

RESEARCH ARTICLE

Clustering and correlations: Inferring resilience from spatial patterns in ecosystems

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Abstract

1. In diverse ecosystems, organisms cluster together in such a manner that the frequency distribution of cluster sizes is a power law function. Spatially explicit computational models of ecosystems suggest that *a loss of such power law clustering* may indicate a loss of ecosystem resilience; the empirical evidence in support for this hypothesis has been mixed. On the other hand, a well-known dynamical feature of systems with reduced resilience is the slower recovery from perturbations, a phenomenon known as *critical slowing down* (CSD). Here, we examine the relationship between spatial clustering and CSD to better understand the use of cluster size distributions as indicators of ecosystem resilience.
2. Local positive feedback is an important driver of spatial clustering, while also affecting the dynamics of the ecosystem: Studies have demonstrated that positive feedback promotes abrupt regime shifts. Here, we analyse a spatial model of ecosystem transitions that enables us to disentangle the roles of local positive feedback and environmental stress on spatial patterns and ecosystem resilience.
3. We demonstrate that, depending on the strength of positive feedback, power law clustering can occur at any distance from the critical threshold of ecosystem collapse. In fact, we find that for systems with strong positive feedback, which are more likely to exhibit abrupt transitions, there may be no loss of power law clustering prior to critical thresholds.
4. Our analyses show that cluster size distributions are unrelated to the phenomenon of CSD and that loss of power law clustering is not a generic indicator of ecosystem resilience. Further, due to CSD, a power law feature does occur near critical thresholds but in a different quantity; specifically, a power law decay of spatial covariance of ecosystem state. Our work highlights the importance of links between local positive feedback, emergent spatial properties and how they may be used to interpret ecosystem resilience.

KEYWORDS

criticality, early warning signals, ecosystem resilience, patch size distribution, percolation, power-spectrum, power law, regime shift

1 | INTRODUCTION

Desertification of semi-arid ecosystems (van de Koppel et al., 2002), eutrophication of lakes (Carpenter, Ludwig, & Brock, 1999), spread of diseases (Chaves, Hashizume, Satake, & Minakawa, 2012), invasion (Hansen, Ives, Vander Zanden, & Carpenter, 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 are also known as critical transitions in the ecology literature. They happen when a system crosses a certain threshold, called *critical threshold*, 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; Chen, Jayaprakash, Yu, & Guttal, 2018; Dakos et al., 2012; Dakos, Kéfi, Rietkerk, Van Nes, & Scheffer, 2011; Eby, Agrawal, Majumder, Dobson, & Guttal, 2017; Guttal & Jayaprakash, 2008, 2009; Kéfi et al., 2014; Kéfi, Rietkerk, Alados, et al., 2007; Kéfi, Rietkerk, Baalen, & Loreau, 2007; Scheffer et al., 2009; Van Belzen et al., 2017; Weerman et al., 2012). One such method is based on the idea that patterns of self-organization in ecosystems can offer signatures of resilience (Corrado, Cherubini, & Pennetta, 2014; Génin, Majumder, Sankaran, Danet, et al., 2018; von Hardenberg, Meron, Shachak, & Zarmi, 2001; Kéfi et al., 2014; Kéfi, Rietkerk, Alados, et al., 2007; Kéfi, Rietkerk, Baalen, et al., 2007; Rietkerk, Dekker, Ruiter, & Koppel, 2004). Self-organized patterns themselves often result from an interplay of facilitative and competitive interactions among organisms (von Hardenberg, Kletter, Yizhaq,

Nathan, & Meron, 2010; Manor & Shnerb, 2008; Scanlon, Caylor, Levin, & Rodriguez-Iturbe, 2007). Therefore, a comprehensive understanding of how local interactions between organisms scale to their spatial distribution and affect ecosystem resilience is of broad ecological interest.

Of the many varieties of self-organization found in nature (D'Odorico, Okin, & Bestelmeyer, 2012; Foti, Jesus, Rinaldo, & Rodriguez-Iturbe, 2013; von Hardenberg et al., 2010, 2001; Kéfi, Rietkerk, Alados, et al., 2007; Kéfi, Rietkerk, Baalen, et al., 2007; Rietkerk & van de Koppel, 2008; Scanlon et al., 2007), we focus on spatial patterns where organisms exhibit clustering of irregular size and shape; these are found in many ecosystems such as semi-arid ecosystems, mussel beds or seagrass (Figure 1). Here, the frequency distributions of these cluster sizes may follow a power law function (henceforth referred to as *power law clustering*). These are interesting because they may imply that systems lack characteristic size (see Box 1 for a summary of properties of power laws). Some simulation and empirical studies suggest that when ecosystems are stressed, clusters fragment leading to loss of large patches (Kéfi et al., 2014; Kéfi, Rietkerk, Alados, et al., 2007; Kéfi, Rietkerk, Baalen, et al., 2007). This results in a qualitative change in the properties of cluster size distribution: from a power law to an exponential distribution. The progressive truncation of the tail of the power law clustering has, therefore, been hypothesized to represent loss of resilience in ecosystems (Fernández & Fort, 2009; Kéfi et al., 2014, 2011; Kéfi, Rietkerk, Alados, et al., 2007; Kéfi, Rietkerk, Baalen, et al., 2007; Lin, Han, Zhao, & Chang, 2010; Weerman et al., 2012).

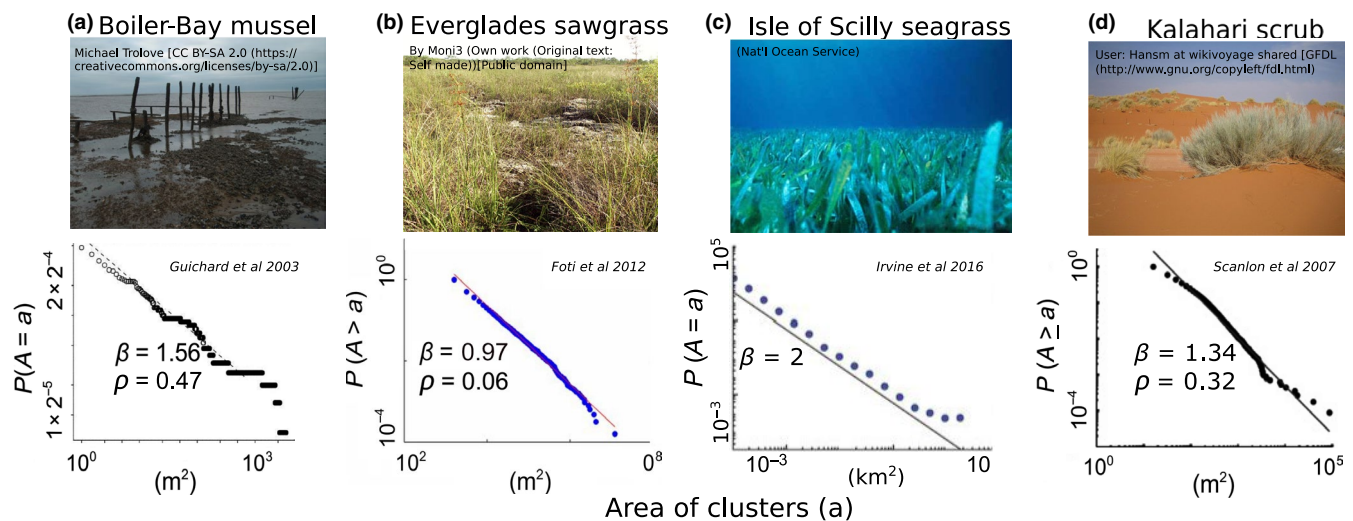


FIGURE 1 Power law cluster size distributions in different ecosystems (bottom panel) and representative snapshots which are not necessarily from the same study area or time period (top panel). (a) Boiler bay mussel bed, USA (Guichard et al., 2003), © (2003) UNIVERSITY OF CHICAGO PRESS (b) Sawgrass in Everglades wetlands, USA (Foti, Jesus, Rinaldo, & Rodriguez-Iturbe, 2012), © (2012) National Academy of Sciences (c) West Broad Ledges seagrass near the Isle of Scilly (Irvine et al., 2016) CC BY-SA 2.0 and (d) Vegetation in Kalahari, Namibia (Scanlon et al., 2007) © (2007) SPRINGER NATURE. Top row image credits: (a) From Michael Trolove [CC BY-SA 2.0 (<https://creativecommons.org/licenses/by-sa/2.0/>)] (b) <https://doi.org/10.1016/j.ecss.2017.11.001> [CC BY] <http://creativecommons.org/licenses/by/4.0/>, (c) Nat'l ocean service <http://www.sanctuaries.nos.noaa.gov/oms/omsflorida/omsfloridanatset.html>, sourced from https://commons.wikimedia.org/wiki/File:Floridian_seagrass_bed.jpg (d) User: Hansm at wikivoyage shared [CC BY-SA 3.0 (<https://creativecommons.org/licenses/by-sa/3.0/>)] Data (1995–2014) (Scanlon et al., 2007)

Empirical evidence for this hypothesis, however, is ambiguous (Maestre & Escudero, 2009; Meloni, Nakamura, Granzotti, & Martinez, 2017; Weerman et al., 2012). Additionally, simulation studies in more complex models suggest that details of systems matter, thus questioning the generality of these cluster-based indicators (Génin, Majumder, Sankaran, Schneider, et al., 2018; Schneider & Kéfi, 2016). Nevertheless, the possibility of inferring ecosystem resilience from a single snapshot and the increasing availability of low-cost remotely sensed spatial datasets, where these methods can be applied, is attractive. Therefore, an evaluation of the generality and robustness of clustering properties as a signature of ecosystem resilience is needed.

To understand issues of generality, we must discuss another class of power law behaviours that are considered universal features near/at *critical points* of phase transitions. Here, we emphasize that the theoretical underpinnings of ecosystem dynamics and indicators of stability are based on principles derived from the theory of phase transitions and bifurcations (Scheffer et al., 2009; Strogatz, 1994). This theory predicts that as a system nears a critical point of phase transitions, it takes increasingly longer to recover from perturbations. This phenomenon of slowed recovery is called *critical slowing down* (CSD) in the context of continuous phase transitions in the physics literature. However, a similar effect of slowed recovery appears even in ecological models that show abrupt transitions (Scheffer et al., 2009; Strogatz, 1994; Wissel, 1984). Consequently, CSD has been widely used to devise methods to detect the approach of critical thresholds in ecosystems (Scheffer et al., 2009; Wissel, 1984). An aspect of CSD that is much less known in the ecology literature is that close to, and at the critical point, the strength of a perturbation decays as a power law function of time – indicating a very slow recovery (Ma, 2000; Sethna, 2006; Stanley, 1999); this is in contrast to systems far away from thresholds where perturbations decay exponentially fast. In fact, many power law behaviours arise near/at continuous phase transitions (Ma, 2000; Sethna, 2006; Stanley, 1999).

Let us highlight an interesting contrast between the two power law relationships we have discussed thus far: While the power laws associated with CSD are expected to *emerge near/at critical points* of phase transitions (Ma, 2000; Sethna, 2006), the power laws in clustering are hypothesized to be *lost near/at critical thresholds* of ecosystem collapse (Kéfi, Rietkerk, Alados, et al., 2007; Kéfi, Rietkerk, Baalen, et al., 2007). (Please see Glossary and Methods sections for the difference in our usage of critical points and critical thresholds.) It is now fairly well-established that many mechanisms cause emergence of power laws even away from critical thresholds (Newman, 2005; Pascual & Guichard, 2005; Roy, Pascual, & Franc, 2003). However, the theoretical basis for why a loss of power law clustering can indicate approach to a critical threshold in ecosystem models is unclear. Furthermore, elucidating relationships (if any) between the dynamical phenomenon of CSD and cluster size properties has not gained attention in the literature. Such an exercise will not only prove helpful in evaluating the generality of ecosystem resilience indicators but also reveal the crucial role of local positive feedback in ecosystem patterning.

In this article, we probe the relationship between positive feedback, clustering and resilience. To do so, we use a spatially explicit

model which, unlike previous relatively complex models, decouples the effects of positive feedback and environmental stress. We show that power law clustering (or loss thereof) is unrelated to resilience. We then demonstrate how CSD – a universal feature of dynamical systems near thresholds – manifests as a power law decay of spatial correlations. Owing to the interdisciplinary nature of the study, we introduce important terms and concepts via a Box and a Glossary.

Glossary

1. Regime shifts: Changes in qualitative nature of ecosystem states. These changes can be abrupt or gradual functions of the underlying drivers.
2. Critical threshold: The value of an environmental condition (e.g. rainfall) and/or state variable (e.g. woody cover) at which a system undergoes an abrupt regime shift. In some ecology papers, it is used interchangeably with critical point (see below) but here we avoid doing so.
3. Resilience: The amount of change a system can withstand without transitioning to an alternative state.
4. Stability: The rate at which a system recovers to its original equilibrium from small perturbations.
5. Critical point: In the physics literature, this term refers to the value of driver at which the system undergoes a continuous phase transition from one state to the other.
6. Critical slowing down: The phenomenon in which systems near threshold of transitions are slow to recover from perturbations.
7. Positive feedback: Interactions between individuals that result in enhanced reproduction and/or reduced death rates of both individuals.
8. Cluster: A set of individuals who are within a minimum distance (typically the nearest neighbour distance) of at least one member of the same set.
9. Scale-free: A quantity having infinite average value, thus lacking a characteristic scale. Also see Box 1.
10. Percolation: In the physics literature, percolation is the movement/spread of an agent through the extent of the system via a connected path of sites.
11. Percolation density: The lowest density of occupied sites at which percolation occurs. At the same density, we observe a scale-free distribution of cluster sizes in the landscape.
12. Spatial autocovariance function: Covariance between states at two locations as a function of the distance between them.
13. Power-spectrum/Spectral density function: Strength of fluctuations as a function of frequency; it is the Fourier transform of the autocovariance function.

2 | METHODS AND RESULTS

2.1 | The model

We employ a spatially explicit model of ecosystem dynamics with probabilistic update rules for local states (Eby et al., 2017; Majumder, Tamma, Ramaswamy, & Guttal, 2019; Sankaran, Majumder, Kéfi, &

BOX 1 Power-law and scale-free behaviours

Biology is replete with examples of self-organized spatial clustering (Guichard, Halpin, Allison, Lubchenco, & Menge, 2003; von Hardenberg et al., 2010; Rietkerk & van de Koppel, 2008). In some cases, clusters have a wide range of sizes such that the frequency of occurrence of clumps of a particular size (denoted by x) decays as a power function of the size, that is, $f(x) = cx^{-\beta}$ (defined for all clusters above a size $x > x_{\min}$ with c and β being constants). Below, we describe two interesting properties of this function.

Heavy-tailedness

The power law frequency distribution has much higher occurrences of extreme events than predicted by commonly used distributions such as Gaussian or exponential distributions (Figure 2); this feature of the power law distribution is also called *heavy-tailedness*.

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 (normalized) power law probability density function, denoted by $p(x)$, are given by

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

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

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 common and have been documented in various ecosystems (Figure 1).

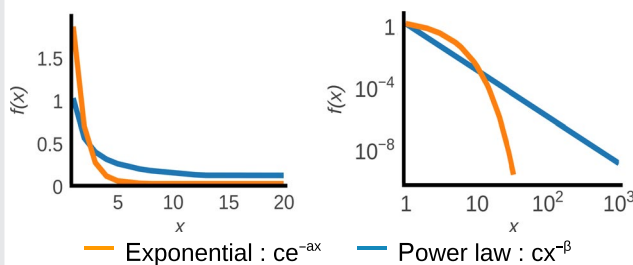


FIGURE 2 The plot on the left shows that the power law function has a heavier tail, that is, higher frequency ($f(x)$) of occurrence of large events, than in an exponential function. The plot on the right shows that power law function is a straight line on log-log axes; the heavier tail of power law is evident here too

Guttal, 2018). We consider our landscape to be a discrete two-dimensional space, consisting of $N \times N$ grid cells. Each grid cell can be either in an occupied state (representing an organism and denoted by 1) or in an unoccupied state (denoted by 0). The update rules for these local states consist of a baseline probability of reproduction described by a parameter p : If a randomly chosen cell is occupied, the organism gives birth with a probability p and the offspring colonizes one of the randomly chosen nearest neighbour cells; alternatively, the organism in the chosen cell dies with a probability $1 - p$.

The update rules also incorporate local positive feedback, via a second parameter q : If near-neighbours of the chosen cell are occupied, the probability of local birth is enhanced and that of death is reduced. See Appendix A for detailed model description, update rules, a simulation protocol and a schematic of the probabilistic update rules. This model was first described in the physics literature in Lübeck (2006) and has been recently adopted in the context of regime shifts (Eby et al., 2017; Majumder et al., 2019; Sankaran et al., 2018).

Although several spatial models in ecology try to explain power law clustering, due to their relative complexity, it is often difficult to clearly elucidate the role of positive feedback on clustering and resilience (Guichard et al., 2003; Kéfi, Rietkerk, Alados, et al., 2007; Kéfi, Rietkerk, Baalen, et al., 2007; Manrubia & Solé, 1997; Scanlon et al., 2007). The simplicity of our model allows us to independently tune, and thus, study the effects of an environmental driver and local positive feedback on spatial patterns via two parameters p and q respectively. We can think of p , which represents baseline reproduction probability of organisms, as being determined by key environmental conditions such as resource availability. Consequently, the parameter $1 - p$ can be interpreted as environmental stress.

Our model captures basic features of ecological transitions, consistent with previous studies. A stronger positive feedback in ecosystems is known to cause nonlinear and even abrupt responses to stress (Kéfi, Eppinga, Ruiters, & Rietkerk, 2010; Kéfi, Holmgren, & Scheffer, 2016; Xu, Van Nes, Holmgren, Kéfi, & Scheffer, 2015). To see this, we compute *density* of organisms in the landscape as the proportion of occupied cells in steady-state conditions (see Appendix A). In our model, when local positive feedback is weak ($q = 0$), the system undergoes a continuous transition from non-zero densities to a bare state as we increase environmental stress ($1 - p$) (Figure 3a,b). As the strength of local positive feedback (q) increases, the system can maintain a high density state even for higher levels of stress (similar to previous models; Corrado, Cherubini, & Pennetta, 2013); but the system also exhibits an abrupt transition to a bare state when the stress exceeds the critical threshold. Henceforth, we refer to the point of transition (defined by either driver value (p) or density (ρ)) as a *threshold*. When we specifically refer to a continuous transition, we call the threshold a *critical point* whereas the corresponding term for the discontinuous transition is *critical threshold* (also see Glossary).

To reveal the links between positive feedback, clustering and resilience, we use this model to investigate the relationship between (a) positive feedback and the emergence of power law clustering and

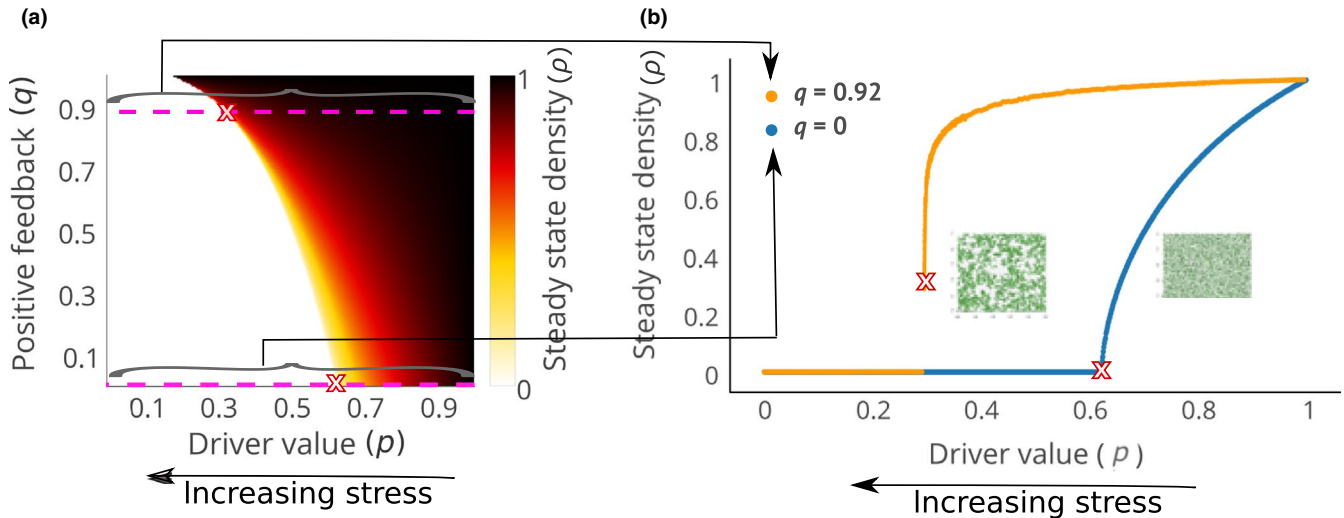


FIGURE 3 Positive feedback increases the nonlinearity and causes an abrupt collapse in response to stress. (a) Steady-state density (shown as heatmap) as a function of driver value (p) and positive feedback (q). Pink-dashed lines in (a) represent two values of q which are magnified and shown in (b): $q=0$ (continuous transition) and $q=0.92$ (abrupt transition). The red crosses in both panels represent critical point/threshold for these two values of q . Lattice size $1,024 \times 1,024$

(b) the power law clustering and thresholds of regime shifts. Finally, we demonstrate the implication of CSD on spatial correlations. Going forward, we present our findings to each of these investigations as separate subsections. Given that each investigation required us to draw methods from seemingly disparate concepts, we provide a brief explanation of the theory, methods and then present each finding.

2.2 | Positive feedback lowers the percolation density

To investigate the effect of positive feedback on power law clustering in ecosystems, we must first understand clustering in 'null models', that is, spatial models that are devoid of any interactions among organisms. The simplest way to implement such a null model is to merely distribute individuals on a two-dimensional discrete lattice *at random*, with the number of individuals determined by the desired densities on the landscape. Spatial null models correspond to classic models in the physics literature in the context of a phenomenon called percolation (Stauffer, 1979). This phenomenon refers to the emergence of a 'spanning cluster' – a single cluster that spans the extent of the system; other non-connected, smaller clusters may continue to exist on the landscape. The *lowest density* at which such a spanning cluster can occur is called the *percolation density* (denoted by ρ_p); the value of ρ_p depends on the model and the geometry of the landscape.

In null models with a square lattice – a geometry relevant to many ecological contexts – the percolation density (denoted by ρ_p) is 0.59. We ask the question – how does percolation density depend on the strength of local positive feedback (q) in our model? To address this question, we use the concept of *percolation probability* which is defined as the probability of occurrence of a spanning cluster in the landscape (see Appendix A for details of simulations). In Figure 4, we display the percolation probability as a function of density of

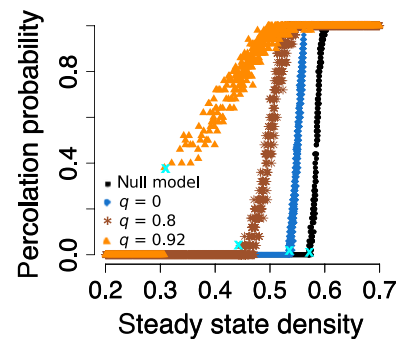


FIGURE 4 Percolation probability changes from zero to non-zero at an approximate density of 0.59 for the spatial null model, at 0.53 for the spatial model with low positive feedback ($q=0$), at 0.45 for higher positive feedback ($q=0.8$), and at 0.31 with very high positive feedback ($q=0.92$). Cyan-coloured crosses represent the approximate location of the percolation densities. For each of these cases, these transitions in percolation probability occur exactly at the density where power law cluster size distributions are observed; see Figure 5a and b. Lattice size 256×256

occupied cells on the landscape (ρ) for three different values of positive feedback (q) and the spatial null model. From this graph, we identify percolation density (ρ_p) as the lowest density at which this probability is non-zero.

We find that our model also exhibits a transition in percolation probability as a function of density (Figure 4). Based on the trends in the null model, together with the three values of positive feedback, we conclude that the percolation density (ρ_p) decreases with increasing local positive feedback (q). Based on the results of percolation (spatial null) models (Stauffer, 1979), we expect to see scale-free spatial clustering emerging at the percolation density in our spatial model as well. This quantification of percolation density is thus helpful for the next analysis concerning relationship between clustering and ecosystem resilience.

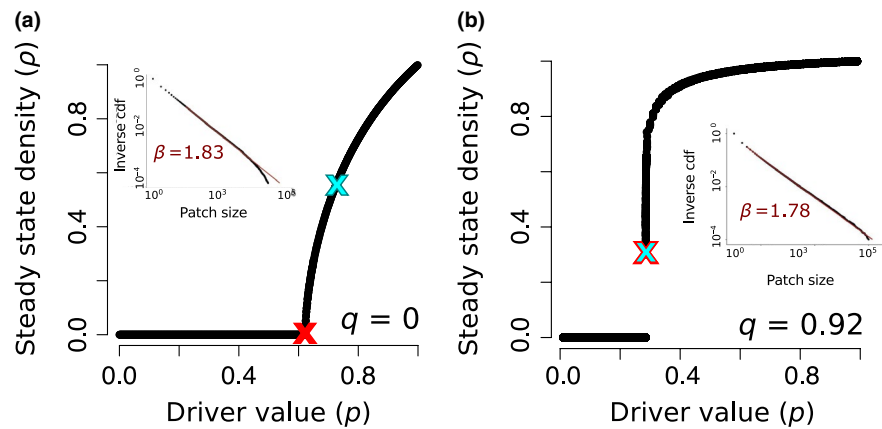


FIGURE 5 Strength of positive feedback, rather than distance to thresholds, determines the density at which power law (scale-free) clustering occurs. The values of driver and density at which we find a power law distribution (percolation point) are shown as cyan-coloured crosses in the phase diagrams (a) and (b), with their insets showing the corresponding inverse cumulative distribution function (CDF) of the patch sizes. (a) When positive feedback is weak ($q=0$), power law clustering occurs far from ecosystem transition, consistent with previous hypotheses. (b) When positive feedback is strong ($q=0.92$), power law clustering can occur close to (or even at) the critical threshold of collapse. For the fitted function $kx^{-\beta}$ wherein $k=(\beta-1)x_{\min}^{\beta-1}$, $x_{\min}=17$ in (a) and 3 in (b); lattice size = $1,024 \times 1,024$. See Appendix C for cluster size distributions at other values of p and q

2.3 | Cluster size distributions are not generic indicators of ecosystem resilience

Let us now consider how positive feedback affects both spatial clusters and resilience. As we showed in the above result, positive feedback promotes abrupt transitions and increases the threshold value of density at which the regime shift happens (Figure 3). Additionally, positive feedback can lower the percolation density (Figure 4). We find that power law clustering occurs at the percolation threshold irrespective of the density at which the threshold occurs (Figure 5a,b). It follows from this that, power law clustering can, therefore, occur at any distance from the threshold of regime shift.

In Figure 6, we display how positive feedback (q) affects the link between patterns, dynamics and resilience in a qualitative way. Based on this, we make predictions for two scenarios: we predict that in systems with *weak positive feedback* (q is low/zero), the distance between percolation density (ρ_p) and threshold of regime shift (ρ_c) will be relatively large. Thus, an approach to threshold follows the previously expected pattern of loss of power law clustering (Kéfi et al., 2014) (Figure 5b and inset). In contrast, for systems with *strong positive feedback* (q is high), which are most likely to exhibit abrupt transitions, the distance between percolation density and the critical threshold of collapse will be negligible or even zero (Figure 5b and inset). Hence, power law clustering may occur at the critical threshold itself and the loss of power law clustering cannot be used as a resilience indicator.

Our model confirms our expectations, that the distance between the density and threshold of transition and percolation density/threshold reduces as a function of positive feedback and becomes even zero for large values of positive feedback (Figure 6b). Consequently, the qualitative features of cluster-size distribution (e.g. being a power law, truncated power law or exponential) do not follow a general trend as a function of ecosystem

stress (see Appendix C). In Figure 5b and inset, we show a case where a strong positive feedback scenario shows a power law clustering occurring very near, even possibly at, the critical threshold of collapse.

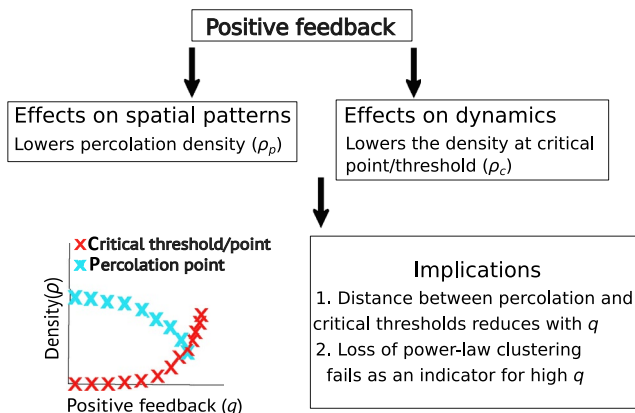
Put together, our model analyses suggest that the relationship between cluster sizes and ecosystem resilience heavily depends on the strength of positive feedback in the ecosystem. This questions the generality of cluster size distributions as indicators of ecosystem resilience. Notably, systems most prone to abrupt transitions (i.e. systems with strong positive feedback) are also systems where properties of cluster size distributions are least likely to be useful as indicators. Furthermore, since cluster size distributions do not primarily depend on proximity to critical threshold in these stochastic and spatial ecological models, we conclude that it is also unrelated to critical slowing down (CSD); we recall that CSD is a generic dynamical feature of systems near critical thresholds. See next section on how CSD influences spatial properties and causes power law features in them.

2.4 | Scale-free spatial correlations arise at critical thresholds of ecosystem collapse

The theory of phase transitions posits the emergence of scale-free features near/at critical points. Here, we illustrate how critical slowing down – a canonical feature of dynamical systems near thresholds – causes scale-free behaviour in the spatial autocovariance function (Figure 7; Appendix E).

As an ecosystem approaches a critical threshold, its return to equilibrium state, when perturbed, becomes increasingly slow. This phenomenon of critical slowing down (Ma, 2000; Scheffer et al., 2009; Wissel, 1984) has two implications – increased spatial correlations (Dakos, Nes, Donangelo, Fort, & Scheffer, 2010) and increased spatial variance (Guttal & Jayaprakash, 2009). The spatial

(a) Conceptual framework



(b) Result

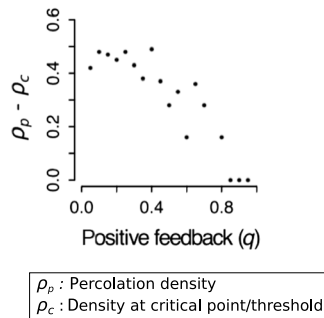


FIGURE 6 (a) Conceptual diagram of our hypothesis. This cartoon illustrates the qualitative features of the effect of positive feedback on thresholds (red crosses) and percolation points (cyan crosses). (b) shows that indeed in our model, as hypothesized conceptually, the difference between the density at which patches follow a power law distribution (ρ_p) and the density at the critical point/threshold (ρ_c) reduces as positive feedback (q) increases. For this result, lattice size of 256×256 was chosen to reduce computational time. See Appendix D for how difference between driver value at critical and percolation points/thresholds changes as a function of q

autocovariance function, defined as covariance of local densities at two locations separated by a distance r (Appendix E), captures both spatial variance and correlations. Calculation of the spatial autocovariance function, however, is often beset with statistical and computational difficulties. Therefore, we focus on a mathematically equivalent measure – power-spectrum (Kéfi et al., 2014). It can be shown that the power-spectrum is the Fourier transform 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 thresholds, the low frequency modes begin to dominate their power-spectrum (Carpenter & Brock, 2010; Kéfi et al., 2014). However, the full functional form of the power-spectrum is rarely quantified (but see Barbier, Couteron, Lejoly, Deblauwe, and Lejeune (2006), Bonachela et al. (2015), Couteron (2002) in the context of periodic and multi-scale patterns of dryland vegetation).

Simulations of our model show that the power-spectrum indeed becomes scale-free at critical thresholds for systems with both weak and strong positive feedback (Figure 7; see Appendix F for details of statistical fitting). It is well known that a scale-free power-spectrum is indicative of a scale-free autocovariance function (Reif, 2009; also see Appendix E). In other words, we may conclude that the autocovariance function is also scale-free near/at critical thresholds of ecosystem collapse in our model. Note that, unlike the cluster-size distribution which shows positive feedback and density-dependent trends (Figure S2 and S3 in Appendix C), the power-spectrum is consistently scale-free at the critical threshold.

3 | DISCUSSION

In this study, we investigated the generality of the hypothesis that loss of power law clustering in ecosystems is indicative of reduced resilience. We revealed that cluster size distributions are in fact unrelated to ecosystem resilience. Furthermore, when ecosystems are in the vicinity of critical thresholds of collapse, critical slowing down causes a power law (scale-free) behaviour in a different metric – the spatial autocovariance, or spectral function, of local densities.

3.1 | Local positive feedback and clustering

Previous ecological models that have attempted to resolve these connections include complex interactions often specific to particular ecosystems (Kéfi, Rietkerk, Alados, et al., 2007; Kéfi, Rietkerk, Baalen, et al., 2007; Kéfi et al., 2011; Meloni et al., 2017; Scanlon et al., 2007; Schneider & Kéfi, 2016). In such models, many parameters contribute to local positive feedback and environmental stress, thus making it difficult to disentangle causal links between local processes and macroscopic patterns. Here, we deliberately used a simple model which enabled us to unravel the effects of environmental stress and local positive feedback on clustering and resilience. It is worth highlighting another contrast with seminal ecological models that try to explain power law clustering observed in ecosystems (Kéfi, Rietkerk, Alados, et al., 2007; Kéfi, Rietkerk, Baalen, et al., 2007; Scanlon et al., 2007); they assume that local births/deaths of trees, in addition to being positively influenced by local density, are negatively regulated by *global-scale feedback*. Mechanisms such as rapid spread of water in the landscape (von Hardenberg et al., 2010) or a uniform global density-dependent grazing pressure (Kéfi, Rietkerk, Alados, et al., 2007; Kéfi, Rietkerk, Baalen, et al., 2007) are offered as potential explanations for negative regulation of local growth due to global-scale vegetation density. Based on our results in Figure 5, consistent with Manor and Shnerb (2008, 2009), we argue that there is no need to invoke global-scale feedback; in fact, local positive feedback 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, Holmgren, et al., 2015) nor the expected shifts of cluster size distributions with increasing stress (Casey,

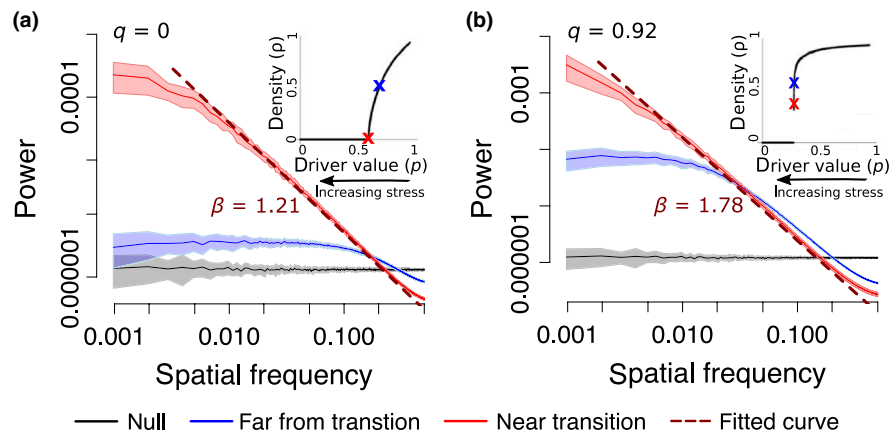


FIGURE 7 The power-spectrum of systems very near (or at) the threshold of transitions decays as a power law function of spatial frequency, (a) for $q=0$ and (b) for $q=0.92$. Lines represent the mean trend and bands, the SD. Insets show the location of parameter values for which power-spectrum is plotted. Blue is far from transition (0.73 for $q=0$ and 0.2862 for $q=0.92$), red is close/at the threshold (0.6225 for $q=0$ and 0.2852 for $q=0.92$) and grey represents the spatial null model. For the fitted function $kx^{-\beta}$ (dashed dark red line), $k=2.02 \times 10^{-7}$ when $q=0$ and 4.65×10^{-8} when $q=0.92$. We used a $1,024 \times 1,024$ lattice. See Appendix F for details on statistical fitting

Cohen, Acharya, Kaplan, & Jawitz, 2016). However, they attribute this to an absence/disruption of global negative feedback in their systems (Casey et al., 2016; von Hardenberg et al., 2010; Weerman et al., 2012) (but also see Moreno-de las Heras, Saco, Willgoose, & Tongway, 2011). As we argued in the previous paragraph, negative feedback is not a necessary condition for scale-free clustering. Further, based on our results that cluster sizes do not relate to resilience, we posit that these empirical results are not surprising.

3.2 | Cluster size distributions in other contexts

Many different processes can result in the emergence of power law cluster size distributions (Mitzenmacher, 2004; Newman, 2005). Consequently, the interpretation of the loss of power law clustering could differ across systems. Broadly, for correct interpretations of power law clustering (or loss of power laws), it is important to understand how local interactions and processes scale to macroscopic clustering properties. Previous studies have shown that power law cluster size distributions arise when clusters grow in proportion to their size, also called proportionate growth (Manor & Shnerb, 2009). Our simple model and as well as those presented in several studies, (for e.g. Corrado et al., 2014; Guichard et al., 2003; Kéfi et al., 2014; Kéfi, Rietkerk, Alados, et al., 2007; Kéfi, Rietkerk, Baalen, et al., 2007; Scanlon et al., 2007), are likely to be consistent with the generic feature of proportionate growth in clusters. We expect that our conclusions on the lack of relationship between cluster size distributions and resilience will be applicable to these spatially explicit models.

There could, however, be system-specific cases where trends in cluster size distributions may function as an indicator of ecosystem health. For example, in ecosystems with relatively weak local positive feedback, the distance between percolation point and critical thresholds could be large (see Figure 6); here, cluster size distributions, which qualitatively change from a power law to an exponential

distribution as a function of reducing density and therefore, will show a loss of power law clustering as the system approaches the critical threshold. However, even in spatial null models with no local interactions and no thresholds of regime shifts, cluster size distributions show the same behaviour, that is, a loss of power law clustering as a function of reducing density (Kéfi et al., 2014, 2011). Hence, one must exercise caution in drawing causal relationships between cluster size distributions and resilience. Even in such specific instances where cluster size distributions may offer indicators of ecosystem health, monitoring of critical slowing down-related measures such as spatial variance and correlations (also see next section) is likely to be helpful by providing an additional assessment of ecosystem resilience.

We, however, reiterate that many processes can lead to power law relationships. A detailed exposition of the emergence of various power law relationships and the local processes underlying the dynamics of these systems are beyond the scope of this manuscript. We refer the reader to Newman (2005) for a review on the topic.

3.3 | Cluster sizes and critical slowing down

How do scale-free correlations in density and scale-free clustering relate to each other? They both indicate the emergence of large spatial scales in the system. In our model, however, they capture fundamentally different properties. Scale-free correlations in density indicate that perturbations spread to large distances in ecosystems as a consequence of critical slowing down. 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. In our model, we showed that the dynamics of how perturbations decay do not relate to distribution of cluster sizes. Based on this, we hypothesize this to be true for associated models such as dryland vegetation and mussel bed models. (Guichard et al., 2003; Kéfi, Rietkerk, Alados, et al., 2007; Kéfi, Rietkerk, Baalen, et

al., 2007; Scanlon et al., 2007; Scheffer, Rinaldi, Gragnani, Mur, & Nes, 1997). Future studies may explore the validity of this hypothesis in other ecosystem models and how system-specific processes may affect these results.

How efficient is it to use scale-free features of density correlations as an early warning signals (EWS) of regime shifts or critical transitions (Scheffer et al., 2009)? The purpose of early warning signals is to detect signatures of approach to critical thresholds. In that sense, computing simpler metrics of spatial autocorrelation between neighbouring sites (Dakos et al., 2010) or spatial variance (Guttal & Jayaprakash, 2009) may have advantages such as ease of computation and better statistical reliability in comparison to characterizing 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) and hence confound interpretations. Further investigations can reveal the relative efficacy of different spatial metrics.

Long-range and even scale-free spatial correlations have indeed been documented in some ecological contexts. For example, orientations of birds in starling murmurations show scale-free correlations (Cavagna et al., 2010). In population ecology, patterns of tree yield may show a long-range spatial synchrony (Noble, Rosenstock, Brown, Machta, & Hastings, 2018). In these cases too, spatial autocorrelation essentially measures the spread of perturbations from one individual to nearby individuals and the resultant long-range patterns. With the increase in the availability of large-scale spatial datasets in ecology, especially remotely sensed images, we expect that measures of spatial clustering and correlations can be obtained with statistical rigour, potentially offering insights on local ecological interactions and ecosystem resilience.

3.4 | Concluding remarks

Our study helps us disentangle processes that generate power law cluster sizes, scale-free correlations and how they relate to ecosystems' critical thresholds. With the increasing availability of high-resolution spatial datasets, from satellites to drone-based imagery, of various ecosystems, spatial analyses are likely to be widely deployed in the future. Such data will enable us to quantify not only patterns, as described above, but also dynamics of clusters and correlations (Manor & Shnerb, 2009; Van Belzen et al., 2017; Weissmann, Kent, Michael, & Shnerb, 2017; Weissmann & Shnerb, 2016). Our study reveals that naive association of observed scale-free behaviours with either criticality or stability can be misleading. Furthermore, we highlight the importance of having a clear understanding of how local interactions drive macroscopic behaviours to infer resilience of ecosystems.

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AUTHORS' CONTRIBUTIONS

S.S. conceived the idea. S.S. wrote codes with key contributions from S.M. (model), A.V. (statistical fitting) and V.G. (power-spectrum). S.S. conducted analyses and produced figures. S.S. and V.G. synthesized the literature review and model results. S.S. and V.G. wrote the manuscript with comments from S.M. and A.V. All authors gave final approval for publication and have no conflict of interests to declare. We thank Sonia Kefi for many insightful discussions. We thank the Associate Editor of the manuscript and Hari Sridhar for helpful comments on the manuscript.

DATA AVAILABILITY STATEMENT

All simulation analyses codes, with simulation datasets corresponding to results presented in this paper, have been made publicly available at: <https://doi.org/10.5281/zenodo.3387085> (Sankaran, Majumder, Viswanathan, Guttal, 2019). Detailed instruction on execution of these codes is also provided.

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SUPPORTING INFORMATION

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