *et al.* (2007) showed that very different spatial structures may be observed at similar vegetation cover, leading to important consequences in term of erosion, runoff and more generally ecosystem functioning. In the models we studied, along a gradient of increasing stress, there are indeed areas where the cover hardly changes but important changes in the spatial structure occur (typically at the percolation points), and conversely, showing that the two indicators are complementary and more informative in concert. Additionally, because changes in cover with time are typically gradual and slow, not only is it difficult to tell how close, or far, an ecosystem currently is from a transition, but the changes may also reflect cyclical or some other form of endogenous fluctuating dynamics, in which decreases are temporary. In this regard, it is especially relevant that the temporal variance of variables such as cover tend to increase when systems approach a transition (Carpenter & Brock 2006; Fig. 6 in Appendix S3), which suggests that following cover only might be difficult and potentially misleading close to extinction. By contrast, the indicator points describe directional, and exogenously driven, transitions in the connectivity patterns, separated by (statistically) distinct bounds in cover, and therefore, provide a reliable link between changes in the cover and possible ecosystem transition.

Additionally, the patch size distribution can provide some information about underlying ecological mechanisms. We showed that systems with the same cover (but different underlying ecological mechanism) can be described by different distributions (Fig. 2; Appendix S3). Considering a real ecosystem and knowing its fractional cover, the patch size distribution can be compared with the patch size distribution generated by a null model for the same fractional cover. An excess in large patches compared with the null model would mean that local interactions might be at play, as a mechanism promoting longer spatial correlations than expected otherwise.

These results open up the prospect of comparing predicted and observed patch size distributions to infer the health of the ecosystem, or equivalently the level of stress exerted on it, as well as the dominant mechanisms that might be at play.



**Figure 2** Succession of patterns for decreasing environmental stress from left to right. Patch size distributions at steady state on a log–log scale, and the corresponding snapshots of the system at the end of the simulations. (a) Local facilitation model; from left to right:  $b = 0.4$ ,  $b = 0.5$ ,  $b = 0.54$ ,  $b = 0.6$ . (b) Mussel bed model; from left to right:  $\delta_o = 0.041$ ,  $\delta_o = 0.029$ ,  $\delta_o = 0.025$ ,  $\delta_o = 0.021$ . (c) Predator–prey model; from left to right:  $s = 0.024$ ,  $s = 0.15$ ,  $s = 0.27$ ,  $s = 0.8$ . (d) Null model;  $m = 0.6$  (note that the  $m$  value of null model is different than the one used in Fig. 1); from left to right:  $r = 0.17$ ,  $r = 0.56$ ,  $r = 0.70$ ,  $r = 0.94$ . In the snapshots: black: vegetated/mussels/prey/occupied cells; white: degraded/empty cells; grey: recolonizable/disturbed/predators (no grey cell in the null model). To each column corresponds a given cover of occupied cells (the same in the four models); from left to right: cover = 0.22, cover = 0.48, cover = 0.54, cover = 0.61. See Appendix S1 for other parameter values.

### The percolation points

Although the percolation points are not linked to a drastic change in the actual cover or abundance of individuals, it is noteworthy that the sudden change in the system-wide connectivity, including the average size of the patches, might have important functional consequences. Indeed, the spatial organization and connectivity of an ecosystem modulate whether 'contagious disturbances' such as fires, diseases, insect outbreaks, species invasions or fluid shear can propagate throughout the system (e.g. Newman & Watts 1999; Peterson 2002; Newman 2003). We provide some examples hereafter.

The percolation concept has been used to address the issue of habitat fragmentation. Bascompte & Solé (1996) showed that as the fraction of destroyed sites in a habitat reaches a threshold value, a percolation cluster of destroyed sites forms which crosses the lattice from one edge to the other. At that point, suitable habitat patches are essentially isolated and this change in the landscape's connectivity affects the survivorship of populations by influencing their dispersal success (Achter & Webb 2006).

In the case of arid ecosystems, the connectivity of the vegetation may play an important role in the functioning of the ecosystems. In many arid ecosystems, patches of vegetation play an important function by capturing and retaining limited resources such as rainwater, organic matter, soil sediments and nutrients (e.g. Schlesinger *et al.* 1990; Tongway *et al.* 2001; Bautista *et al.* 2007; Mayor *et al.* 2008). Ludwig *et al.* (2002) propose that the functionality of an arid ecosystem can be evaluated as its ability to retain vital ecological resources such as rainwater and soil: healthy or functional landscapes conserve water and soil resources, whereas dysfunctional landscapes easily lose these resources. Because the vegetation connectivity as well as the connectivity of empty (degraded) sites dramatically changes at the percolation points, it is possible that the functioning of the ecosystem is affected, e.g. the landscape could become disproportionately leakier and therefore poorly retain resources.

In other words, the percolation points correspond to areas where small changes in cover but large changes in spatial structure occur, potentially corresponding to large functional changes for the ecosystem. Note that these functional changes could affect other species in the ecosystem (e.g. not the ones modelled but other depending on the spatial structures, such as herbivores in a vegetation system).

### The truncation point

Closer to the extinction threshold, as environmental conditions deteriorate further, there is a point where the patch size distribution changes from a power law to a power law with an exponential cutoff, which has remnants of the scaling for smaller patches but has lost the larger patches of the power law itself. When these power laws with exponential cutoffs occur, the power-law pattern has degenerated sufficiently to indicate that the system is now closer to extinction. The last spatial pattern to occur just before extinction is characterized by spanning clusters of empty (or degraded) sites (Fig. 4 in Appendix S3).

Interestingly, in a system characterized by power laws in the patch size distribution, patches of all sizes (or a broad range of sizes as we move away from the percolation point) are present in the system. Under stress, when the patch size distribution is best described by a power law with an exponential cutoff, the range of possible sizes of these patches is reduced. The fact that the range of patch sizes becomes smaller under these harsh environmental conditions suggests that the vegetation patches might tend towards a characteristic size and shape, as already suggested by other studies (von Hardenberg *et al.* 2001).

### The generality of this behaviour towards extinction

We showed that the same sequence of changes in the spatial patterns was present in a range of systems, independently from the specific mechanisms involved, including the arid ecosystem model of Kéfi *et al.* (2007c), the predator-prey model studied in Pascual *et al.* (2002), the mussel bed model of Guichard *et al.* (2003) and a null model lacking spatial interactions (Fig. 4 in Appendix S3).

We conjecture (but did not prove mathematically) that this behaviour of patch size distribution can be generalized to at least all the so-called 'robust critical systems' (Pascual & Guichard 2005). However, we still need to better understand the characteristics of these systems and their essential ingredients. For now, we conjecture that systems combining local stochastic processes of birth and death, extremely common in ecology, will have percolation-like transitions, and that a combination of local interactions and finite size effects, will lead to a less drastic decay of the power laws than expected for classical percolation. In other words, percolation-like transitions may be in part responsible for the ubiquitous nature of patterns resembling power laws.

### Caveats of the proposed approach and technical challenges

There are technical issues to be addressed before being able to test these ideas on field data. We acknowledge that the absolute location of the indicators (and thus the size of the different regions) might depend on the choice of the statistical test and power and will vary with overall system size. Therefore, there are no absolute values of the cover that can be expected to conform to a given spatial distribution. Yet, importantly, we expect the sequence of the patch size distributions to be independent of the statistical test and system size (Appendix S4). Therefore, the indicators we propose are

meaningful when one observes the change of the distributions in a given system in time or in space. Also, when comparing different ecosystems, the fact that they are described by different distributions does not necessarily mean that one is more or less degraded than the other. Some ecosystems might generally have lower cover than others (e.g. we expect very arid ecosystems to have in general lower vegetation covers than sub-humid ecosystems). However, in the same ecosystem (similar species composition, same climate and abiotic characteristics), the fact that two systems have a different amount of deviation from a power law means that one of them can bare less perturbation than the other.

The question remains of a more quantitative characterization of the relationship between the percolation point at which the power laws arise and the extinction point. More specifically, we need to identify what controls the size of the different regions along transition (Appendix S3). Further efforts should be directed at quantifying the distance from the extinction point. We know now that the vegetation patch size distribution and the system's connectivity change towards the extinction point, and that the proposed indicators reflect this. However, we do not know yet how to evaluate (and what determines) the absolute distance in parameter space between these points and extinction.

As we mentioned earlier, White *et al.* (2008) demonstrated that binning and least square fitting on binned data lead to biased estimates of the exponents of the power law; MLE should be used instead. However, currently MLE are not available for power laws with exponential cutoffs. Other distributions may be better able to describe the deviations from power laws when the ecosystem approaches extinction. Robust and routine statistics are required for testing these hypothesis and their potential applications.

### Applicability of the approach to the field: practical challenges

It is now important to verify these behaviours along transitions to extinction in the field, for instance by analysing aerial photographs or satellite imagery (Appendix S4). The results from Scanlon *et al.* (2007) suggest that this could be a promising perspective, but the potential success of the approach will rely on the use of data with appropriate resolution. In all the models considered here (and the sampling of the systems the models were confronted to, in nature), the resolution was sufficiently fine-grained in at least one of the following ways: (1) either one cell was approximately the size of an individual (e.g. arid vegetation study; Kéfi *et al.* 2007b) or (2) the cell size was below the typical size of the smaller patch in the system (Guichard *et al.* 2003). When these conditions do not apply, the poor sampling resolution will degrade the quality of the size distributions and compromise the applicability of the indicators related to those distributions. There are now aerial pictures and satellite images with a resolution that is high enough to reach the required level of precision for many of ecosystems.

Moreover, natural systems are confronted to heterogeneity, disturbance and noise, and very little is known about how they affect the shape of the patch size distributions. We expect the approach presented in this article to be applicable especially to self-organized ecosystems, where self-organization can counteract the effect of noise or spatial heterogeneity, but we also expect the signal to be blurred or difficult to detect in ecosystems with strong stochasticity or underlying spatial heterogeneity. The fact that power laws and deviations from them have been observed in a wide range of ecosystems, independent from soil, vegetation or climate type (Kéfi *et al.* 2007b; Scanlon *et al.* 2007) is already encouraging and suggests that our approach might be applicable to at least a range of natural systems.

### CONCLUSION

Under increasing environmental change at global scales, it is a pressing issue to understand the response of ecological systems to these changes (Adeel *et al.* 2005). In the last years, several indicators of ecosystem shifts have been proposed (e.g. Carpenter & Brock 2006; Van Nes & Scheffer 2007; Carpenter *et al.* 2008; Guttal & Jayaprakash 2008). When a system approaches a shift, the variance of its time series (of a relevant variable such as cover), its skewness and auto-correlation increase [see Scheffer *et al.* (2009) for a review]. These indicators typically rely on time-series analyses and require long and well-defined time series to be reliable (Guttal & Jayaprakash 2008). The spatial equivalents of these quantities (spatial variance, spatial skewness and spatial auto-correlation) have also been recently investigated and shown to exhibit clear trends towards a shift (Oborny *et al.* 2005; Guttal & Jayaprakash 2009; Dakos *et al.* 2010).

All these indicators, temporal and spatial, have been proposed to help predicting the occurrence of shifts and have been tested in some data sets (Scheffer *et al.* 2009). Changes in these indicators usually occur gradually as the shift is approached. As a consequence, a trend in the indicators may serve as a warning but the absolute distance to the shift remains impossible to predict. This is a common caveat of all the indicators currently available. Moreover, Hastings & Wysham (2010) showed that most of these indicators (the 'general leading indicators') are unlikely to occur in a wide range of ecosystems because systems including nonlinearities and environmental variability might not exhibit smooth potentials (on which the general leading indicators depend).

In conclusion, it seems quite clear that not a single indicator is likely to be sufficient. On the contrary, we probably need a set of indicators that are sensitive to different aspects of ecosystems vulnerabilities. Combinations of these indicators might be what will help us get reliable estimations of the stress level experienced by ecosystems. For example, Guttal & Jayaprakash (2009) showed that a combination of increasing spatial variance and a peak in skewness is a clear signature that the system is close to a transition. For spatially organized ecosystems, spatial patterns could also provide important indicators of the level of degradation of the ecosystem (Rietkerk *et al.* 2004; Oborny *et al.* 2005; Kéfi *et al.* 2007b; Manor & Shnerb 2008; Guttal & Jayaprakash 2009). Here, we propose complementary quantities based on the changes in the spatial organization. Specifically, we propose a set of indicators based on the patch size distribution and on the connectivity of the system at a snapshot in time, which provide a relative measure of the distance to extinction. Although the question remains of a more quantitative distance to extinction, this set of indicators will be especially relevant in ecosystems with spatial self-organization and critical transitions.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

- Appendix S1** Definitions of the three models with local interactions.
- Appendix S2** Regions of the patch size distributions in the local facilitation model along continuous and discontinuous transitions.
- Appendix S3** Comparison of the regions in the different models.
- Appendix S4** Effect of the lattice size and of sampling resolution on the patch size distribution.

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