Patchiness and scale-free correlations: characterising criticality in ecosystems

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Abstract

A variety of ecosystems exhibit spatial clustering devoid of characteristic sizes, also known as scale-free clustering. In physics, scale-free behaviour is known to arise when a system is at a critical point, which occurs at the edge of two phases of matter. Scale-free clustering in physics therefore indicates that a system is not resilient. Spatial ecological studies, however, posit that scale-free clustering arises away from critical points and is therefore an indicator of robustness. This inconsistency is troubling. Here, we synthesize the literature on cluster-size distributions together with analyses of a spatial ecological model that incorporates local birth, death and positive feedbacks. We argue that scale-free clustering in real ecological systems is driven by strong positive feedbacks. Using the model, we demonstrate that power-law relations may occur far away from, near or at the critical point of ecosystem collapse depending on the strength of local positive feedbacks. We therefore infer that clustering patterns are unrelated to critical points of ecosystem collapse. Power-law clustering, instead, indicates a different critical point, called a percolation point, that signifies the onset of spanning clusters in a landscape. Finally, we show that a collapse or a regime shift in an ecosystem is characterized by the emergence of scale-free spatial correlations in the system, reflected in a scale-free power-spectrum.

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I.   INTRODUCTION

Desertification of semi-arid ecosystems [1], eutrophication of lakes [2], spread of diseases [3], invasion [4] and community shifts in coral reefs [5] are some examples of state transitions in ecological systems. Some of these transitions can be abrupt and irreversible, leading to the catastrophic loss of wildlife, habitats, and ecosystem services. In ecology, much of our understanding of the dynamics of such transitions, which are also called regime-shifts or critical transitions, is based on principles derived from the theory of phase transitions and bifurcations [6–9]. This theory predicts that the interactions that stabilize a system become increasingly weak as the system nears a critical point. This results in the emergence of properties, that are independent of system-specific details, such as delays in the system's recovery from perturbations. More specifically, perturbations decay as a power-law function of time in critical systems, in contrast to stable systems where perturbations decay exponentially fast. This phenomenon, which is called critical slowing down, has been widely used to devise early warning signals for ecosystems approaching transition points [6–8]. It is, however, only one of several power-law relations that arise at critical points. This emergence of archetypal features in critical systems is called criticality [10–12]. In the physics literature, criticality is often used synonymously with power-law relations (see Box I) [13–15].

Contrastingly, in ecology, power-law clustering is often considered characteristic of resilient rather than critical ecosystems [16–20]. Power-law clustering refers to aggregations of individuals, called patches or clusters, over a landscape such that there is a power-law relationship between the size of clusters and their frequency of occurrence (see Box I). Previous studies suggest that such clustering emerges in ecosystems under conditions of high resilience [16, 17]. When ecosystems are stressed, clusters fragment leading to loss of large patches. This results in a gradual shift from a power-law to an exponential cluster-size distribution, as stressors increase. The disappearance of power-law clustering is, therefore, hypothesised to represent loss of resilience in ecosystems [16, 18, 19, 21–23]. Further, the emergence of power-laws away from critical points has been referred to as 'robust criticality', i.e. the appearance of critical properties over a broad range of conditions, not in the vicinity of critical points [12, 22]. Power-law relations in

these systems thus seem at variance with classical physics theories.

Although some empirical studies in ecology contest the generality of the association between power-law clustering and resilience [24–27], the theory has gained much traction in the ecology community. In this paper, we show that power-law clustering cannot be a signature of resilience. Via a synthesis of recent literature [16, 17, 28, 29], we argue that the power-law clustering observed in real-world ecosystems is promoted by strong facilitative interactions in these systems. We then demonstrate with a simple spatial model, that depending on the facilitative interactions in the system, such clustering may occur far away from, near or at the critical point of ecosystem collapse and is thus independent of resilience. Scale-free power-law clustering (Box I) is instead always indicative of the emergence of clusters that span the landscape, also known as the percolation threshold. We finally show that properties of systems at collapse thresholds are best captured by a different metric - the spectral density - which decays as a power-law function of spatial frequency.

Glossary

1. Regime shifts: Qualitative changes in ecosystem state. These shifts can be abrupt or gradual functions of the underlying drivers.

2. Phase transition: A discontinuous change in a macroscopic property of a system. Some ecological relevant macroscopic quantities are canopy cover, biomass density, connectivity, etc.

3. 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.

4. Criticality: Characteristic features of a system at a critical point. These features are often independent of the system-specific details.

5. Robust criticality: The appearance of critical features over a broad range of conditions, and not only near the critical point.

6. Scale-free: Lacking a characteristic scale, or a quantity having infinite average value.

7. Diverge: Tending to infinity.

8. Percolation: Existence of a path (of sites in a particular state) from each edge of a system to all others.

9. Resilience: The amount of disturbance a system can withstand without transitioning to an alternate state.

10. Stability: The rate at which a system recovers from perturbations.

11. Facilitation: Interactions between individuals resulting in enhanced reproduction and/or reduced death rates.

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.

BOX 1: POWER-LAW CLUSTERING

Biology is replete with examples of self-organised spatial clustering ([30–32]; see Fig 1). Often, this clustering occurs in the form of irregular clumps without a characteristic size (Fig 1). 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 $x > x_{min}$ wherein c is a constant. The lower the value of the exponent β, the heavier the tail of the distribution. This distribution cannot be normalised if $\beta < 1$. Additionally, 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

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

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

Thus, there is no characteristic size or typical length scale in this distribution, when $1 < \beta \leq 2$, and the distribution is called *scale-free*. Power-law distributions of biological quantities with exponents ≤ 2 are therefore intriguing. Such distributions, however, are not uncommon and have been documented in various ecosystems (Fig 1).
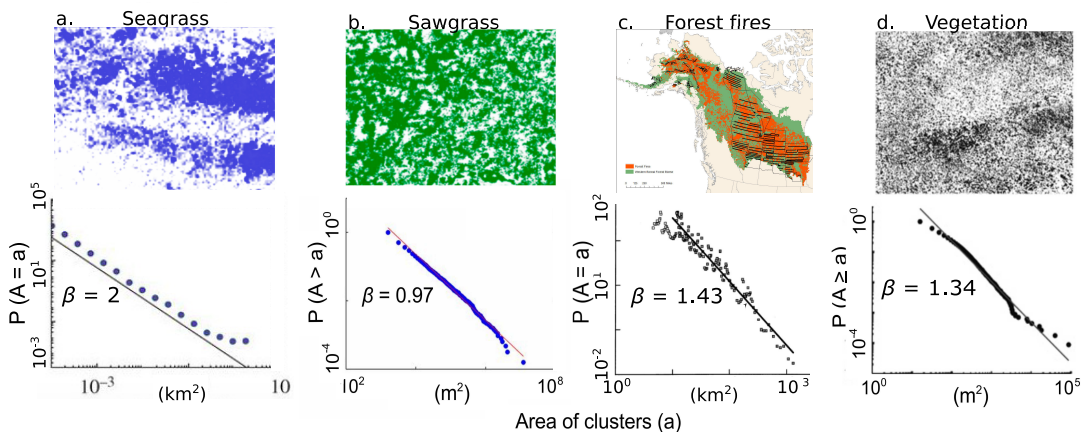

Figure 1: Scale-free cluster size distributions in different ecosystems and representative snapshots (not necessarily from the same study area or time period) of (a) West broad ledges seagrass near the isle of scilly, [33] (b) Saw-grass in everglades wetlands, USA [34] (c) Forest fires in Alaskan boreal forests, USA (1990-91) [35] and (d) Vegetation in Kalahari, Namibia [17] Top row image credits: modified from [36] https://doi.org/10.1016/j.ecss.2017.11.001 [CC BY] http://creativecommons.org/licenses/by/4.0/, [34], U.S. Geological Survey,Department of the Interior/USGS U.S. Geological Survey Map created by Tyler Lewis/USGS. Data (1995-2014), [17]

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II. POSITIVE FEEDBACKS PROMOTE POWER-LAW CLUSTERING AT RELATIVELY LOW DENSITIES

Power-law clustering in the real world (Figure 1 in Box 1) is predominantly seen in ecosystems with strong positive interactions [17, 31, 34, 37]. Power-law cluster-size distributions, however, 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 [22, 38]. 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 [39]. Despite the lack of positive feedbacks in these null models (henceforth called percolation models), power-law clustering occurs at a particular density of the occupied sites, known as percolation density. For ecological contexts, a relevant geometry is that of two dimensional square lattice for which the percolation density is 0.59 [38].

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 [17]. Spatial ecological models of ecosystems that aim to explain these scale-free clustering all assume varying degrees of positive-feedback interactions in the system [16, 17, 40–42]. 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 [28]. 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 [29]. In percolation models, proportionate growth occurs only at the percolation density, which is 0.59 for a square lattice [28, 38]. In models with local facilitation, proportionate growth and thus scale-free clusters occur at lower densities than 0.59 [17], offering 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 [5, 16, 17, 31, 34, 37, 43–45]. 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 [37, 43]. 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 [42]. 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 [44, 45]. Thus, models together with empirical data indicate that positive feedbacks lower the density at which power-law clustering in ecosystems.

BOX 2: SPATIAL MODEL WITH POSITIVE FEEDBACK

Several spatial models in ecology try to explain power-law clustering in the context of facilitation and/or ecosystem resilience [16, 17, 31, 41]. These models incorporate detailed ecological processes that are relevant to some focal ecosystems. Owing to their complexity, however, it is difficult to infer generic relationships between different microscopic processes (facilitation) and macroscopic patterns (e.g. clustering and ecosystem resilience). 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 2). 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 2 and described in Appendix B. Detailed model description and analytical methods can be found in [46]

Facilitation induces abrupt regime shifts: Local positive feedbacks in ecosystems are known to cause non-linear responses to stress [47–49]. Consider the example of plants in a semi-arid ecosystem. The presence of neighbours offsets water and heat stress to
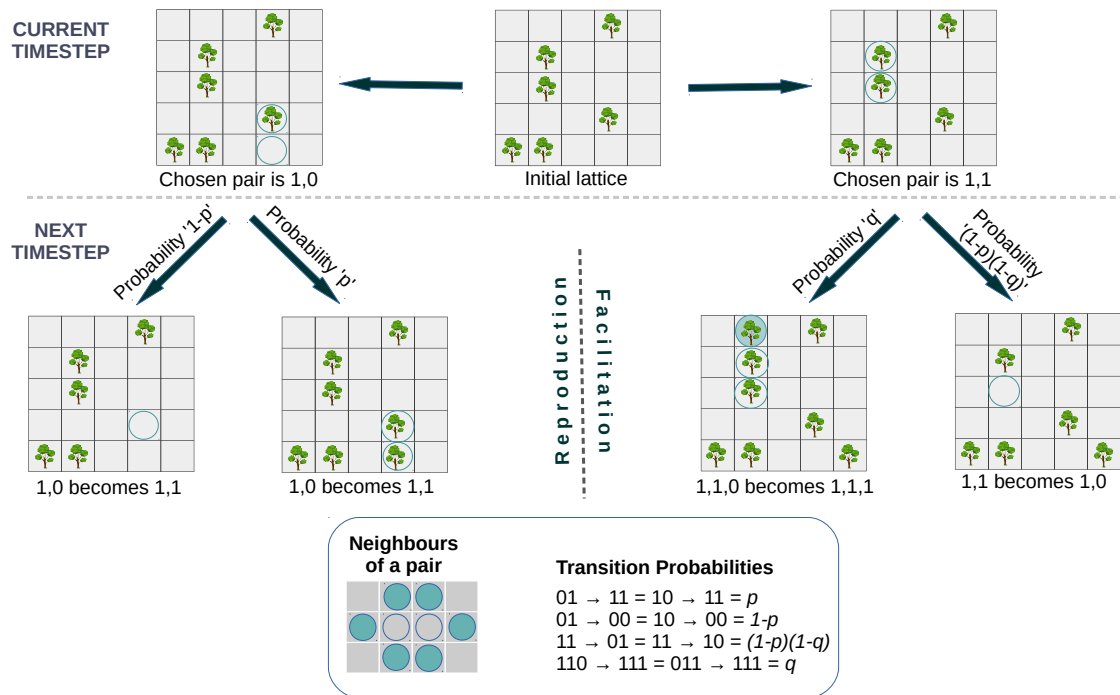
Figure 2: Schematic representation of the model and simulation procedure, for a given 'Initial lattice' shown at the centre of the top row. Light blue circles represent (randomly) chosen cells to update. Depending on the states of chosen cells, the update scheme results in reproduction (left part of 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.

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 with a minimum threshold of neighbourhood density for plants to survive and increasing stress can then potentially collapse the entire system [48].
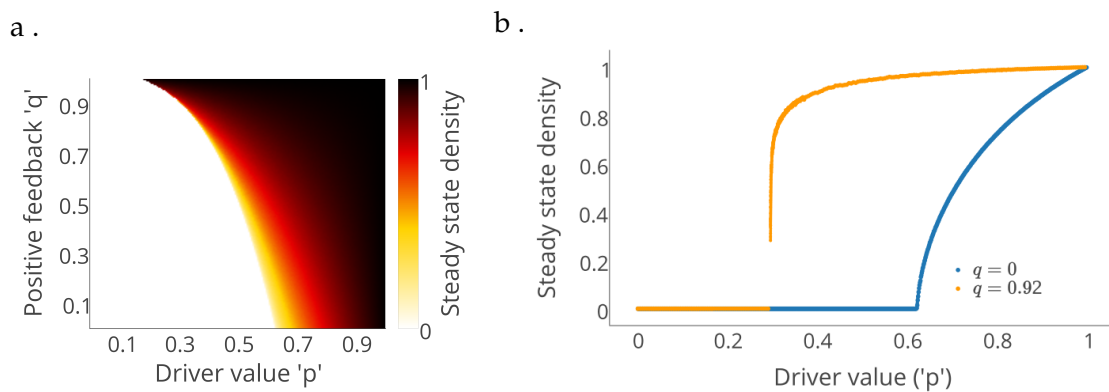

Figure 3: (a) shows steady state density as a function of changing driver value for different values of positive feedback. (b) shows a close look at the nature of this change for two values of positive feedback, $q = 0$ and 0.92. We find that facilitation increases the non-linearity and may even cause an abrupt collapse in response to stress.

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Indeed, our model too shows that when facilitation is weak, the system undergoes a continuous transition from an occupied to a bare state (Fig 3). 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.

III.   POWER-LAW CLUSTERING IS RELATED TO PERCOLATION POINT AND NOT 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 [16–18]. Researchers have argued for a phenomenon they called 'robust criticality', based on the emergence of power-laws over a range of driver conditions in certain types of systems [12, 22], to explain the counter-intuitive shift away from a power-law pattern as the system approaches a transition. 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 [16, 18], while others do not [24–27]. Based on our model analyses, we argue 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*.

Few ecological studies have examined the association between power-law clustering and percolation in (non-null) models with spatial-interactions (but see [50]). As we argued in Section II, facilitation lowers the density at which clusters grow proportionally to their size. This reflects as a reduction in the density at which power-law clustering emerges. Further, as we have shown for our model as well (see Box II), positive feedbacks also promote non-linearities in the system's response to stress, thus promoting abrupt collapse from high densities (Fig 3 b). Consequently, depending on the strength of facilitation, power-law clustering can occur at any distance from the critical density of collapse; for example, the inset of Fig 4a shows the emergence of power-law clustering far from the critical point whereas the inset of Fig 4b shows power-law clustering very near, even possibly at, the critical point of collapse. Thus, cluster-size distribution reveals little about the ecosystem's resilience.
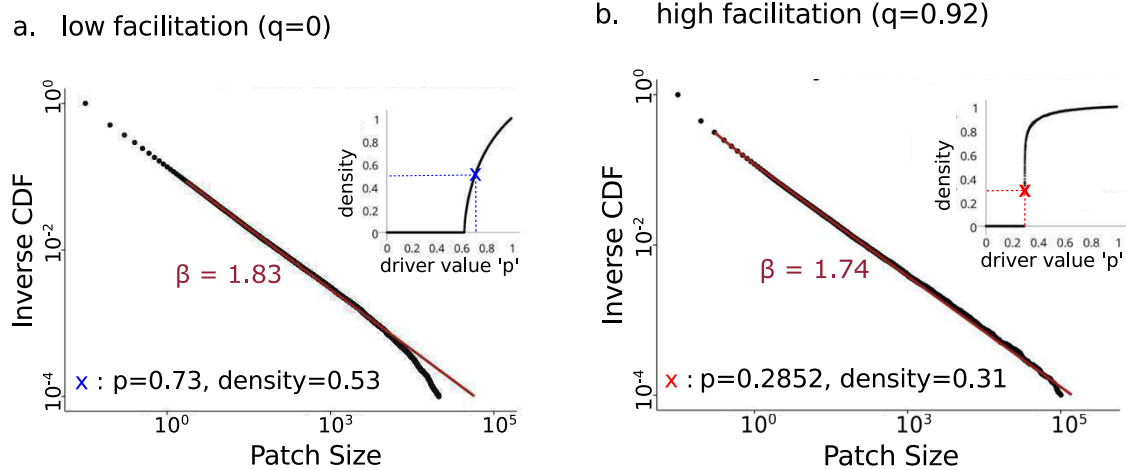
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Figure 4: Strength of facilitation, rather than distance to critical transition, determines the cluster size distribution. The Inverse CDF is the inverse cumulative distribution function. The values of driver and density at which we find a scale-free 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 [12, 16, 17]. (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.

Cluster size distributions, however, are frequently associated with a critical phenomenon called percolation. 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 power-law clustering. Consequently, the average cluster size diverges and the system exhibits no scale, or is called scale-free. In other words, power-law 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 5). Just as in null model, 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, $q = 0$ to 0.95, and we expect it to be true for all the entire range (i.e, up to $q = 1$).
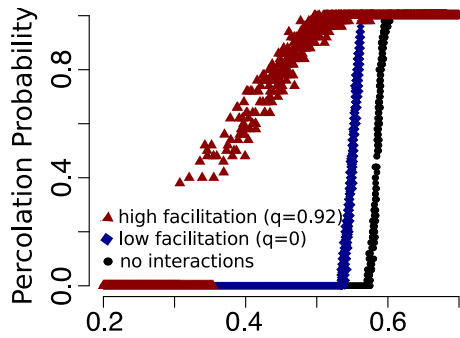
Figure 5: Percolation transition for different strengths of facilitation and a null model. Percolation transition occurs close to density 0.59 for the null model, 0.53 for low facilitation ($q = 0$) and 0.31 for high facilitation ($q = 0.92$). We note that the percolation transition is exactly at that density where power-law cluster size distributions are observed; see Fig 4.

The percolation density is lower for the system with higher facilitation (Fig 5), 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 5).

Thus, power-law cluster size distributions are indeed a signature of criticality but associated with a percolation transition. At the percolation point, the average cluster size diverges and the system becomes scale-free (Fig 5). However, 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., cover) collapses.

IV. 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 can not 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 6; Appendix E).

As an ecosystem approaches a critical point, its return to equilibrium state, when disturbed, becomes progressively slower. This phenomenon, known as critical slowing down [8, 9, 13, 51], has two implications - increased spatial correlations [52] and increased spatial variance [53]. 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 [13, 14]. A measure of perturbation spread, the correlation length, rapidly increases [52]. Second, as the

perturbations persist for longer, further disturbances enhance the amplitudes of the ripples. This manifests as increasing spatial variance in the ecosystem as it moves towards the critical point [53]. Here, we consider the spatial autocovariance function, defined as covariance of densities at two locations separated by a distance r (Box I). 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 [14]. 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 [50]. 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*. So far critical slowing down has been well demonstrated in both models and empirical systems of even discontinuous ecological transitions. Here, using our ecological model, we demonstrate that scale-free behaviour characterises critical points of both the continuous and 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 [18] (Appendix E). It can be shown that the power spectrum is the Fourier transformation of the autocovariance function [54]. 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 [18, 55]. However, the full functional form of the power-spectrum is rarely quantified but is crucial to inferring critical behaviour. Simulations of our model described above shows that the power-spectrum becomes scale-free at critical points (Fig 6). We explain in Appendix E that a scale-free power spectrum is indicative of a scale-free autocovariance func-

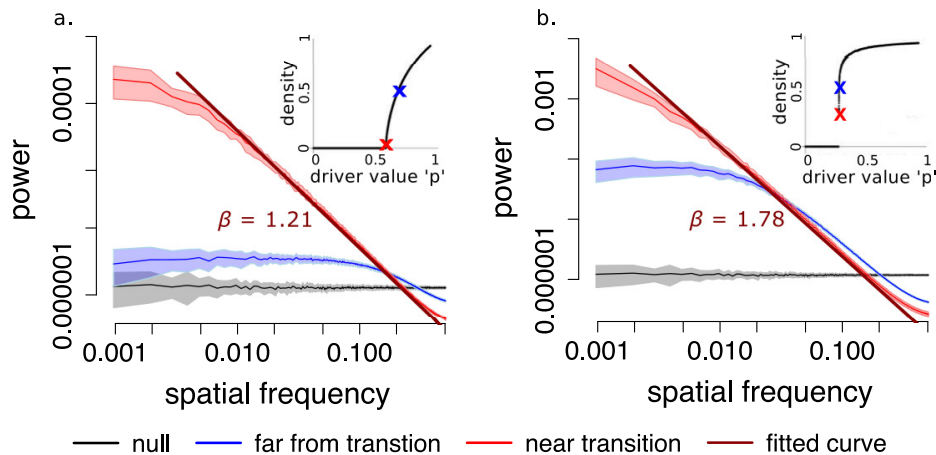tion. Criticality associated with density collapse of an ecosystem is thus captured in its power-spectrum.

Figure 6: 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.

V. DISCUSSION

Scale-free behaviour is known to occur in critical systems. It is thus intriguing that several ecological studies associate scale-free clustering with resilient ecosystems. We show in this paper that scale-free clustering 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.

A. Positive feedbacks and clustering

Previous ecological models that have attempted to resolve these connections include complex interactions often specific to particular ecosystems [17, 22, 26, 27,

56]. 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. Specifically, seminal models relating clustering and resilience [16, 17] also assumed that local birth/death of trees was negatively regulated by global density of vegetation in the landscape. Mechanisms such as rapid spread of water in the landscape [57] are offered as potential explanation for global-scale feedbacks. However, based on our synthesis([28, 29] and Fig 4), we posit that local positive feedbacks alone can explain the emergence of scale-free clustering in these systems.

A recent theoretical study found that this association of cluster-size distributions with resilience can fail [26]. This study investigated the effect of incorporating grazing in a previous model of dryland vegetation dynamics. Here, 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 [16, 17], 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. In other words, any form of cluster size distribution (exponential, scale-free, etc) can occur at the critical point of ecosystem collapse .

Some studies extend and aim to generalise the idea of cluster size distributions to infer resilience [19]. They argue that fragmentation and concomitant loss of large patches, or shift in mean-patch size, has a wider applicability extending even to systems with Turing-like (regular) patterns. That the geometry of clusters can reflect resilience-loss was in fact first proposed for systems with Turing-like spatial structures [58]. A few empirical studies that have quantified such patterns, however, don't find the expected shifts in the cluster shapes/size-distributions with increasing stress in the ecosystem [19, 20, 25]. Nevertheless, they do not question the premise of the original hypothesis. Instead, some studies invoke explanations based on the relative strengths of local versus long-range negative feedbacks in the ecosystem [19, 20] or based on geographical constraints

imposed by the landscapes [25]. We think that complexity of previous models was the limiting factor in revealing the absence of a link between resilience and cluster properties. Our model analysis shows that facilitative interactions alone can alter cluster properties. Although we investigated systems with irregular sized clusters, our result that cluster properties do not relate to resilience can potentially extend even to Turing-like systems.

B. Relevance of cluster sizes

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 [3, 59]. 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. 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 [10]. Here too, unlike the hypothesis of [16–18], scale-free clusters do not indicate resilient systems.

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C. Critical transitions and early warning signals

Our analyses show 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 [8]? The EWS of critical transitions (as noted in the Introduction), as well as the emergence of scale-free correlations (Section IV), arise from critical slowing down. Although we argue that scale-free correlations are a reliable signature of criticality, we do not intend to propose that they offer better early warning signals of critical transitions. 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 [52] or spatial variance [53] 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 [18, 52] and hence confound interpretations. Therefore, further investigations are required to reveal the relative efficacy of looking for features like scale-free correlations. The key focus of our synthesis, however, is to disentangle processes that generate scale-free cluster sizes, scale-free correlations and how they relate to criticality.

D. Concluding remarks

Real world analyses can sometimes misleadingly yield power-laws due to sampling artefacts [60] or misfitting [61–63]. Various ways in which patterns are misconstrued as power-laws have been discussed in detail in multiple other forums [61, 64, 65]. Where there is a true power-law with an exponent less than 2, 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 [66, 67]. Naive association of observed scale-free behaviours with either criticality or stability are both problematic. Our study highlights the importance of having a clear understanding of how local-interactions drive macroscopic behaviours. Criticality can then be inferred by measurements and analyses of appropriate ecological quantities.

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VI. DATA AND CODES

All simulation analyses codes, with simulation datasets corresponding to results presented in this paper, have been made publicly available at https://github.com/ssumithra/PowerLawCriticalityPaper. Detailed instruction on execution of these codes are also provided.

VII. ONLINE SUPPLEMENTARY MATERIALS

Appendix A: Power-law Vs exponential functions.

Appendix B: Detailed model description.

Appendix C: Statistical fitting of cluster-size distributions.

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

Appendix E: Power-spectrum fitting.

VIII. COMPETING INTERESTS

We have no competing interests.

IX. AUTHOR CONTRIBUTIONS

SS conceived the idea. SS wrote codes with key contributions from SM (model), AV (statistical fitting) and VG (power spectrum). SS conducted analyses and produced figures. SS and VG synthesised the literature review and model results. SS and VG wrote the manuscript with comments from SM and AV. All authors gave final approval for publication.

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[1] van de Koppel J, Rietkerk M, van Langevelde F, Kumar L, Klausmeier C, Hearne JW, van Andel J, de Ridder N, Skidmore A, Stroosnijder L, Prins HHT. 2002 Spatial heterogeneity and irreversible vegetation change in semiarid grazing systems. *American Naturalist* **159**, 209–218.

[2] Carpenter SR, Ludwig D, Brock WA. 1999 Management of eutrophication for lakes subject to potentially irreversible change. *Ecological applications* **9**, 751–771.

[3] Chaves LF, Hashizume M, Satake A, Minakawa N. 2012 Regime shifts and heterogeneous trends in malaria time series from Western Kenya Highlands. *Parasitology* **139**, 14–25.

[4] Hansen GJ, Ives AR, Vander Zanden MJ, Carpenter SR. 2013 Are rapid transitions between invasive and native species caused by alternative stable states, and does it matter?. *Ecology* **94**, 2207–2219.

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

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

[7] Strogatz S, Friedman M, Mallinckrodt AJ, McKay S et al.. 1994 Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry, and Engineering. *Computers in Physics* **8**, 532–532.

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

[9] Dakos V, Kéfi S, Rietkerk M, van Nes E, Scheffer M Slowing Down in Spatially Patterned Ecosystems at the Brink of Collapse. .

[10] Solé RV, Manrubia SC, Benton M, Kauffman S, Bak P. 1999 Criticality and scaling in evolutionary ecology. *Trends in Ecology & Evolution* **14**, 156–160.

[11] Christensen K, Moloney NR. 2005 *Complexity and criticality* vol. 1. Imperial College Press.

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

[13] Ma SK. 2000 *Modern theory of critical phenomena*. Da Capo Press.

[14] Sethna J. 2006 *Statistical mechanics: entropy, order parameters, and complexity* vol. 14. Oxford University Press.

[15] Stanley HE. 1999 Scaling, universality, and renormalization: Three pillars of modern critical phenomena. *Reviews of modern physics* **71**, S358.

[16] Kéfi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasis VP, ElAich A, de Ruiter PC. 2007 Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* **449**, 213–217.

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

[18] Kéfi S, Guttal V, Brock WA, Carpenter SR, Ellison AM, Livina VN, Seekell DA, Scheffer M, van Nes EH, Dakos V. 2014 Early warning signals of ecological transitions: methods for spatial patterns. *PloS one* **9**, e92097.

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

[20] Yuan J, Cohen MJ. 2017 Spatial metrics for detecting ecosystem degradation in the ridge-slough patterned landscape. *Ecological Indicators* **74**, 427–440.

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

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

[23] Lin Y, Han G, Zhao M, Chang SX. 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.

[24] Maestre FT, Escudero A. 2009 Is the patch size distribution of vegetation a suitable indicator of desertification processes?. *Ecology* **90**, 1729–1735.

[25] Moreno-de las Heras M, Saco PM, Willgoose GR, Tongway DJ. 2011 Assessing landscape structure and pattern fragmentation in semiarid ecosystems using patch-size distributions. *Ecological Applications* **21**, 2793–2805.

[26] Schneider FD, Kéfi S. 2015 Spatially heterogeneous pressure raises risk of catastrophic shifts. *Theoretical Ecology* pp. 1–11.

[27] Meloni F, Nakamura GM, Granzotti CRF, Martinez AS. 2017 Empirical evidence reveals the phase diagram of vegetation patterns in Mediterranean drylands. *bioRxiv* p. 171835.

[28] Manor A, Shnerb NM. 2008a Facilitation, competition, and vegetation patchiness: from scale free distribution to patterns. *Journal of theoretical biology* **253**, 838–842.

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

[30] von Hardenberg J, Meron E, Shachak M, Zarmi Y. 2001 Diversity of vegetation patterns and desertification. *Physical Review Letters* **87**, 198101.

[31] Guichard F, Halpin PM, Allison GW, Lubchenco J, Menge BA. 2003 Mussel disturbance dynamics: signatures of oceanographic forcing fr om local interactions. *The American Naturalist* **161**, 889–904.

[32] Rietkerk M, van de Koppel J. 2008 Regular pattern formation in real ecosystems. *Trends in Ecology & Evolution* **23**, 169–175.

[33] Irvine MA, Jackson E, Kenyon EJ, Cook KJ, Keeling MJ, Bull J. 2016 Fractal measures of spatial pattern as a heuristic for return rate in vegetative systems. *Royal Society open science* **3**, 150519.

[34] Foti R, del Jesus M, Rinaldo A, Rodriguez-Iturbe I. 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.

[35] Malamud BD, Morein G, Turcotte DL. 1998 Forest fires: an example of self-organized critical behavior. *Science* **281**, 1840–1842.

[36] Duffy JP, Pratt L, Anderson K, Land PE, Shutler JD. 2017 Spatial assessment of intertidal seagrass meadows using optical imaging systems and a lightweight drone. *Estuarine, Coastal and Shelf Science*.

[37] Aguiar MR, Sala OE. 1994 Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. *Oikos* pp. 26–34.

[38] Grimmett G. 1999 What is Percolation?. In *Percolation* , pp. 1–31. Springer Berlin Heidelberg.

[39] Stauffer D. 1979 Scaling theory of percolation clusters. *Physics reports* **54**, 1–74.

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

[41] Manrubia SC, Solé RV. 1997 On forest spatial dynamics with gap formation. *Journal of theoretical biology* **187**, 159–164.

[42] Guichard F, Halpin PM, Allison GW, Lubchenco J, Menge BA. 2003 Mussel disturbance dynamics: signatures of oceanographic forcing from local interactions. *The American Naturalist* **161**, 889–904.

[43] Maestre FT, Bautista S, Cortina J. 2003 Positive, negative, and net effects in grass–shrub interactions in Mediterranean semiarid grasslands. *Ecology* **84**, 3186–3197.

[44] Dell CL, Longo GO, Hay ME. 2016 Positive feedbacks enhance macroalgal resilience on degraded coral reefs. *PloS one* **11**, e0155049.

[45] Boada J, Arthur R, Alonso D, Pagès JF, Pessarrodona A, Oliva S, Ceccherelli G, Piazzi L, Romero J, Alcoverro T. 2017 Immanent conditions determine imminent collapses: nutrient regimes define the resilience of macroalgal communities. **284**, 20162814.

[46] Lübeck S. 2006 Tricritical directed percolation. *Journal of statistical physics* **123**, 193–221.

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

[48] Kéfi S, Eppinga MB, de Ruiter PC, Rietkerk M. 2010 Bistability and regular spatial patterns in arid ecosystems. *Theoretical Ecology* **3**, 257–269.

[49] Xu C, Van Nes EH, Holmgren M, Kéfi S, Scheffer M. 2015 Local Facilitation May Cause Tipping Points on a Landscape Level Preceded by Early-Warning Indicators. *The American Naturalist* **186**, E81–E90.

[50] Roy M, Pascual M, Franc A. 2003 Broad scaling region in a spatial ecological system. *Complexity* **8**, 19–27.

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

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

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

[54] Reif F. 2009 *Fundamentals of statistical and thermal physics*. Waveland Press.

[55] Carpenter S, Brock W. 2010 Early warnings of regime shifts in spatial dynamics using the discrete Fourier transform. *Ecosphere* **1**, art10.

[56] Kéfi S, Rietkerk M, van Baalen M, Loreau M. 2007 Local facilitation, bistability and transitions in arid ecosystems. *Theoretical Population Biology* **71**, 367–379.

[57] von Hardenberg J, Kletter AY, Yizhaq H, Nathan J, Meron E. 2010 Periodic versus scale-free patterns in dryland vegetation. *Proceedings of the Royal Society of London B: Biological Sciences* p. rspb20092208.

[58] Rietkerk M, Dekker SC, de Ruiter PC, van de Koppel J. 2004 Self-organized patchiness and catastrophic regime shifts in ecosystems. *Science* **305**, 1926–1929.

[59] Turcotte DL, Malamud BD. 2004 Landslides, forest fires, and earthquakes: examples of self-organized critical behavior. *Physica A: Statistical Mechanics and its Applications* **340**, 580–589.

[60] Plank MJ, Codling EA. 2009 Sampling rate and misidentification of Lévy and non-Lévy movement paths. *Ecology* **90**, 3546–3553.

[61] Clauset A, Shalizi CR, Newman ME. 2009 Power-law distributions in empirical data. *SIAM review* **51**, 661–703.

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

[63] Meloni F, Granzotti CRF, Bautista S, Martinez AS. 2017 Scale dependence and patch size distribution: clarifying patch patterns in Mediterranean drylands. *Ecosphere* **8**.

[64] Stumpf MP, Porter MA. 2012 Critical truths about power laws. *Science* **335**, 665–666.

[65] Breed GA, Severns PM, Edwards AM. 2015 Apparent power-law distributions in animal movements can arise from intraspecific interactions. *Journal of the Royal Society Interface* **12**, 20140927.

[66] Petrovskii S, Mashanova A, Jansen VA. 2011 Variation in individual walking behavior creates the impression of a Lévy flight. *Proceedings of the National Academy of Sciences* **108**, 8704–8707.

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