Patchiness and scale-free correlations: characterising criticality in ecosystems

20th March, 2018

Manuscript type: **Synthesis**

Manuscript elements: Figure 1, figure 2, figure 3, figure 4, figure 5, figure 6, online appendices A to D (including Appendix Tables 1,2 and Figures A1 to A5).

Number of words in main text: 8253

Number of sections in main text: Six sections, three boxes and one glossary.

Keywords: Criticality, Power-law, Regime Shift, Patch Size Distribution, Power Spectrum, Percolation, Early Warning Signals.

Prepared using the suggested LaTeX template for *Am. Nat.*

Abstract

Diverse ecosystems exhibit clusters that follow scale-free size distributions and lack a characteristic scale. In phase-transition theory, it is well known that scale-free behaviours arise at critical points. Scale-free behaviours, therefore, typically indicate a lack of resilience. Yet, many ecological studies associate loss of scale-free clustering with reduced resilience, presenting an intriguing inconsistency with the physics literature. Our synthesis of literature on cluster sizes in physics and ecology reveals that empirically observed scale-free clustering in ecosystems can be parsimoniously explained by facilitative interactions. Our synthesis of theory, aided by analyses of a minimal spatial model, shows that scale-free clustering may occur far away from, near or at the critical point of ecosystem collapse depending on the strength of local facilitation. Thus, contrary to current thinking in the literature, we conclude that clustering patterns are unrelated to critical points of ecosystem collapse. Scale-free clustering, instead, indicates a different threshold called a percolation point, which signifies the onset of spanning clusters in the landscape. Finally, we suggest that ecosystem criticality can be characterized by scale-free spatial correlations in the system. Our synthesis resolves subtle links between local facilitative interactions and macroscopic patterns of scale-free clustering, scale-free correlations and ecosystem resilience, and offers future directions to investigate these phenomena.

Introduction

Desertification of semi-arid ecosystems (van de Koppel et al., 2002), eutrophication of lakes (Carpenter et al., 1999), spread of diseases (Chaves et al., 2012), invasion (Hansen et al., 2013) and community shifts in coral reefs (Knowlton, 2004) are some examples of state transitions or regime shifts in ecological systems. Some of these transitions can be abrupt and irreversible, leading to catastrophic loss of wildlife, habitats, and ecosystem services. Such transitions, also known as critical transitions, happen when a system crosses a certain threshold or critical point of environmental conditions. Over the last decade, several studies have devised and validated methods to detect the vulnerability of ecosystems to transitions (Carpenter et al., 2011; Dakos et al., 2012; Eby et al., 2017; Guttal and Jayaprakash, 2009; Kéfi et al., 2007; Kéfi et al., 2014; Scheffer et al., 2009). One such method is based on the idea that self-organised clustering in ecosystems can offer signatures of resilience (Kéfi et al., 2007; Kéfi et al., 2014; Rietkerk et al., 2004; von Hardenberg et al., 2001). Such patterns typically result from an interplay of facilitative and competitive interactions among organisms (Manor and Shnerb, 2008*b*; von Hardenberg et al., 2010*a*). However, these interactions not only shape clumping of organisms on a landscape but also fundamentally affect the stability of ecosystems (Kéfi et al., 2016; Xu et al., 2015*b*). A comprehensive understanding of how local interactions between organisms scale to their spatial distribution and ecosystem stability is of broad interest from the perspectives of both pure and applied ecological sciences.

Recent ecological studies suggest that the resilience of ecosystems can be inferred by measuring spatial clustering properties (Kéfi et al., 2007; Kéfi et al., 2014; Scanlon et al., 2007). While many ecosystems exhibit self-organised clusters of characteristic shape and size (Klausmeier, 1999; Rietkerk and van de Koppel, 2008; van de Koppel and Reitkerk, 2004), several ecosystems also in fact show irregular sized clusters without any characteristic form (see Fig 2). Such clumping patterns without a well-defined scale are called scale-free clustering. Mathematically, these are described by power-law size distributions within a certain range of exponents (see Box for further details on power-laws and scale-free patterns). Some theoretical and empirical studies in Ecology suggest

that power-law cluster size distributions are indicative of resilient ecosystems (Kéfi et al., 2007; Scanlon et al., 2007). When ecosystems are stressed, however, clusters fragment leading to loss of large patches. This results in a qualitative change the properties of cluster sizes, from a power-law to an exponential distribution. The disappearance of power-law clustering is, therefore, hypothesised to represent loss of resilience in ecosystems (Fernández and Fort, 2009; Kéfi et al., 2007; Kéfi et al., 2011, 2014; Lin et al., 2010; Weerman et al., 2012).

The association of power-law clustering with resilience in dynamical systems, from a theoretical perspective, is puzzling. To understand why, we need to revisit the theoretical underpinnings of ecosystem dynamics and indicators of resilience, much of which is based on principles derived from the theory of phase transitions and bifurcations (Dakos et al.; Scheffer et al., 2009; Strogatz et al., 1994; Wissel, 1984). This theory predicts that the interactions that stabilize a system become increasingly weak as the system nears a critical point. Consequently, there is a delay, or slow down, in the system's recovery from perturbations. Eventually, very close to or at the critical point, the perturbations decay as a power-law function of time (see Box); this is unlike stable systems in which perturbations decay exponentially fast. This phenomenon, called *critical slowing down*, has been widely used to devise methods to forecast the approach of critical transitions in ecosystems (Scheffer et al., 2009; Strogatz et al., 1994; Wissel, 1984). It is, however, only one of several power-law relations that arise at critical points (Ma, 2000; Sethna, 2006; Stanley, 1999). The emergence of archetypal features in critical systems, that are, surprisingly, independent of system-specific details, is called criticality (Christensen and Moloney, 2005; Pascual and Guichard, 2005; Solé et al., 1999). Among these, an ecologically relevant quantity is the spatial autocovariance function of the ecosystem state variable; it measures how perturbations decay over distance. The covariance function becomes scale-free at/near critical point, implying that perturbations spread over extended spatial scales. Put simply, theories predict emergence of various power-law relations in critical systems, but typically not in resilient systems. Therefore, at the outset, it is intriguing that resilient ecosystems are distinguished by power-law clustering and it will be useful to understand how this phenomenon relates to scale-free correlations.

Scale-free clustering has previously been investigated in two class of models. One is the so called percolation model in the physics literature (Grimmett, 1999; Stauffer, 1979), which in ecological terms can be thought of as a spatial null (no interactions) model that produces clustering even when occupancy of space is random. Second is in the context of ecosystem pattern formations (Guichard et al., 2003; Pascual and Guichard, 2005; Scanlon et al., 2007) where it is referred to as 'robust criticality' (Kéfi et al., 2011; Pascual and Guichard, 2005). Robust criticality is the phenomenon of properties associated with criticality (Pascual and Guichard, 2005; Roy et al., 2003), such as scale-free patterns (in clustering), occurring over a broad region of environmental conditions, even away from critical points. Furthermore, some of these models predict that the loss of scale-free and power-law behaviours can be used as signatures of reduced resilience of ecosystems (Kéfi et al., 2007; Kéfi et al., 2011, 2014). These models of ecosystem dynamics incorporate various ecological processes that are relevant to the focal ecosystem. For example both dryland vegetation and mussel-bed dynamics models incorporate processes such as dispersal, birth, disturbance and death of vegetation/mussel at local sites. These processes depend on multiple facilitative and competitive interactions operating at local and global scales. While these studies make insightful and empirically testable predictions about spatial patterns in these ecosystems, they are not amenable to analyses of generic relationships between microscopic processes (facilitation) and macroscopic patterns (e.g. clustering and ecosystem resilience). Consequently, even though some studies fail to find the expected trends of cluster size distributions with decreasing resilience (Maestre and Escudero, 2009; Meloni et al., 2017*b*; Schneider and Kéfi, 2015; Weerman et al., 2012), such exceptions are argued on a case-by-case basis. We argue that this is due to the absence of a unified perspective on how the observed scale-free clusters in ecosystems, the phenomenon of percolation, as well as the theoretically expected scale-free correlations at criticality, all relate to each other. Moreover, with increasing availability of high resolution spatial images and empirical data from several regions across the globe, a comprehensive understanding of these matters is crucial not only for conceptual unification but also to enable correct application of these theories.

Based on these considerations, the main purpose of our *Synthesis and Perspective* article is to investigate the emergence of spatial clustering and its link to resilience or criticality of ecosystems. To do so, we first review and synthesise the literature on how local ecological processes lead to the formation and dynamics of clusters. Further, following earlier studies (Roy et al., 2003), we use the percolation theory from physics literature as a baseline framework to understand scale-free clustering. Owing to interdisciplinary nature of various concepts, we present important terms and concepts including power-laws, scale-free patterns, correlations and glossary of terms via summaries in boxes and tables (Table 1; Boxes 1, 2 and 3). Our synthesis reveals the importance of facilitative interactions in the emergence of scale-free clustering in various ecosystems. To probe the relationship between facilitation, clustering and resilience, we use a minimal spatially-explicit model which, unlike previous complex models of irregular pattern formations, decouples the essential processes of facilitation and environmental stress. This enables us to establish that, counter to current thinking in the literature, clustering is in fact unrelated to resilience. Scale-free clustering is indicative of a different critical point, the percolation threshold. We then investigate the emergence of scale-free spatial correlations at criticality. Finally, we discuss future directions of research to quantify patterns and dynamics of clustering to infer ecological interactions.

Glossary

1. Cluster: A group of organisms who are connected via at least one near-neighbour. Near-neighbours are typically defined as those within a threshold distance.
2. Regime shifts: Qualitative changes in ecosystem state. These shifts can be abrupt or gradual functions of the underlying drivers.
3. Phase transition: A continuous or a discontinuous transition in a macroscopic property of the system. Even continuous transitions are necessarily characterised by a discontinuity in some macroscopic quantities such as rate of change of state variable. Ecologically relevant macroscopic quantities are canopy cover, biomass density, connectivity, etc.
4. Critical point: The value of a state variable (such as density) or the value of an environmental condition (such as rainfall) at which a system undergoes a phase transition.
5. Criticality: Characteristic features of a system at a critical point. These features are often independent of the system-specific details.
6. Robust criticality: The appearance of critical features over a broad range of conditions, and not only near the critical point.
7. Scale-free: Lacking a characteristic scale, or a quantity having infinite average value.
8. Diverge: Tending to infinity.
9. Percolation: Existence of a path (of sites in a particular state) from each edge of a system to all others.
10. Resilience: The amount of disturbance a system can withstand without transitioning to an alternate state.

11. Stability: The rate at which a system recovers from perturbations.
12. Facilitation: Interactions between individuals resulting in enhanced reproduction and/or reduced death rates of both individuals. Here, also referred to as positive feedbacks.
13. Spatial autocovariance function: Covariance between states at two locations as a function of the distance between them.
14. Power spectrum/Spectral density function: Strength of fluctuations as a function of frequency; it is the Fourier transform of the autocovariance function.

Box 1: Power-law and scale-free behaviours

Biology is replete with examples of self-organised spatial clustering (Guichard et al., 2003; Rietkerk and van de Koppel, 2008; von Hardenberg et al., 2001). Often, this clustering occurs in the form of irregular clumps with a wide range of sizes. Such a pattern is mathematically described as a power-law function of clump sizes - i.e the frequency of clumps of a particular size (denoted by x) decays as a power function of the size i.e. $f(x) = c\,x^{-\beta}$, for all clusters above a size $x > x_{min}$ with c and β being constants. This function has several characterisitic properties which we describe below.

Heavy-tailedness

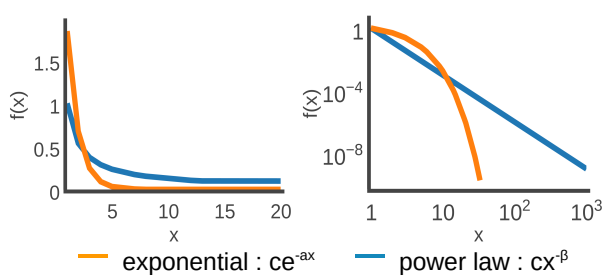


Figure 1: The plot on the left shows that the power-law function has a heavier tail, i.e. higher frequency ($f(x)$) of occurrence of large events, than in an exponential function. The plot on the right shows that power-law function is a straight line on double logarithmic axes; the heavier tail of power-law is evident here too.

The power-law frequency distribution has much higher occurrences of extreme events than predicted by commonly used distributions such as Gaussian or exponential distributions (Fig 1); this feature of the power-law distribution is also called *heavy tailedness*.

Scale-invariance

The functional form and the exponent of power-law functions are unaffected by changes in the scale of observation. Consider the mathematical expression of the function, $f(x) = c\,x^{-\beta}$. Now if the scale of observation is changed from x to kx, where k is a constant, then $f(kx) = ck^{-\beta}\,x^{-\beta} =$

$k^{-\beta} f(x)$. This property, common to all power-laws, is known as *scale-invariance*.

Scale-free power-laws

Power-laws with an exponent $\beta \leq 2$ mathematically describe features *that lack a characteristic size/length scale*. To see this, we observe that when $\beta \leq 2$ the mean of this distribution is infinite. Exact expressions for the mean ($\bar{x}$) and variance (σ_x^2) of the normalised power-law distribution, denoted by $p(x)$, are given by

$$\bar{x} = \int_{x_{min}}^{\infty} x p(x) dx = \begin{cases} x_{min} \frac{\beta-1}{\beta-2} & \text{if } \beta > 2 \\ \infty & \text{if } 1 < \beta \leq 2 \end{cases}$$

$$\sigma_x^2 = \int_{x_{min}}^{\infty} (x - \bar{x})^2 p(x) dx = \begin{cases} x_{min}^2 \frac{\beta-1}{(\beta-3)(\beta-2)^2} & \text{if } \beta > 3 \\ \infty & \text{if } 1 < \beta \leq 3 \end{cases}$$

Thus, there is no characteristic size or typical length scale in this distribution, when $\beta \leq 2$, and therefore the distribution is called *scale-free*. Power-law distributions of biological quantities with exponents $\beta \leq 2$ are therefore intriguing. Such distributions, however, are not uncommon and have been documented in various ecosystems (Fig 2)

In this review, we focus only on scale-free patterns. However, scale-invariant and scale-free patterns are often not clearly distinguished in the literature. It is *only power-laws with an exponent* $\beta \leq 2$ that are scale-free and this distinction is particularly important when trying to understand critical phenomena.

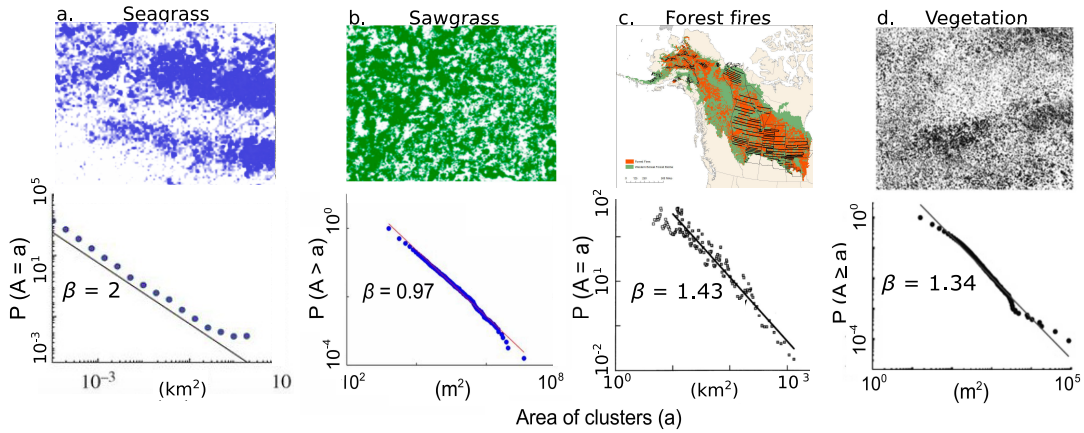


Figure 2: Scale-free cluster size distributions in different ecosystems and representative snapshots (not necessarily from the same study area or time period) of (a) West broad ledges seagrass near the isle of scilly, (Irvine et al., 2016) (b) Saw-grass in everglades wetlands, USA (Foti et al., 2013) (c) Forest fires in Alaskan boreal forests, USA (1990-91) (Malamud et al., 1998) and (d) Vegetation in Kalahari, Namibia (Scanlon et al., 2007)
Top row image credits: modified from (Duffy et al., 2017) https://doi.org/10.1016/j.ecss.2017.11.001 [CC BY] http://creativecommons.org/licenses/by/4.0/, (Foti et al., 2013), U.S. Geological Survey,Department of the Interior/USGS U.S. Geological Survey Map created by Tyler Lewis/USGS. Data (1995-2014), (Scanlon et al., 2007)

Positive feedbacks promote power-law clustering at relatively low densities

Scale-free clustering is seen in diverse ecosystems, including drylands, mussel beds, seagrass beds, sawgrass and forest fires (see Box , (Guichard et al., 2003)). Although these systems are often shaped by strong positive interactions (Aguiar and Sala, 1994; Foti et al., 2013; Guichard et al., 2003; Scanlon et al., 2007), we first discuss how scale-free cluster-size distributions are also realised in 'null models' that are devoid of any interactions in space. In null models, birth and death rates are density independent and individuals occupy space randomly. Consequently, the density of occupied sites changes from large values to a bare state as a gradual/smooth function of local birth/death rates (Grimmett, 1999; Kéfi et al., 2011). These null models are widely studied in the physics literature in the context of percolation. Percolation is the movement or spread of an agent through a system via a connected path of sites, from any edge of the system to all others (Stauffer, 1979). Despite the lack of positive feedbacks in these null models (henceforth called percolation models), scale-free clustering occurs at a particular density of the occupied sites, known as per-

colation density. For ecological contexts, a relevant geometry is that of two dimensional square lattice for which the percolation density is 0.59 (Grimmett, 1999).

The densities that correspond to power-law clustering in ecosystems are typically lower than the above mentioned percolation density. For example, regions in the Kalahari, ranging in density from 0.14 to 0.54, all show power-law size distributions of vegetation clusters (Scanlon et al., 2007); a bulk of these systems exhibit exponent of the power-law $\beta < 2$, and are thus scale-free. Spatial ecological models of ecosystems that aim to explain these scale-free clustering all assume varying degrees of positive-feedback interactions in the system (Grassberger, 1993; Guichard et al., 2003; Kéfi et al., 2007; Manrubia and Solé, 1997; Scanlon et al., 2007). Although these models often incorporate system-specific processes and are consequently complex involving many parameters, they have commonalities. For example, they all assume, in some form, increased birth (or reduced death) rates of individuals who are surrounded by others (Box 2). Below, we explain how positive feedbacks lower the density at which scale-free clustering can occur.

The emergence of clustering depends on how local interactions between individuals scale to cluster dynamics. In percolation (null) models, bigger clusters are more likely to merge with other clusters, resulting in larger growth rates for larger clusters. This baseline difference in growth rates between clusters of different sizes is determined only by the density of the landscape (Manor and Shnerb, 2008*b*). Facilitation further increases these size-dependent differences in cluster growth rates, at all densities. Theory predicts that scale-free clustering emerges whenever clusters grow in proportion to their size, known as proportionate growth (Manor and Shnerb, 2008*a*). In percolation models, proportionate growth occurs only at the percolation density, which is 0.59 for a square lattice (Grimmett, 1999; Manor and Shnerb, 2008*b*). In models with local facilitation, proportionate growth and thus scale-free clusters occur at lower densities than 0.59 (Scanlon et al., 2007), offering a potential explanation for the lowered densities at which scale-free clustering is seen in ecosystems.

Indeed, there is ample empirical evidence of such local facilitative interactions in these ecosystems (Aguiar and Sala, 1994; Boada et al., 2017; Dell et al., 2016; Foti et al., 2013; Guichard et al.,

2003; Kéfi et al., 2007; Knowlton, 2004; Maestre et al., 2003; Scanlon et al., 2007). For example, in semi-arid landscapes, seed germination and seedling survival probabilities are higher in the neighbourhood of other plants than out in the open (Aguiar and Sala, 1994; Maestre et al., 2003). This results from reduced light and heat stress as well as increased water availability to young saplings in the vicinity of adult plants. Similarly, in mussel-beds, steadfast attachment of mussel to the substrate is directly dependent on the attachment of neighbours (Guichard et al., 2003). Moving beyond terrestrial landscapes, in macroalgal beds, recruitment and survival of macroalgal fronds shows density dependence due to the protection offered by neighbours from herbivory by sea urchin and fish (Boada et al., 2017; Dell et al., 2016). Thus, models together with empirical data indicate that positive feedbacks lower the density at which power-law clustering occurs in ecosystems.

Box 2: Spatial model with positive feedback

As we mentioned in the Introduction section, several spatial models in ecology try to explain power-law clustering but due to their relative complexity, it is difficult to clearly elucidate the role of facilitation on clustering and resilience (Guichard et al., 2003; Kéfi et al., 2007; Manrubia and Solé, 1997; Scanlon et al., 2007). To address this problem, we employ a simple spatially-explicit model with only two parameters - one to control baseline reproduction rates, and the other to control strength of local positive feedbacks. Each cell in this cellular automata model is updated probabilistically depending on states of cells in its neighbourhood and all interactions are local (see Fig 3). The simplicity of this model allows us to decouple the effects of environmental stress and facilitation on spatial patterns in ecosystems. The simulation rules and sequence are illustrated in Fig 3 and (Eby et al., 2017). Detailed model description and analytical methods can be found in (Lübeck, 2006)

Facilitation induces abrupt regime shifts: Local positive feedbacks in ecosystems are known to cause non-linear responses to stress (Kéfi et al., 2010, 2016; Xu et al., 2015*b*). Consider the

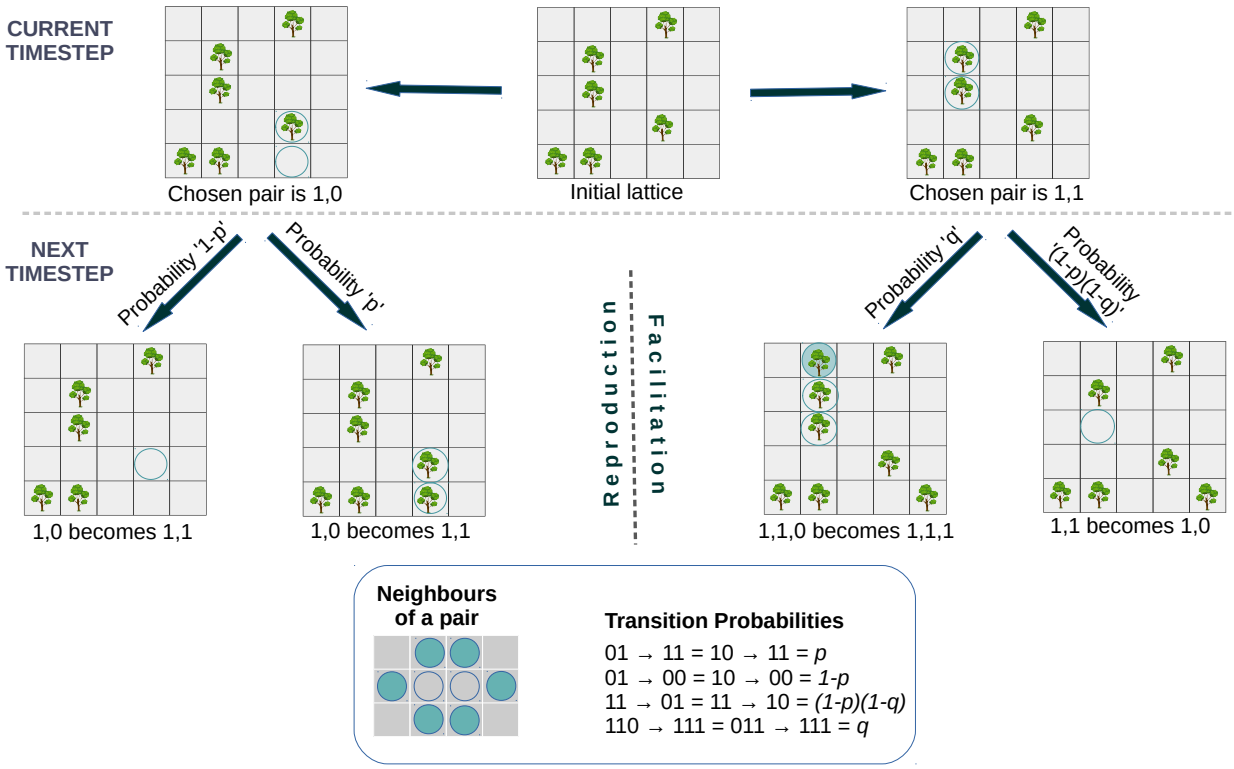


Figure 3: Schematic representation of the model and simulation procedure, for a given 'Initial lattice' shown at the centre of the top row. Light blue circles represent (randomly) chosen cells to update. Depending on the states of chosen cells, the update scheme results in reproduction or death (left part of second row) or facilitation (right part of the second row). The box at the bottom shows (i) neighbours of a focal pair of cells and (ii) state dependent transition probabilities of chosen cells.

example of plants in a semi-arid ecosystem. The presence of neighbours offsets water and heat stress to individual plants. Consequently, reproduction and death rates are heterogeneous over the landscape with local areas of high plant density having a higher rates of reproduction (and lower death rates) than the landscape's average. Strong positive feedback interactions, thus, offset the effects of environmental stressors like aridity. However, this produces an Allee effect on the landscape such that plants require a minimum threshold of neighbourhood density to survive. Increasing stress can then potentially collapse the entire system (Kéfi et al., 2010).

Indeed, our model too shows that when facilitation is weak, the system undergoes a continuous transition from an occupied to a bare state (Fig 4). As facilitation strength increases, the system can maintain a high density state even for higher levels of stress; but the system also exhibits an abrupt transition to a bare state when the stressor crosses a threshold.

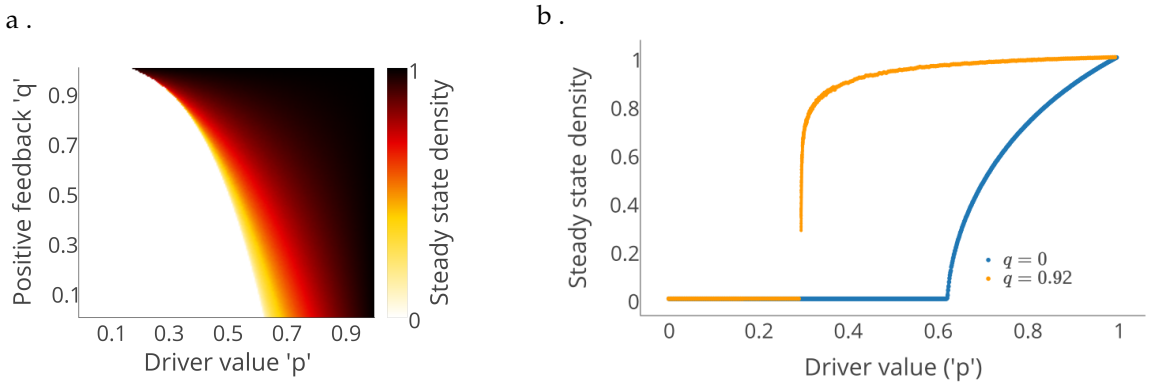


Figure 4: (a) shows steady state density as a function of changing driver value for different values of positive feedback. (b) shows a close look at the nature of this change for two values of positive feedback, $q = 0$ and 0.92. We find that facilitation increases the non-linearity and may even cause an abrupt collapse in response to stress.

Scale-free clustering is not related critical point of ecosystem collapse

As mentioned in earlier sections, several studies over the last decade have suggested that a power-law distribution of patch sizes indicates a resilient ecosystem (Kéfi et al., 2007; Kéfi et al., 2011, 2014; Scanlon et al., 2007). Further, they suggest that the fragmentation of large patches and consequent thinning of the tail of the cluster-size distribution could serve as an indicator of a stressed ecosystem on the brink of collapse (Kéfi et al., 2007; Kéfi et al., 2011, 2014). Several studies, however, do not find evidence, in either models or data, for this hypothesis (Maestre and Escudero, 2009; Meloni et al., 2017*b*; Moreno-de las Heras et al., 2011; Schneider and Kéfi, 2015). Therefore, the generality of relationship between cluster sizes and resilience remains unresolved. To resolve this, we analyse the model presented in Box . This model simplifies the more complex and system-specific interactions of other models to two key processes: local reproduction and facilitation. Our analysis of this model reveals that a) there is no relationship between spatial clustering and transitions in the overall density of the ecosystem, and b) power-law clustering is indeed associated with a transition, but in a different quantity which is known as the *percolation probability*.

To examine the relationship between spatial clustering and ecosystem resilience, let us consider at the role of facilitation in shaping both spatial clusters and resilience. As we argued in Section 2 , facilitation lowers the density at which scale-free clustering emerges. Further, as is well

known and also seen in our model (see Box 4), positive feedbacks also promote non-linearities in the system's response to stress, thus promoting abrupt collapse from higher densities (Fig 4. Putting the above two observations together, we hypothesise that depending on the strength of facilitation, power-law clustering can occur at any distance from the critical density of collapse. Indeed, our model analyses confirms this: the inset of Fig 5a shows the emergence of power-law clustering far from the critical point whereas the inset of Fig 5b shows power-law clustering very near, even possibly at, the critical point of collapse. Thus, cluster-size distribution reveals the existence of positive feedbacks in the ecosystem but very little about its resilience.

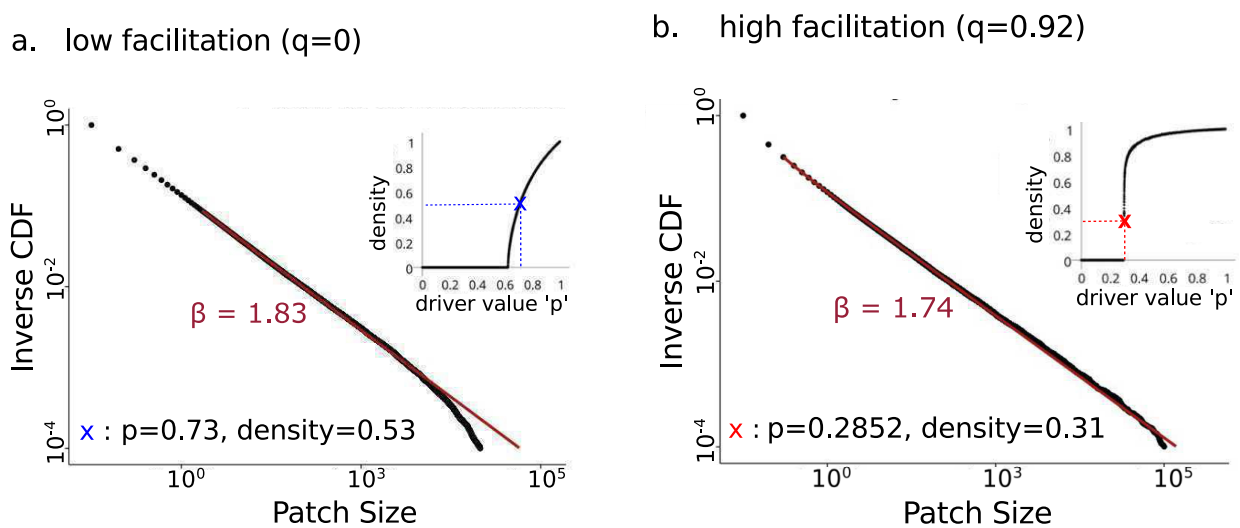


Figure 5: Strength of facilitation, rather than distance to critical transition, determines the cluster size distribution. The Inverse CDF is the inverse cumulative distribution function. The values of driver and density at which we find a scale-free cluster size distribution are shown as crosses in the insets of (a) and (b). (a) shows that when facilitation is weak ($q = 0$), scale-free clustering is seen far from ecosystem transition, consistent with previous hypotheses (Kéfi et al., 2007; Pascual and Guichard, 2005; Scanlon et al., 2007). (b) shows that when facilitation is strong ($q = 0.92$), scale-free clustering can occur right at the transition point; this contradicts previous hypotheses associating scale-free cluster size distributions with resilience. For the fitted function $kx^{-\beta}$ wherein $k = (\beta - 1)x_{min}^{\beta-1}$, $x_{min} = 17$ in (a) and 3 in (b). See Appendix D for cluster size distributions at other values of p and q.

Scale-free clustering emerges at the percolation point

Few ecological studies have examined the association between scale-free clustering and percolation in (non-null) models with spatial-interactions (but see (Roy et al., 2003)). Percolation probability is the probability that an agent (e.g. fire) permeates through a substance (forest). This depends

on the availability of a connected path of sites in a conducive state (e.g. vegetated) from one edge of the system to all others. The percolation probability can, therefore, be measured by the probability of occurrence of a spanning cluster of occupied cells in the system. As stated previously, for a square lattice, null models exhibit a phase transition from zero percolation probability to finite values at a density of 0.59. This is exactly the density, also called percolation density, at which the system exhibits scale-free clustering. Consequently, the average cluster size diverges and the system exhibits no scale, or is called scale-free. In other words, scale-free clustering characterises the percolation transition in null models.

We show that our spatial ecological model too exhibits a transition in percolation probability as a function of density (Fig 6). Just as in null models, this transition is associated with scale-free clustering. We find this association to be true for a wide range of values of strengths of facilitation.

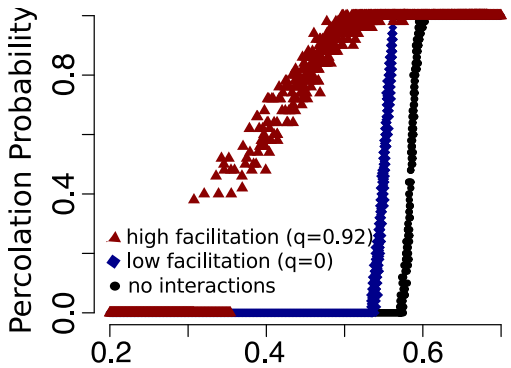


Figure 6: Percolation transition for different strengths of facilitation and a null model. Percolation transition occurs close to density 0.59 for the null model, 0.53 for low facilitation ($q = 0$) and 0.31 for high facilitation ($q = 0.92$). We note that the percolation transition is exactly at that density where power-law cluster size distributions are observed; see Fig 5.

The percolation density is lower for the system with higher facilitation (Fig 6), consistent with our synthesis of empirical results in the previous section . Weak facilitation leads to continuous change in percolation probability whereas strong facilitation, owing to stronger nonlinear response of the system, makes it discontinuous (Fig 6).

Thus, scale-free cluster-size distribution is a signature of criticality, but that associated with the percolation point. At this threshold, the average cluster size diverges (Fig 6). The density at which percolation point occurs is mediated by the strength of local facilitation in the system. We reiterate that cluster size distributions are not associated with the regime shift or critical transition typically studied in the context of ecosystems where a global density variable (e.g., vegetation cover) collapses.

Several studies posit that the emergence of scale-free clustering at the percolation point represents a case of robust criticality, i.e. the existence of scale-free clusters over a broad range of

conditions (Pascual and Guichard, 2005; Roy et al., 2003). We find that in our model, scale-free clustering occurs only at the percolation point. At this juncture, we emphasize the distinction between scale-free clustering and scale-invariant clustering. Whereas scale-invariance is a property of all power-laws, scale-free patterns occur only for power-laws with exponents less than two (Box 1). Scale-free behaviours are associated with diverging quantities and thus, critical phenomena. This distinction between scale-free and scale-invariant patterns is sometimes not made sufficiently clear, leading to the confusion where all power-laws are referred to as scale-free (Kéfi et al., 2011, 2014; Pascual and Guichard, 2005; Roy et al., 2003) and thought to reflect properties of critical phenomena.

Scale-free spatial correlations arise at critical points of ecosystem collapse

So far, we have demonstrated that scale-free cluster sizes do not represent resilience and hence cannot indicate imminent regime shifts. However, the theory of phase transitions posits the emergence of scale-free features near/at critical points. Here, we argue that the right way to characterise criticality associated with regime shifts is by scale-free behaviour in spatial autocovariance function (Fig 7; Appendix E).

As an ecosystem approaches a critical point, its return to equilibrium state, when disturbed, becomes progressively slower. This phenomenon of critical slowing down (Dakos et al.; Ma, 2000; Scheffer et al., 2009; Wissel, 1984) has two implications - increased spatial correlations (Dakos et al., 2010) and increased spatial variance (Guttal and Jayaprakash, 2009). To understand this, consider how a perturbation at any location in the ecosystem will spread in space. First, as the system approaches a critical point, ripples caused by each perturbation will propagate to ever larger distances in the system (Ma, 2000; Sethna, 2006). A measure of perturbation spread, the correlation length, rapidly increases (Dakos et al., 2010; Ma, 2000; Sethna, 2006). Second, as the perturbations persist for longer duration, further disturbances enhance the amplitudes of the ripples. This man-

ifests as increasing spatial variance in the ecosystem as it moves towards the critical point (Guttal and Jayaprakash, 2009). Here, we consider the spatial autocovariance function, defined as covariance of densities at two locations separated by a distance r (Box). This function captures both spatial variance and correlations. Below we argue that spatial autocovariance function at the critical point becomes a power-law function of distance (r), with an exponent that reflects an infinite correlation length (Sethna, 2006). Thus, the system has scale-free spatial correlations at critical points of ecosystem collapse.

Before we show calculations of spatial autocovariance for our model, we make a couple of technical remarks. First, physicists often refer to the autocovariance function as the 'correlation function'; some theoretical papers in ecology also do the same (Roy et al., 2003). Here, we have adopted the standard terminology that is used in quantitative ecology literature (see Appendix E for the definition). Second, the theory of phase transition predicts critical slowing down and consequent scale-free behaviour at critical points of *continuous phase transitions*. Here, using the simple ecological model presented in Box , we demonstrate that scale-free behaviour characterises critical points of not only continuous but also discontinuous transitions.

Calculation of the spatial autocovariance function is often beset with statistical and computational difficulties. Therefore, we focus on a mathematically equivalent measure of correlations in spatial patterns via its power spectrum (Kéfi et al., 2014) (Appendix E). It can be shown that the power spectrum is the Fourier transformation of the autocovariance function (Reif, 2009). The power spectrum of a spatial pattern provides a measure of the relative contribution of fluctuations at different spatial frequencies in the system, to its overall pattern. It is known in the ecology literature that as systems approach critical points, the low frequency modes begin to dominate their power spectrum (Carpenter and Brock, 2010; Kéfi et al., 2014). However, the full functional form of the power-spectrum is rarely quantified (but see (Couteron, 2002) in the context of periodic patters of dryland vegetation). This quantity is crucial to inferring critical behaviour. Simulations of our model shows that the power-spectrum becomes scale-free at critical points (Fig 7). We explain in Appendix E that a scale-free power spectrum is indicative of a scale-free autocovari-

ance function. Criticality associated with density collapse of an ecosystem is thus captured in its power-spectrum.

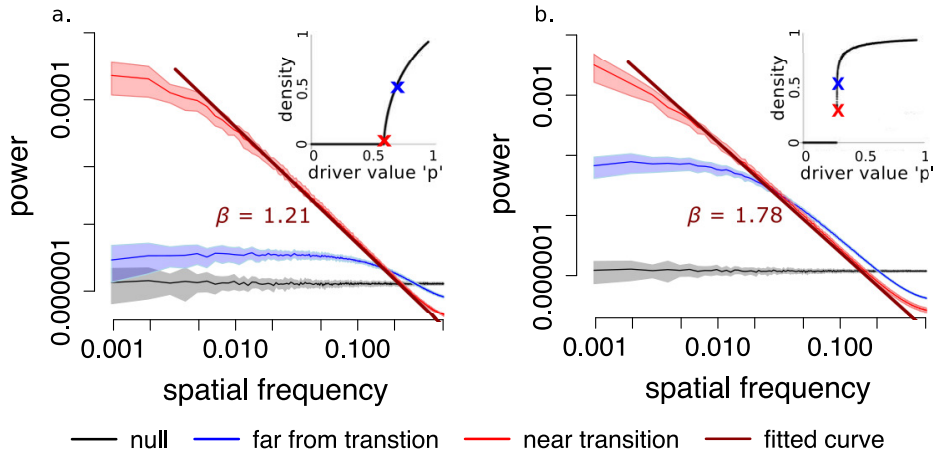


Figure 7: The power-spectrum of systems very near/at the critical point decays as a power-law function of spatial frequency. This is independent of the nature of interactions in the system, with (a) showing the model with low facilitation i.e. $q = 0$ and (b) showing high facilitation i.e. $q = 0.92$). Lines represent the mean trend and bands, the SD. For the fitted function $kx^{-\beta}$, $k = 2.02 * 10^{-7}$ when $q = 0$ and $4.65 * 10^{-8}$ when $q = 0.92$. Grey colour represents trends for the null model.

Scale-free correlations in density (described above) and scale-free clustering (Section) both indicate emergence of large spatial scales in the system. However, they capture fundamentally different properties. Scale-free correlations in density indicate that *perturbations* spread to large distances in ecosystems; therefore, it captures the dynamics of perturbations and hence can be used to infer stability or lack thereof. In contrast, scale-free clusters indicate the presence of large clusters. Therefore, clustering properties are unrelated to resilience, as we indeed demonstrate in Fig 5.

BOX 3: Covariance, correlation and spectral function

One way to capture the spread of disturbance in a system or the length scale of spatial fluctuations, is by constructing the spatial covariance function. The spatial autocovariance function for density ρ for a distance r is defined as

$$C(r) = \langle (\rho(\mathbf{x}) - \bar{\rho})(\rho(\mathbf{x}') - \bar{\rho}) \rangle \tag{1}$$

where $\bar{\rho}$ represents mean density over the entire landscape, angular brackets denote average over all locations $\mathbf{x}$ and $\mathbf{x}$ in the landscape that are separated by a distance r. Ecologists widely use the correlation function which is defined as

$$K(r) = \frac{\langle(\rho(\mathbf{x}) - \bar{\rho})(\rho(\mathbf{x}') - \bar{\rho})\rangle}{\sigma^2}) \tag{2}$$

where σ^2 is the spatial variance of densities in the ecosystem. Thus the covariance function is a production of the correlation function and the variance.

The mean of the covariance function is called the correlation length, or the average distance to which local fluctuations spread. The correlation length becomes infinite at the critical point. This means that the covariance function then follows a power-law with an exponent less than 2 [see Box].

The power spectrum, denoted by $S(k)$, is the Fourier transform of its autocovariance function (Baugh and Murdin, 2006; Reif, 2009). Therefore, it can be calculated as

$$S(k) = \int C(r)e^{-ikr}dr \tag{3}$$

At the critical point, we expect the spatial covariance function to exhibit a power-law relation with distance

$$C(x) = c_0 x^{-\alpha} \tag{4}$$

where c_0 is a constant and α is an exponent less than two. The corresponding spectral function for an n-dimensional system is given by

$$|S(\mathbf{k})| \sim \mathbf{k}^{-(n-\alpha)}$$

Thus, at criticality, the spectral function also follows a power law with an exponent $\alpha - n$. Therefore, evidence of a power-law spectral function is also evidence of a power-law autocovariance function.

Discussion

Scale-free behaviour is known to occur in critical systems. It is thus intriguing that several ecological studies associate loss of scale-free clustering with reduced resilience. Our synthesis reveals that scale-free clustering (or lack thereof) is unrelated to ecosystem resilience. When ecosystems are in the vicinity of a critical point of collapse, we do indeed observe scale-free behaviour but in the spatial autocovariance, or spectral function, of local densities. Scale-free clustering, on the other hand, is associated with the emergence of spanning clusters, also called percolation, which represents a phase transition in a different state variable and is not necessarily associated with a collapse. We argue that an understanding of how local facilitation scales to macroscopic patterns reveals intricate connections between scale-free clustering, ecosystem resilience and critical phenomena.

Local positive feedbacks, clustering and resilience

Seminal ecological models generating scale-free clustering observed in ecosystems (Kéfi et al., 2007; Scanlon et al., 2007) assume that local birth/death of trees, in addition to being positively influenced by local density, is negatively regulated by *global-scale feedbacks*. Mechanisms such as rapid spread of water in the landscape (von Hardenberg et al., 2010*b*) are offered as potential explanations for negative regulation of local growth due to global-scale vegetation density. However, some theoretical studies show that irregular clusters cannot even occur under conditions of strong negative feedbacks (Manor and Shnerb, 2008*a*). Indeed, based on our synthesis ((Manor and Shnerb, 2008*a*,*b*) and Fig 5), we demonstrate that there is no need to invoke global-scale feedbacks; in fact, local positive feedbacks alone can explain the emergence of scale-free clustering in these systems.

Several empirical studies find neither scale-free clustering (Weerman et al., 2012; Xu et al., 2015*a*) nor the expected shifts of cluster-size distributions with increasing stress (Casey et al., 2016). However, they attribute this to an absence/distruption of global negative feedbacks in their sys-

tems (Casey et al., 2016; von Hardenberg et al., 2010*b*; Weerman et al., 2012)(but also see (Moreno-de las Heras et al., 2011)). As we argued in the previous paragraph, negative feedbacks aren't even a necessary condition for scale-free clustering. Furthermore, recent theoretical studies too have found the association of cluster-size distributions with resilience to be tenuous (Génin et al., 2018; Schneider and Kéfi, 2015). These studies investigate the effect of incorporating heterogeneous stressors in previous models of dryland vegetation and forest gap dynamics. Here, for example, grazing-induced mortality is lowered for individuals with more neighbours, called associative protection. When the associative protection is high, they find scale-free clustering at the critical point. These results are consistent with our synthesis because associative protection in their model is analogous to increased positive feedback (q) in our model. Indeed, with low positive-feedbacks, our model results match that of previous studies (Kéfi et al., 2007; Scanlon et al., 2007), away from the critical point. However, increasing the strength of positive feedbacks can result in scale-free clustering occurring at lower densities, closer and even at the critical point of ecosystem collapse. In other words, any form of cluster size distribution (exponential, scale-free, etc) can occur at the critical point. This conclusion of our synthesis overturns the current understanding in the literature (Kéfi et al., 2007; Kéfi et al., 2011, 2014).

Cluster-size distributions are nevertheless relevant in ecological contexts where connectivity or porosity of the landscape is of focal interest, such as in the case of forest fires or disease spread (Chaves et al., 2012; Turcotte and Malamud, 2004). We showed that scale-free clustering in our ecological model is associated with a transition in percolation probability, representing the emergence of a spanning cluster in the system. This is also seen in spatial models of predator-prey interactions (Roy et al., 2003). In the context of fire or disease outbreaks, presence of a cluster of vegetation (susceptible individuals) allows fire (disease) to easily spread within each cluster. Consequently, scale-free clustering, which indicates a highly connected landscape, signals the possibility of catastrophic fire (or disease) outbreaks. As we discuss below, these models represent a fundamentally different class of models from what we have discussed in this paper.

Our model, as well as those reviewed in our syntheses such as those of dryland vegetation and

mussel bed dynamics, all exhibit critical transitions when parameter values of the model are tuned to specific values (critical points). There are however several models where, surprisingly, the dynamics always take the system to a critical state, even without tuning any parameters. Therefore these models are called 'self-organised critical systems'. A classic example relevant to ecology is that of forest fire models. Here, criticality is characterised by the simultaneous occurrence of power-laws associated with both percolation and collapse transitions (Solé et al., 1999). Here too, unlike the hypothesis of (Kéfi et al., 2007; Kéfi et al., 2014; Scanlon et al., 2007), scale-free clusters do not indicate resilient systems.

Future directions

Our synthesis suggests some exciting directions for future research. The focus of recent research, as reviewed in this paper, has been to understanding how local interactions produce clustering properties, and how clustering properties can be used to infer resilience. However, the inverse problem of inferring ecological interactions from spatial images of ecosystems remains poorly studied. For example, the occurrence of power-law or such heavy-tailed distributions can itself be used to infer the role of local facilitative interactions in the ecosystem. Indeed, one recent study does suggest that skewness of cluster-size distributions can suggest facilitation in vegetation systems (Xu et al., 2015*a*). The bigger question remains open: can we quantify the strengths and spatial scales of facilitation and other ecological interactions between organisms by analysis of spatial images, for example via geometrical properties of clusters such as cluster sizes, fractal dimension of clusters, and the strength of spatial correlations in the system.

With recent advancements in remote sensing and reducing costs of procuring spatial images, we can also procure extensive high-resolution spatial data over time. This will enable us to quantify not only patterns, as described above, but also dynamics of various cluster properties. Unlike static properties available from a single image, dynamical properties may reflect stability of ecosystems by capturing how systems respond to perturbations. Theoretical works, inspired by studies of domain growth in phase transitions, predict rich dynamics of clusters in simple eco-

logical models exhibiting continuous and discontinuous transitions (Shnerb-JTB and Plos ONE). However, much remains to be done in integrating these studies with real data. This requires extensive theoretical and computational studies to identify suitable metrics of clustering properties, development of statistical frameworks including appropriate spatial null models and finally, empirical validations/applications based on analyses of aerial images of ecosystems.

Our synthesis predicts that scale-free behaviour in spatial correlations, measured via autocovariance or spectral functions, can characterise criticality. How does this relate to the relatively vast literature on early warning signals (EWS) of regime shifts or critical transitions (Scheffer et al., 2009)? The EWS of critical transitions (as noted in the Introduction), as well as the emergence of scale-free correlations (Section), arise from critical slowing down. The purpose of early warning signals is to detect signatures of approach to critical points. In that sense, computing simpler metrics of spatial autocorrelation at lag-1 (Dakos et al., 2010) or spatial variance (Guttal and Jayaprakash, 2009) may have advantages such as ease of computation and better statistical reliability in comparison to characterising the complete form of autocovariance or spectral functions. On the other hand, simpler metrics are also easily affected by external factors, such as increased spatial heterogeneity or external variability (Dakos et al., 2010; Kéfi et al., 2014; Sheffer et al., 2013) and hence confound interpretations. Further investigations can reveal the relative efficacy of different spatial metrics.

Concluding remarks

Our synthesis helps us disentangle processes that generate scale-free cluster sizes, scale-free correlations and how they relate to criticality. Our synthesis also offers several exciting directions of research on how geometric and dynamics of clustering can potentially reveal underlying interactions. Real world analyses however can sometimes misleadingly yield various patterns, including power-laws and scale-free behaviours due to sampling artefacts (Plank and Codling, 2009) or misfitting (Clauset et al., 2009; Meloni et al., 2017*a*; White et al., 2008). Various ways in which patterns are misconstrued as power-laws have been discussed in detail in multiple other forums (Breed

et al., 2015; Clauset et al., 2009; Stumpf and Porter, 2012). Where there is a true power-law with an exponent less than two, since it is indicative of diverging quantities, there is a tendency to associate such a pattern with a critical phenomenon. However, scale-free patterns can also arise when underlying processes operate at multiple scales and due to landscape heterogeneity (Khaluf et al., 2017; Petrovskii et al., 2011). Naive association of observed scale-free behaviours with either criticality or stability are both problematic. With the increasing availability of high-resolution spatial data, from satellites to drone based imagery, data of various biotic and abiotic drivers of ecosystems are becoming available and thus are likely to be widely deployed in the future. Our study highlights the importance of having a clear understanding of how local-interactions drive macroscopic behaviours to infer ecological interactions and resilience of ecosystems.

Data and codes

All simulation and analyses codes, with simulation datasets corresponding to results presented in this paper, have been made publicly available. Detailed instruction on execution of these codes are also provided. The repository link has been provided to the journal and will be included in the final submission.

Online Supplementary Materials

Appendix A: Detailed model description.

Appendix B: Statistical fitting of cluster-size distributions.

Appendix C: Cluster-size distributions across the phase-diagram for low and strong facilitation.

Appendix D: Power-spectrum fitting.

Competing Interests

We have no competing interests.

Online Appendix A: Detailed model description

We model the landscape as a two dimensional grid of of N x N cells, where each cell represents a discrete site that an individual (mussel, plant, etc.) can occupy. An occupied cell is denoted by 1 and an unoccupied cell, by 0. Each cell is updated probabilistically depending on states of cells in its neighbourhood (see Fig 2 of main text). Individuals can spread from an occupied cell to an empty cell in their immediate four-cell neighbourhoods (equivalent to a seed dispersal followed by germination) with probability p, or die with probability $1 - p$; we call this process of birth or death, *baseline reproduction*. *Facilitation* is incorporated as an increase of reproduction wherein each pair of individuals can spread to an empty cell in their immediate six-cell neighbourhood with a probability q, or die with a reduced probability $(1 - p)(1 - q)$. Thus, the model has two parameters, p, which controls baseline reproduction, and q, which controls the strength of facilitation. Competition manifests in this model as the decreased availability of sites for reproduction with increased local density. The simulation sequence runs as described below:

Step 1: Select a cell at random.

Step 2: If this cell is unoccupied, return to step 1. If occupied, proceed to step 3.

Step 3: Select at random, one of the four nearest neighbors of the chosen cell cell.

Step 4: If this selected neighbor cell is empty (0), update its state to 1 by probability p, else update the state of the first chosen cell to 0 (the probability of this is then $1 - p$). Return to step 1 for a new iteration.

Step 5: If the first chosen cell (in step 1) and the neighbor cell (selected in step 2) are both occupied, (a) with probability 'q' select one of the six possible nearest neighbors of the pair and make it occupied (if it it was already occupied, nothing changes), else update the first chosen cell (in step 1), to 0

The cells are, thus, updated asynchronously. Each discrete time step implies that the update rules are iterated N^2 number of times sequentially; this procedure ensures that, on an average, all sites are updated once per discrete time step.

We ran our simulations with a 1024×1024 system size at increasing resolutions of p and q to construct the steady-state phase diagrams of mean density of the landscape and identify the critical driver values. The system was considered to have reached a steady-state once the mean density had saturated. Cluster-size distributions and Power-Spectrum functions were computed from 50 replicate spatial snapshots of the system at steady-state. To compute the spanning cluster probabilities alone, we ran another set of simulations with 256×256 system-size and calculated these probabilities from 25 replicate spatial snapshots of the system at steady-state.

Onilne Appendix B: Statistical fitting of cluster-size distributions

Cluster size distributions were fit using methods proposed in (Clauset et al., 2009). It is worth recalling the methods of fitting power-laws have attracted much scrutiny in the literature. Therefore, we chose the statistical methods proposed by (Clauset et al., 2009) which are widely accepted as rigorous to fit power-law distributions and to compare with other model candidates.

Is power-law a good fit?: First step in the process is to find out if power-law is even a good fit. The exponent of the distribution was estimated using Maximum Likelihood Estimation (MLE), and x_{min} was identified by minimising the KS distance between the fitted model and data. We assessed goodness of fit for our power-law model by re-fitting synthetic power law distributions (which we generated) with the with the same estimated exponent and xmin values. The fraction of synthetic datasets that result in a fitted model with a K.S distance larger than the K.S distance calculated when fitting our dataset, was considered the p-value of our fit. As described in (Clauset et al., 2009), a p-value above 0.1 represents a good fit, and only when this condition was satisfied, we proceeded to compare with alternative models of cluster size distributions. Indeed, we found p-values of 0.49 for the low positive feedback model ($q = 0$)[see Fig 4a in main text] and 0.53 for the high positive feedback model ($q = 0.92$)[see Fig. 5b in main text]. This suggests good power-law fit of cluster size distributions for both values of facilitation, but one of them is away from critical point (Fig 4a) and the other is right at the critical point (Fig 4b).

Is power-law the best fit?: We compared power-law (PL) fit of the cluster size distributions with three different model fits: exponential (EXP), log-normal (LN) and power-law with an exponential cut off (PLE). Each of the candidate models was fit using MLE. Since power-law is a nested model of power-law with a cut-off, these two were compared using log-likelihood ratio. The other two candidate models were compared with the power-law model using Vuong test. We refer readers to (Clauset et al., 2009) for further technical details.

We know from percolation models that cluster size distributions typically shift from a bimodal to a power-law to a power-law with exponential cut off to an exponential as density in the system reduces (Kéfi et al., 2011; Stauffer, 1979). Thus, in our investigations of effects of positive feedbacks on clustering, these were obvious candidate distributions to fit to the data. In addition, we also fit and compare log-normal as a candidate function in order to make the reported results comparable with other studies discussed in (Clauset et al., 2009). However it must be noted that, till date, there exist no mechanistic processes that can yield a log-normal cluster size distribution in these systems . On the other hand, based on the theory of phase transitions, there is a well-reasoned expectation of scale-free behaviour at critical points.

Realising a true scale-free distribution requires, ideally, an infinitely large system. Our datasets consist of 50 replicates of identically sized lattices (of 1024 x 1024 cells). Even a true power-law distribution in these replicates would inevitably be best fit as a truncated power-law distribution, due to the limit imposed by the system-size. Given these finite size constraints in our data, a power-law as the best fit is inferred based on (a) the closeness of estimated parameters between the fitted power-law function and fitted power-law with exponential cut off function and (b) the range over which the power-law dominates the truncated power-law function.

For the data presented in Fig 4 of main text, power-law with exponential cut off was identified as the best fit model for both cases ($q = 0, p = 0.7225$ and $q = 0.92, p = 0.2852$). Given in Table 1 is the comparison statistics for the power-law (PL) fit with the other three considered models - exponential (EXP), Power-law with exponential truncation (PLE) and Log-normal (LN) fits.

[0]but see (Xu et al., 2015*a*) where there is an in-built scale in the model that could explain log-normal distributions

Dataset	PL Vs Exp vuong test statistic	PL Vs PLE log-likelihood ratio	PL Vs LN vuong test statistic
q=0, p=0.7225	34.31***	-53.92 ***	-2.69 (p=0.996)
q=0.92, p=0.2852	41.33608 ***	-9.71**	-15.22 (p=0.999)

Appendix Table 1: Results of likelihood ratio test for fitted power-law vs other models. Positive values suggest that the power-law is a the better fit and negetive values favour the alternative model. Significance levels are as follows : '***' for $p < 0.001$, '**' for $p < 0.01$ '*' for $P < 0.1$ and '' ' for $P > 0.1$. For both datasets, log-normal could not be ruled out as a potential fit (p value given in brackets), while power-law with exponential cut-off was found to be the best fit

We see from the estimated rate (Table 2) of the fitted power-law with exponential cut-off model, $x^{-\beta}e^{-x/X_{max}}$, that the X_{max} is larger than the largest patch-size in the system. The power-law behaviour persists without any effect of the exponential truncation till atleast four orders of magnitude in patch sizes.

Dataset	Fitted model	Exponent	Rate	X_{min}
q=0, p = 0.7225	Power law with exponential cut off	1.84	9.3×10^{-6}	17
	Power law	1.83		17
q=0.92, p = 0.2852	Power law with exponential cut off	1.75	2.9×10^{-6}	3
	Power-law	1.77		3

Appendix Table A2: Estimated parameter values of fitted power-law and power-law with exponential cut-off functions. The exponent estimates are very close for both model fits. The rate of exponential cut-off is very low, suggesting that the power-law persists over a large range of patch sizes.

Online Appendix C: Cluster-size distributions

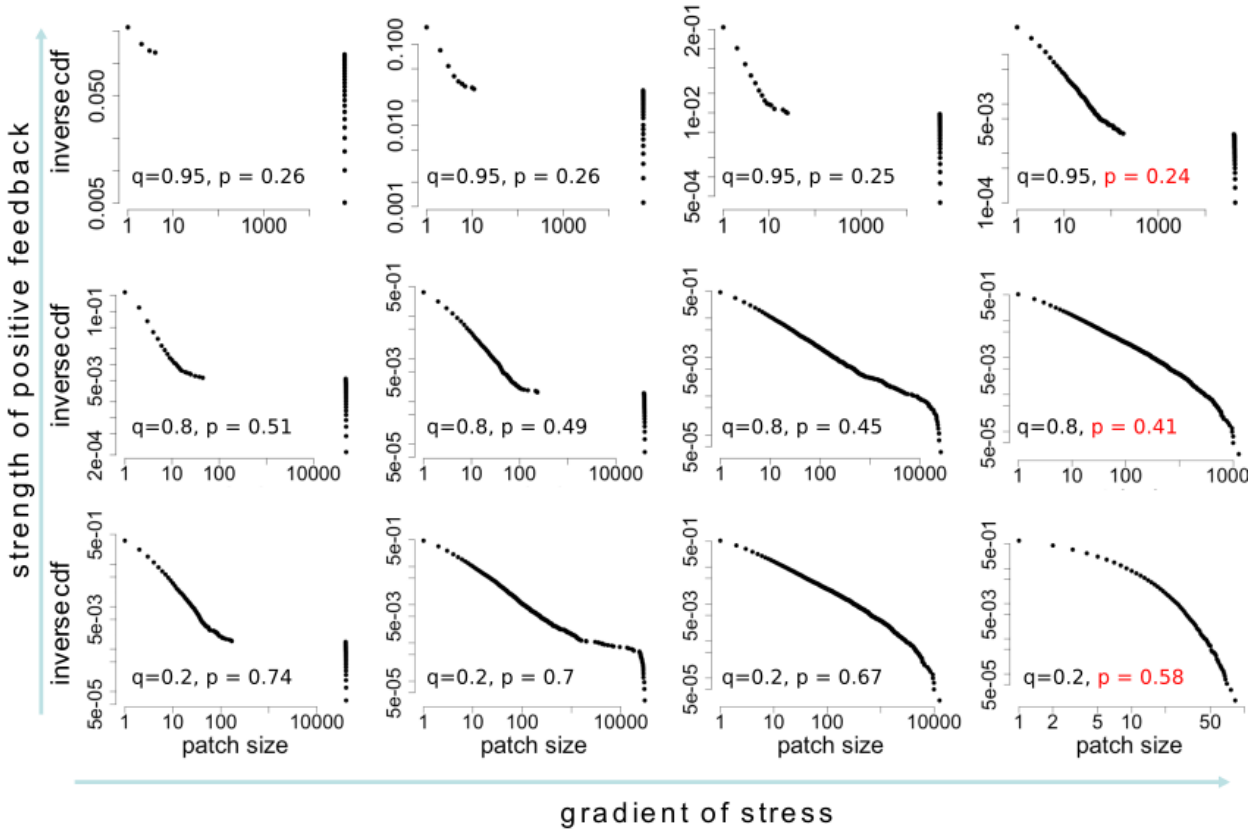


Figure A1: Cluster size distributions realised in square lattices of 250x250 cells. The right most column of plots is of systems very near/at critical points, with the driver value shown in red. When facilitation (q) is low, we see the entire range of cluster-size distributions: bimodal at very high density, far from the critical point, power-law, truncated power-law and exponential, as we move towards the critical point. As q increases, 1. high densities prevail for lower and lower p values, 2. system begins to collapse from higher density states (see Fig 4 of main text). This results in a shift in observed cluster size distributions, with fat-tailed distributions persisting for the entire range of realised non-zero densities. We then see power-law or, with very high facilitation, even bimodal clustering at the point of collapse.

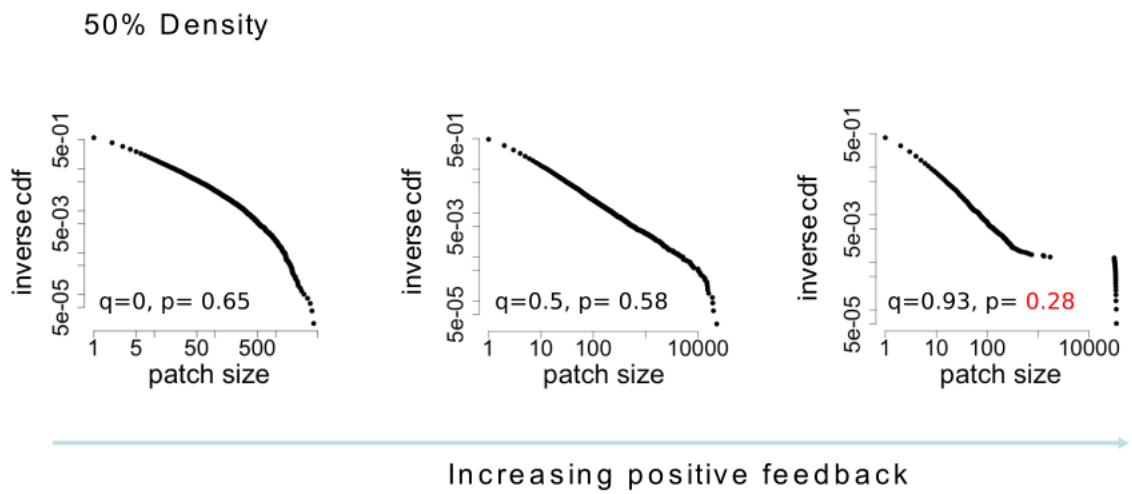


Figure A2: Cluster size distributions realised in square lattices of 250x250 cells. At the same density, different cluster size distributions can be observed depending on facilitation strength (q). Since facilitation also results in the system collapsing from higher densities, increasing facilitation causes fat tailed distributions to occur closer and closer to the critical point. This results in a complete reversal of previously proposed (Kéfi et al., 2007; Kéfi et al., 2014) trends in cluster size distibutions.

Online Appendix D: Power-spectrum fitting

0.1 Resilient systems (far from transition points)

It is well known that in systems far from transition the power-spectrum typically exhibits a lorentzian functional form . Theoretically it is also expected that as the system reaches a critical point, its spectral function shifts to a power-law form. In our model too we found the lorentzian function to be a good fit for resilient systems (both, with high and low positive feedback, Fig.A3). The function was fit by running a non-linear least squared regression on the data. We present the results of the analyses below:

Dataset low positive feedback($q = 0$)
Formula: $y = k * a/((x - x0)^2 + a^2)$
Parameters:

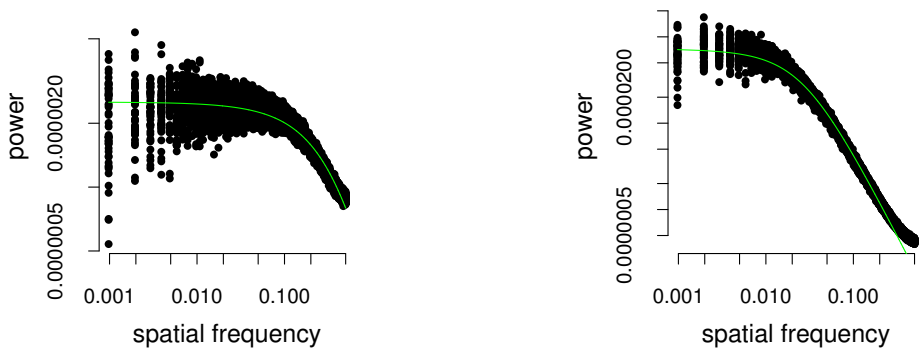
	Estimate	Std. Error	t value	Pr(¿—t—)
k	$1.36\text{x}10^{-6}$	$1.6\text{x}10^{-8}$	87.97	¡2e-16 ***
x0	-0.2308	0.0051	-45.35	¡2e-16 ***
a	0.4116	0.0073	564.89	¡2e-16 ***

Signif. codes: 0 '∗ ∗ ∗' 0.001 '∗∗' 0.01 '∗' 0.05 '.' 0.1 ' ' 1
Residual standard error: 0.0001061 on 25647 degrees of freedom
Number of iterations to convergence: 8
Achieved convergence tolerance: 0.0000000149

Dataset high positive feedback ($q = 0.92$)
Formula: $y\ k * a/((x - x0)^2 + a^2)$
Parameters:

	Estimate	Std. Error	t value	Pr(¿—t—)
k	$2.06\text{x}10^{-6}$	$1.13\text{x}10^{-8}$	182.99	¡2e-16 ***
x0	-0.0085	0.00017	-49.67	$2.72\text{x}10^{-11}$ ***
a	0.0254	$6.79\text{x}10^{-5}$	374.72	¡2e-16 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 0.0004837 on 25647 degrees of freedom
Number of iterations to convergence: 8
Achie



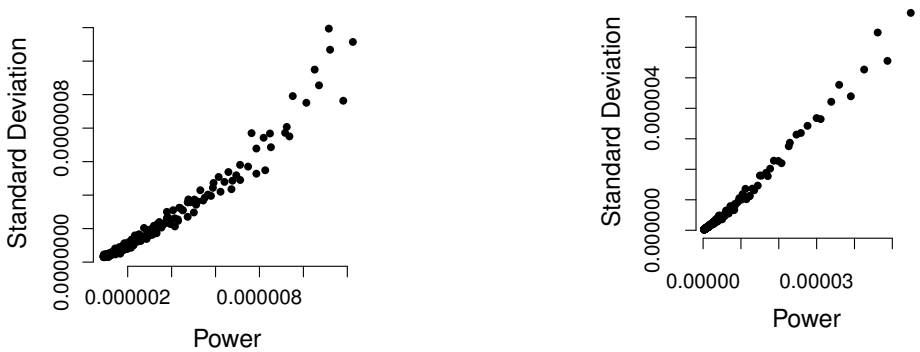
(a) $q = 0, p = 0.7225$ (b) $q = 0.92, p = 0.2865$

Figure A3: The lorentzian fit (green line) of power spectrum data (black dots) of resilient systems with low and high facilitation, see main text Fig 6. The plotted data correspond to the data shown in blue in Fig 6.

0.2 *Critical systems (very near/at transition points)*

For systems near transition, as expected, we found that the power-law function was a good fit over a large range of the data. There are two approaches to fitting power-law relations: one is by log transforming the data and then fitting a linear model and the other, by directly fitting a non-linear model. Several studies demonstrate that log-transforming power-law distributions or frequency data violates assumptions underlying linear regressions such as normally distributed residuals. This, however, is not always the case. More precisely, fitting power-law data using non-linear least squares regressions assumes that the data have a constant standard deviation, whereas log

transformation followed by linear regression is valid for data with a constant coefficent of variation (Bolker et al., 2013). Since our spectral data for systems near/at critical points, like other $1/f^{\beta}$ spectra (Van der Schaaf and van Hateren, 1996), show an increasing trend of standard deviation with average power (see Fig.A4), we used the linear regression method on log-transformed values. The range of the power-law function was estimated in the same way as described in the previous section, by identifying the x-value (spatial frequency) which minimises the KS distance between the predicted function and the data but an upper frequency limit of 0.3 was kept fixed for all datasets.



(a) $q = 0, p = 0.62275$

(b) $q = 0.92, p = 0.2852$

Figure A4: Varying SD and constant coefficient of variation ($SD/mean$) of power-spectra of systems near transition

Dataset: low positive feedback($q = 0$)
Formula: $y = (k * x^{a})$
lm(formula = log(y) log(x), weights = x)
Parameters:

	Estimate	Std. Error	t value	Pr(¿—t—)
a	-1.2103	0.00096	-1265	¡2e-16 ***
$\log k$	-15.4159	0.00159	-9688	¡2e-16 ***

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 0.01954 on 15698 degrees of freedom
Multiple R-squared: 0.9932, Adjusted R-squared: 0.9932
F-statistic: 1.6x10^{6} on 1 and 15698 DF, p-value: ¡ 2.2e-16

Dataset: high positive feedback ($q = 0.92$)
Formula: $y = (k * x^{a})$
lm(formula = log(y) log(x), weights = x)
Parameters:

	Estimate	Std. Error	t value	Pr(¿—t—)
a	-1.7819	0.00128	-1392	¡2e-16 ***
$\log k$	-16.8830	0.00283	-5976	¡2e-16 ***

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 0.1006 on 14798 degrees of freedom
Multiple R-squared: 0.9944, Adjusted R-squared: 0.9944
F-statistic: 1.938e+06 on 1 and 1 DF, p-value: ¡ 2.2e-16

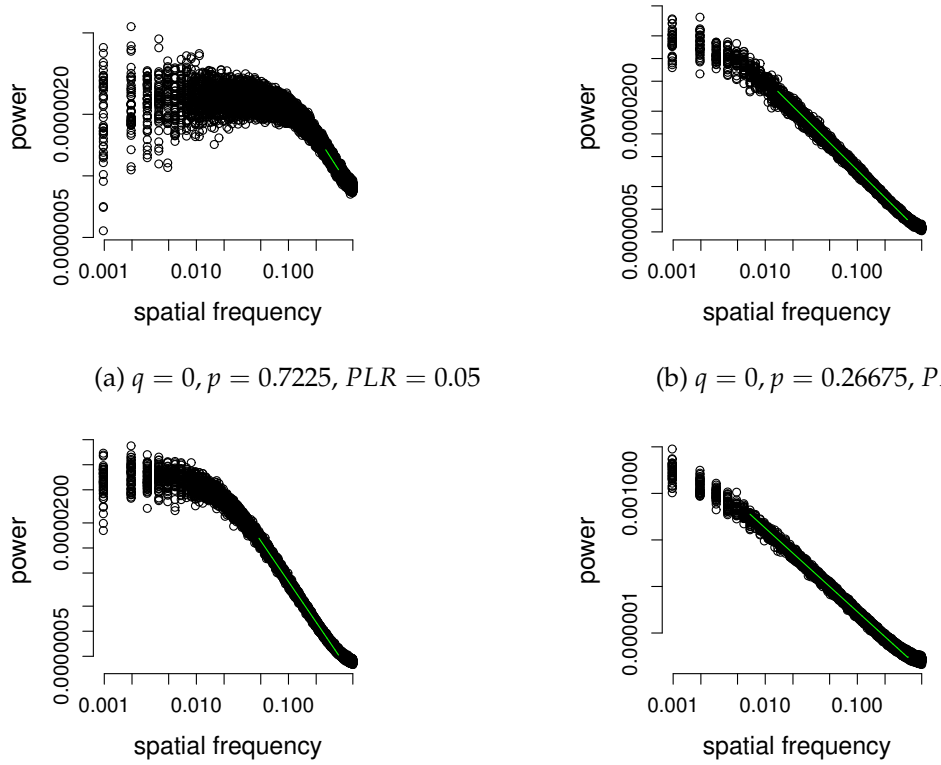
0.3 Comparing lorenztian and scale-free spectra

Comparison of the models (Lorentzian vs power-law) for the different data-sets is impossible as the models not only have a different number of parameters, but are also not fit over the same range of data. One way to get around this is to consider the theory underlying the emergence of scale-free power-spectra in critical systems. Even data that follow a lorentzian function, will follow a power-law over some (small) range of spatial frequencies. However, as the system approaches a critical point, low frequency interactions begin to dominate, thus increasing in power and leading to a shift in the spectrum such that the extent of the power-law region sharply increases (see section 4 on "scale-free spatial correlations in critical systems" in main text). Thus to compare the power-spectra behaviour in systems near/at the critical point with that of resilient systems, one can examine the range over which the power-law fit extends.

To compare the range of power law (PLR), we use the method proposed by (Berdugo et al., 2017), who define it as:

$$PLR = 1 - \frac{log[x_{min}] - log[x_{smallest}]}{log[x_{max}] - log[x_{smallest}]}$$

PLR varies from 0 (when none of the data fall within the fitted power-law) to 1 (when all the data are fall within the power-law region). We see in our power-spectra that as the system approaches a critical point, smaller and smaller spatial frequencies fall within the power-law range (Fig A5). This is congruent with theoretical predictions of diverging correlation length at critical points.



(a) $q = 0, p = 0.7225, PLR = 0.05$

(b) $q = 0, p = 0.26675, PLR = 0.56$

(c) $q = 0.92, p = 0.2865, PLR = 0.32$

(d) $q = 0.92, p = 0.2852, PLR = 0.67$

Figure A5: The shift in the functional form of the power-spectrum is captured by the increased range of power-law as systems approach critical points. Data are shown with black dots and the fitted power-law functions, as green lines

Literature Cited

Aguiar, M. R., and O. E. Sala. 1994. Competition, facilitation, seed distribution and the origin of patches in a patagonian steppe. Oikos pages 26–34.

Baugh, C., and P. Murdin. 2006. Correlation function and power spectra in cosmology. Encycl. of Astronomy and Astrophysics. IOP Publishing, Bristol .

Berdugo, M., S. Kéfi, S. Soliveres, and F. T. Maestre. 2017. Plant spatial patterns identify alternative ecosystem multifunctionality states in global drylands. Nature Ecology & Evolution 1:0003.

Boada, J., R. Arthur, D. Alonso, J. F. Pagès, A. Pessarrodona, S. Oliva, G. Ceccherelli, L. Piazzi,

J. Romero, and T. Alcoverro. 2017. Immanent conditions determine imminent collapses: nutrient regimes define the resilience of macroalgal communities 284:20162814.

Bolker, B. M., B. Gardner, M. Maunder, C. W. Berg, M. Brooks, L. Comita, E. Crone, S. Cubaynes, T. Davies, P. Valpine, et al. 2013. Strategies for fitting nonlinear ecological models in r, ad model builder, and bugs. Methods in Ecology and Evolution 4:501–512.

Breed, G. A., P. M. Severns, and A. M. Edwards. 2015. Apparent power-law distributions in animal movements can arise from intraspecific interactions. Journal of the Royal Society Interface 12:20140927.

Carpenter, S., and W. Brock. 2010. Early warnings of regime shifts in spatial dynamics using the discrete fourier transform. Ecosphere 1:art10.

Carpenter, S., J. Cole, M. Pace, R. Batt, W. Brock, T. Cline, J. Coloso, J. Hodgson, J. Kitchell, D. Seekell, et al. 2011. Early warnings of regime shifts: A whole-ecosystem experiment. Science 332:1079–1082.

Carpenter, S. R., D. Ludwig, and W. A. Brock. 1999. Management of eutrophication for lakes subject to potentially irreversible change. Ecological applications 9:751–771.

Casey, S. T., M. J. Cohen, S. Acharya, D. A. Kaplan, and J. W. Jawitz. 2016. Hydrologic controls on aperiodic spatial organization of the ridge-slough patterned landscape. Hydrology and Earth System Sciences 20:4457.

Chaves, L. F., M. Hashizume, A. Satake, and N. Minakawa. 2012. Regime shifts and heterogeneous trends in malaria time series from western kenya highlands. Parasitology 139:14–25.

Christensen, K., and N. R. Moloney. 2005. Complexity and criticality, volume 1. Imperial College Press.

Clauset, A., C. R. Shalizi, and M. E. Newman. 2009. Power-law distributions in empirical data. SIAM review 51:661–703.

Couteron, P. 2002. Quantifying change in patterned semi-arid vegetation by fourier analysis of digitized aerial photographs. International Journal of Remote Sensing 23:3407–3425.

Dakos, V., S. Kéfi, M. Rietkerk, E. van Nes, and M. Scheffer. Slowing down in spatially patterned ecosystems at the brink of collapse .

Dakos, V., E. van Nes, R. Donangelo, H. Fort, and M. Scheffer. 2010. Spatial correlation as leading indicator of catastrophic shifts. Theoretical Ecology 3:163–174.

Dakos, V., S. R. Carpenter, A. M. Ellison, V. Guttal, A. R. Ives, S. Kéfi, V. Livina, D. A. Seekell, E. H. van Nes, and M. Scheffer. 2012. Early warning signals of critical transitions: Methods for time series. PLOS ONE 7:e41010.

Dell, C. L., G. O. Longo, and M. E. Hay. 2016. Positive feedbacks enhance macroalgal resilience on degraded coral reefs. PloS one 11:e0155049.

Duffy, J. P., L. Pratt, K. Anderson, P. E. Land, and J. D. Shutler. 2017. Spatial assessment of intertidal seagrass meadows using optical imaging systems and a lightweight drone. Estuarine, Coastal and Shelf Science .

Eby, S., A. Agrawal, S. Majumder, A. P. Dobson, and V. Guttal. 2017. Alternative stable states and spatial indicators of critical slowing down along a spatial gradient in a savanna ecosystem. Global Ecology and Biogeography doi:10.1111/geb.12570.

Fernández, A., and H. Fort. 2009. Catastrophic phase transitions and early warnings in a spatial ecological model. Journal of Statistical Mechanics: Theory and Experiment 2009:P09014.

Foti, R., M. del Jesus, A. Rinaldo, and I. Rodriguez-Iturbe. 2013. Signs of critical transition in the everglades wetlands in response to climate and anthropogenic changes. Proceedings of the National Academy of Sciences 110:6296–6300.

Génin, A., S. Majumder, S. Sankaran, F. D. Schneider, A. Danet, M. Berdugo, V. Guttal, and S. Kéfi.

2018. Spatially heterogeneous stressors can alter the performance of indicators of regime shifts. Ecological Indicators .

Grassberger, P. 1993. On a self-organized critical forest-fire model. Journal of Physics A: Mathematical and General 26:2081.

Grimmett, G. 1999. What is percolation? In Percolation, pages 1–31. Springer Berlin Heidelberg.

Guichard, F., P. M. Halpin, G. W. Allison, J. Lubchenco, and B. A. Menge. 2003. Mussel disturbance dynamics: signatures of oceanographic forcing fr om local interactions. The American Naturalist 161:889–904.

Guttal, V., and C. Jayaprakash. 2009. Spatial variance and spatial skewness: leading indicators of regime shifts in spatial ecological systems. Theoretical Ecology 2:3–12.

Hansen, G. J., A. R. Ives, M. J. Vander Zanden, and S. R. Carpenter. 2013. Are rapid transitions between invasive and native species caused by alternative stable states, and does it matter? Ecology 94:2207–2219.

Irvine, M. A., E. Jackson, E. J. Kenyon, K. J. Cook, M. J. Keeling, and J. Bull. 2016. Fractal measures of spatial pattern as a heuristic for return rate in vegetative systems. Royal Society open science 3:150519.

Kéfi, S., M. Rietkerk, C. L. Alados, Y. Pueyo, V. P. Papanastasis, A. ElAich, and P. C. de Ruiter. 2007. Spatial vegetation patterns and imminent desertification in mediterranean arid ecosystems. Nature 449:213–217.

Kéfi, S., M. B. Eppinga, P. C. de Ruiter, and M. Rietkerk. 2010. Bistability and regular spatial patterns in arid ecosystems. Theoretical Ecology 3:257–269.

Kéfi, S., M. Rietkerk, M. Roy, A. Franc, P. De Ruiter, and M. Pascual. 2011. Robust scaling in ecosystems and the meltdown of patch size distributions before extinction. Ecology letters 14:29–35.

Kéfi, S., V. Guttal, W. A. Brock, S. R. Carpenter, A. M. Ellison, V. N. Livina, D. A. Seekell, M. Scheffer, E. H. van Nes, and V. Dakos. 2014. Early warning signals of ecological transitions: methods for spatial patterns. PloS one 9:e92097.

Kéfi, S., M. Holmgren, and M. Scheffer. 2016. When can positive interactions cause alternative stable states in ecosystems? Functional Ecology 30:88–97.

Khaluf, Y., E. Ferrante, P. Simoens, and C. Huepe. 2017. Scale invariance in natural and artificial collective systems: a review. Journal of The Royal Society Interface 14:20170662.

Klausmeier, C. A. 1999. Regular and irregular patterns in semiarid vegetation. Science 284:1826–1828.

Knowlton, N. 2004. Multiple ?stable? states and the conservation of marine ecosystems. Progress in Oceanography 60:387–396.

Lin, Y., G. Han, M. Zhao, and S. X. Chang. 2010. Spatial vegetation patterns as early signs of desertification: a case study of a desert steppe in inner mongolia, china. Landscape ecology 25:1519–1527.

Lübeck, S. 2006. Tricritical directed percolation. Journal of statistical physics 123:193–221.

Ma, S.-K. 2000. Modern theory of critical phenomena. Da Capo Press.

Maestre, F. T., and A. Escudero. 2009. Is the patch size distribution of vegetation a suitable indicator of desertification processes? Ecology 90:1729–1735.

Maestre, F. T., S. Bautista, and J. Cortina. 2003. Positive, negative, and net effects in grass–shrub interactions in mediterranean semiarid grasslands. Ecology 84:3186–3197.

Malamud, B. D., G. Morein, and D. L. Turcotte. 1998. Forest fires: an example of self-organized critical behavior. Science 281:1840–1842.

Manor, A., and M. Shnerb. 2008*a*. Facilitation, competition, and vegetation patchiness: From scale free distribution to patterns. Journal of Theoretical Biology 253:838–842.

Manor, A., and N. M. Shnerb. 2008*b*. Facilitation, competition, and vegetation patchiness: from scale free distribution to patterns. Journal of theoretical biology 253:838–842.

Manrubia, S. C., and R. V. Solé. 1997. On forest spatial dynamics with gap formation. Journal of theoretical biology 187:159–164.

Meloni, F., C. R. F. Granzotti, S. Bautista, and A. S. Martinez. 2017*a*. Scale dependence and patch size distribution: clarifying patch patterns in mediterranean drylands. Ecosphere 8.

Meloni, F., G. M. Nakamura, C. R. F. Granzotti, and A. S. Martinez. 2017*b*. Empirical evidence reveals the phase diagram of vegetation patterns in mediterranean drylands. bioRxiv page 171835.

Moreno-de las Heras, M., P. M. Saco, G. R. Willgoose, and D. J. Tongway. 2011. Assessing landscape structure and pattern fragmentation in semiarid ecosystems using patch-size distributions. Ecological Applications 21:2793–2805.

Pascual, M., and F. Guichard. 2005. Criticality and disturbance in spatial ecological systems. Trends in Ecology and Evolution 20:88–95.

Petrovskii, S., A. Mashanova, and V. A. Jansen. 2011. Variation in individual walking behavior creates the impression of a lévy flight. Proceedings of the National Academy of Sciences 108:8704–8707.

Plank, M. J., and E. A. Codling. 2009. Sampling rate and misidentification of lévy and non-lévy movement paths. Ecology 90:3546–3553.

Reif, F. 2009. Fundamentals of statistical and thermal physics. Waveland Press.

Rietkerk, M., and J. van de Koppel. 2008. Regular pattern formation in real ecosystems. Trends in Ecology & Evolution 23:169–175.

Rietkerk, M., S. C. Dekker, P. C. de Ruiter, and J. van de Koppel. 2004. Self-organized patchiness and catastrophic regime shifts in ecosystems. Science 305:1926–1929.

Roy, M., M. Pascual, and A. Franc. 2003. Broad scaling region in a spatial ecological system. Complexity 8:19–27.

Scanlon, T., K. Caylor, S. Levin, and I. Rodriguez-Iturbe. 2007. Positive feedbacks promote power-law clustering of Kalahari vegetation. Nature 449:209–212.

Scheffer, M., J. Bascompte, W. Brock, V. Brovkin, S. Carpenter, V. Dakos, H. Held, E. Van Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. Nature 461:53–59.

Schneider, F. D., and S. Kéfi. 2015. Spatially heterogeneous pressure raises risk of catastrophic shifts. Theoretical Ecology pages 1–11.

Sethna, J. 2006. Statistical mechanics: entropy, order parameters, and complexity, volume 14. Oxford University Press.

Sheffer, E., J. Hardenberg, H. Yizhaq, M. Shachak, and E. Meron. 2013. Emerged or imposed: a theory on the role of physical templates and self-organisation for vegetation patchiness. Ecology letters 16:127–139.

Solé, R. V., S. C. Manrubia, M. Benton, S. Kauffman, and P. Bak. 1999. Criticality and scaling in evolutionary ecology. Trends in Ecology & Evolution 14:156–160.

Stanley, H. E. 1999. Scaling, universality, and renormalization: Three pillars of modern critical phenomena. Reviews of modern physics 71:S358.

Stauffer, D. 1979. Scaling theory of percolation clusters. Physics reports 54:1–74.

Strogatz, S., M. Friedman, A. J. Mallinckrodt, S. McKay, et al. 1994. Nonlinear dynamics and chaos: With applications to physics, biology, chemistry, and engineering. Computers in Physics 8:532–532.

Stumpf, M. P., and M. A. Porter. 2012. Critical truths about power laws. Science 335:665–666.

Turcotte, D. L., and B. D. Malamud. 2004. Landslides, forest fires, and earthquakes: examples of self-organized critical behavior. Physica A: Statistical Mechanics and its Applications 340:580–589.

van de Koppel, J., and M. Reitkerk. 2004. Spatial interactions and resilience in arid ecosystems. American Naturalist 163:112–121.

van de Koppel, J., M. Rietkerk, F. van Langevelde, L. Kumar, C. Klausmeier, J. W. Hearne, J. van Andel, N. de Ridder, A. Skidmore, L. Stroosnijder, and H. H. T. Prins. 2002. Spatial heterogeneity and irreversible vegetation change in semiarid grazing systems. American Naturalist 159:209–218.

Van der Schaaf, v. A., and J. v. van Hateren. 1996. Modelling the power spectra of natural images: statistics and information. Vision research 36:2759–2770.

von Hardenberg, J., E. Meron, M. Shachak, and Y. Zarmi. 2001. Diversity of vegetation patterns and desertification. Physical Review Letters 87:198101:1–4.

von Hardenberg, J., A. Kletter, H. Yizhaq, J. Nathan, and E. Meron. 2010*a*. Periodic versus scale-free patterns in dryland vegetation. Proceedings of the Royal Society B: Biological Sciences 2077:1771–1776.

von Hardenberg, J., A. Y. Kletter, H. Yizhaq, J. Nathan, and E. Meron. 2010*b*. Periodic versus scale-free patterns in dryland vegetation. Proceedings of the Royal Society of London B: Biological Sciences page rspb20092208.

Weerman, E., J. Van Belzen, M. Rietkerk, S. Temmerman, S. Kéfi, P. Herman, and J. V. de Koppel. 2012. Changes in diatom patch-size distribution and degradation in a spatially self-organized intertidal mudflat ecosystem. Ecology 93:608–618.

White, E., B. Enquist, and G. J.L. 2008. On estimating the exponent of power-law frequency distributions. Ecology 89:905–912.

Wissel, C. 1984. A universal law of the characteristic return time near thresholds. Oecologia 65:101–107.

Xu, C., M. Holmgren, E. H. Van Nes, F. T. Maestre, S. Soliveres, M. Berdugo, S. Kéfi, P. A. Marquet, S. Abades, and M. Scheffer. 2015*a*. Can we infer plant facilitation from remote sensing? a test across global drylands. Ecological Applications 25:1456–1462.

Xu, C., E. H. Van Nes, M. Holmgren, S. Kéfi, and M. Scheffer. 2015*b*. Local facilitation may cause tipping points on a landscape level preceded by early-warning indicators. The American Naturalist 186:E81–E90.