Criticality and disturbance in spatial ecological systems

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Classical criticality describes sudden changes in the state of a system when underlying processes change slightly. At this transition, patchiness develops which lacks a characteristic or dominant spatial scale. Thus, criticality lies at the interface of two important subjects in ecology, threshold behavior and patchiness. Most ecological examples of criticality involve processes of disturbance and recovery; the spatial and temporal scales of these processes enable three different types of critical system to be distinguished: classical phase transitions, self organized criticality (SOC) and ‘robust’ criticality. Here, we review the properties defining these three types and their implications for threshold behavior and large intermittent temporal fluctuations, with examples taken from spatial stochastic models for predator–prey, infected–susceptible, and disturbance–recovery interactions. In critical systems, spatial properties of patchiness alone are insufficient indicators of impending sudden changes, unless complemented by the spatial and temporal scales of disturbance and recovery themselves.

Introduction

Ecological systems can exhibit threshold behavior with sudden shifts between states [1,2]. These shifts are characterized by important changes in population abundance and species diversity, and their prediction has become an important focus of ecological science. Threshold behavior originates from the sensitivity of ecological systems to parameters controlling their dynamics, and therefore implies a high sensitivity to environmental perturbations. One theoretical concept of relevance to this type of dynamics is criticality (see Glossary): in its classical form, criticality comprises a drastic shift in state following only slight changes in an underlying process. Mathematical models of wind-disturbed forests predict, for example, the rapid collapse of the area covered by trees when gap cover increases only slightly. Similarly, small changes in predator efficiency [3] or wave force [4] lead to the collapse of the mussel bed in models of the intertidal. Of particular relevance when evaluating the occurrence of these phenomena in nature are the spatial patterns that develop near these critical points of transition. Patchiness develops from local interactions in the complete absence of an underlying blueprint, and exhibits the signature of a complete lack of characteristic, or dominant, spatial scale. In particular, the size distribution of gaps, or that of clusters of trees or mussels, exhibits power-law behavior, with patches of all sizes present and no dominant size. Such patterns have been described for intertidal mussel beds [5] and for wind-disturbed [6] and fire-disturbed [7] forests in nature, within the practical limits of a finite range of scales.

Thus, the concept of criticality lies at the interface of two important subjects in ecology, threshold behavior and patchiness. One central question follows: can spatial patterns be useful indicators of the proximity of a system to catastrophic change (see also [8])?

Most ecological examples of criticality pertain to natural and model systems that incorporate disturbance, whether abiotic, such as fires in forests and wave action in the rocky intertidal zone, or biotic, such as disease and predation [5,9,10]. Disturbance, broadly defined to include biological and physical processes, is fundamental to

Glossary

**Criticality**: in statistical mechanics, the state of a system is said to be critical if poised at a phase transition. Many phase transitions have a critical point associated with them, which separates one or more phases. As a system approaches a critical point, large-scale structures appear despite the fact that the system is driven only by local interactions. At criticality, these patterns are typically characterized by scale invariance (Box 1).

**Lattice (or grid) based models**: a dynamical system in which space is a network of discrete sites. When time is treated as continuous, these models are also known as interacting particle systems or asynchronous cellular automata.

**Phase transition**: an abrupt change in the state of the system as some external parameter is varied. A common example is the gas–liquid phase transition undergone by water in relation to temperature.

**Power law**: a function \(y = f(x)\) is a power law where the dependent variable \(y\) varies as a power of the independent variable \(x\) (i.e. \(y = Ax^{-\alpha}\), where \(A\) is a proportionality constant and \(\alpha\) is a scaling exponent). Power laws are linear functions when the logarithm of both dependent and independent variables are taken.

**Resilience**: the amount of disturbance a system can absorb and still remain within the same state or domain of attraction.

**Scale invariance**: a distribution characterized by a power law is said to be scale invariant (e.g. the frequency distribution of patch sizes in critical systems). It follows that scale-invariant distributions are independent from the resolution, or scale, at which the system is observed.

**State shift**: in an ecosystem, a sudden and drastic change in the state of the system in space or time. The state can be defined as the presence, the abundance or the distribution of one or many species and/or resources.
Box 1. Classical criticality in disturbed ecological systems: some key concepts

The theory of criticality can be applied to explain how local disturbance and recovery processes (Figure Ia) lead to the emergence of long-range correlations in the distribution of organisms (Figure Ib). For example, when a gap in a forest is colonized by a neighboring tree through local dispersal, and wind disturbance occurs only at the edge of a gap, the disturbance-recovery dynamics are local. As wind force changes, a threshold, or critical value, is reached at which the system undergoes a sudden shift called a phase transition (Figure Ic). Near the critical value, or at criticality, the distribution of organisms (Figure Ib) becomes statistically correlated over large scales, and can even become scale invariant, meaning that the distribution will be statistically independent from the resolution, or scale, at which the system is observed. Scale invariance is characterized by power laws in the frequency distribution \( f(S) \) of cluster (patch) sizes \( S \) (Figure Id). Scale invariance and associated long-range correlations resulting from disturbance-recovery processes that are local are considered emergent or self-organized properties, which are characteristic of complex systems.

However, these patterns are not always associated with sudden state shifts and high sensitivity to environmental variation. (Figure Ib and Id adapted, with permission, from [6]).

![Figure I](image)

(a) Local processes
(b) Large-scale patterns
(c) Phase transition
(d) Scale invariance

*We make no attempt to relate our classification to the so-called ‘universality classes’ from physics, which are formally tied to specific values of the scaling exponents. This is partly because exact values of the scaling exponents are difficult to estimate, particularly from finite size systems, and therefore have little practical application in ecology. But, mainly for the purpose of identifying the relevant ecological consequences and assumptions, such finer classification is not needed.*

ecological dynamics, affecting population persistence and species coexistence in dynamic habitats [11–15]. The dynamics of ecological systems at any level of organization typically encompass processes of growth and inhibition that are characteristic of disturbance and recovery. These processes are found, for example, in exploiter–victim (or antagonistic) interactions, in the destruction and recovery of landscapes, and in the adaptive cycle of ecosystems [16].

Although mathematical models of complex systems that incorporate processes of disturbance and recovery are known to exhibit different classes of criticality, the specific ecological mechanisms underlying these differences are not sufficiently recognized. Small differences in the local nature of disturbance and recovery, and in the relative temporal scale of these processes, lead to striking differences in dynamical properties, including the sensitivity to perturbations and the size distribution of temporal change. We argue here that observable properties of patchiness in critical systems, such as spatial power laws and connectedness, are not sufficient to identify these differences. Instead, properties of the processes of disturbance and recovery themselves must be considered to infer properties of the temporal dynamics, and in particular, the possibility of threshold behavior.

Here, we review the different types of critical behavior currently known in ecological systems that incorporate disturbance, including predation, disease and abiotic processes. We use examples from spatial stochastic models, and the systems in nature for which they were proposed, to illustrate three general classes of behavior regarding criticality and associated patterns of spatial self-organization, and to establish both the specific ecological processes underlying these differences and their dynamical consequences. We rely specifically on lattice (or grid) based models [17,18], in which the local nature of recovery and disturbance is easily represented. These systems have been used extensively in population and community ecology to consider individual-based representations. They are also relevant to landscape ecology as implementations of habitat destruction and restoration, and further provide a starting point for spatial extensions of the concept of adaptive cycles developed by Holling and Gunderson to address ecosystem resilience [16]. In this concept, as an ecosystem develops, it also becomes increasingly interconnected among its components. Connectedness is inversely related to resilience and reaches a threshold, driving the system to a large-scale collapse and providing opportunities for growth and innovation [16]. We discuss the generality of this inverse relationship in systems with disturbance.

**The three classes of criticality**

Different types of disturbed systems can be distinguished that differ significantly in their sensitivity to parameter changes and therefore, in their response to external perturbations and environmental change. There are three types of criticality that we consider here: (i) classical criticality; (ii) self-organized (SOC); and (iii) ‘robust’ criticality. Box 1 illustrates classical criticality in the context of disturbed systems, such as wind-disturbed forests. At the critical point, short-range interactions lead
predictions [5]. Here, we use the term ‘robust’ criticality to power-law scalings that are consistent with the model of SOC [5, 21, 22]. Patchiness in an Oregon mussel bed exhibits phase transitions has been recently described in models of similar dynamics and a slow external forcing, such as the migration of infected cases to a local population [10].

SOC behavior is illustrated by the well-known example of a sand pile: as sand grains are slowly added, its slope grows and reaches a critical angle at which avalanches are generated [19, 20]. This critical angle is not imposed by any design of the system but is generated by the interactions among its components. Although most avalanches are small, extreme events occasionally occur. In particular, SOC generates intermittent temporal events of all sizes, such as sand avalanches, fires or epidemics, whose size distribution is a power law. In the spatial propagation of disturbances such as fires and epidemics, SOC further generates spatial power laws in the size distribution of clusters, with long-range correlations arising from short-range interactions. A third type of critical system with similarities and differences to both SOC and classical range interactions. A similar regime has been used in models of wave disturbance in intertidal mussel beds [4], and for biotic disturbance in predator–prey intertidal systems [3]. As for abiotic disturbance, predators (in this case lobsters) can cause the transition of the mussel bed to an empty site by attacking from the edge at any spatial location, as a function of the proportion of neighboring sites that are empty. The mussel bed collapses when predator efficiency increased above a critical value.

In all these systems, disturbance intensity only depends on the local density of susceptible individuals. This means that the mobility of the disturbance agent (e.g. the wind or lobsters) is fast or large scale compared with the recovery process (e.g. tree or mussel colonization) and, therefore, the distribution of the disturbance itself is well mixed over the whole system. A spatial (lattice) model to represent this disturbance regime would require only two states: occupied or empty (Box 2). In this case, disturbance itself is not a state, but is instead determined by the local structure (configuration of trees). These models have at their core the basic contact process [18], which has also been applied to simple susceptible–infective models (SI) of epidemic spread [27].

In the SI contact process, space can be occupied by susceptible or infective individuals, and disturbance results from the spread of the epidemic from infective to susceptible individuals. The recovery of infective individuals can only lead back to susceptibility. These properties of SI models are equivalent to the assumption of well-mixed disturbance, and result from an infective state that does not have a limited lifespan (no mortality) and does not allow immunity. We can think of susceptible sites as those occupied by trees or mussels, and of the infected sites as those that constitute the gaps and propagate disturbance. In these models, there is no refractory or immune state constraining the spatial propagation of disturbance. Knowledge of the distribution of infecteds is not necessary to determine the infection probability of a susceptible individual, which is already fully defined by the local density of susceptibles, because an individual that is not susceptible must be, by definition, infected. Similarly to the predator–prey models described above, disturbance (infection) can attack any susceptible individual located along the edge of a susceptible cluster.

To understand the large-scale spatial and dynamic properties emerging from two-state models, it is useful to note that the contact process is similar to the Ising model used in physics to describe the spin orientation of particles in a ferromagnet [6, 28]. The Ising model is defined by the two possible states of each spin (up or down) and the state to the emergence of long-range correlations characterized by power-law relationships.

With the study of simple physical systems, such as sand piles, but also of forest fires and epidemics, a more robust explanation for the emergence of such scale-free patterns in nature was proposed with the related phenomenon of SOC [19]. Data of measles epidemics in small islands exhibit properties of SOC (in this instance from the Faroe Islands; [9]). In SOC, there is no sudden shift in relation to environmental perturbations, and no fine-tuning of parameters to particular values is required for scale invariance; that is, parameters do not need to be at a critical point. Independently from specific rates of growth (e.g. new trees) and of disturbance (e.g. new fires), the system takes itself to the critical state through its own dynamics and a slow external forcing, such as the migration of infected cases to a local population [10].

Well-mixed disturbance

When is criticality in disturbed systems indicative of low resilience, specifically, of the possibility of a sudden state shift for small parameter changes? To address this question, we begin with an example. Wind-disturbed tropical forests have been described as critical systems [6, 23–26], and viewed as a landscape of trees and gaps corresponding to occupied and unoccupied sites. In real forests, a scale-invariant distribution in tree cover has been observed, suggesting the existence of a critical point. In the corresponding models, disturbances create gaps in the forest at a rate that is only a function of the number of neighboring sites that are themselves a gap. Thus, local tree density in the neighborhood of a single individual determines its susceptibility to wind disturbance. A shift in state is observed at a critical point, from a persistent forest to complete extinction. A similar regime has been used in models of wave disturbance in intertidal mussel beds [4], and for biotic disturbance in predator–prey intertidal systems [3]. As for abiotic disturbance, predators (in this case lobsters) can cause the transition of the mussel bed to an empty site by attacking from the edge at any spatial location, as a function of the proportion of neighboring sites that are empty. The mussel bed collapses when predator efficiency increased above a critical value.

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are unable to accumulate slowly in times between temporarily escape from disturbance. Thus, abundances can always spread into susceptible clusters, no cluster can the susceptible state. Furthermore, because disturbance changes in parameters leading to the complete collapse of sensitivity to perturbations, or low resilience, with small predator efficiency[3]. where a similar change is predicted for small changes in intensity, and for predator–prey intertidal systems[3], predicted to occur over a narrow range of disturbance disturbed tropical forests illustrated in [24].

For disturbance regimes that are not well mixed and are distributed in space, we need to define a disturbed state that spreads into occupied sites and has a limited life span that is independent from the recovery process. The local distribution of susceptibles is not sufficient to determine susceptibility to disturbance, and we need to adopt at least three states. The forest-fire model [32,33] depicted in Figure 1 provides an example, with disturbance propagation represented via an explicit disturbed state (the burning trees) whose lifespan is independent from the recovery process. A site occupied by a burning tree becomes empty before it can recover through growth of a new individual. Distributed disturbance models can, in turn, have well-mixed recovery mechanisms (tree growth), which are associated with SOC.

Here, we also describe a third class of system with distributed disturbance that differs from models exhibiting SOC in that the recovery process is also local (e.g. local seed dispersal) [5,21,22]. An additional difference is the lack of separation between the temporal scales of recovery and disturbance (see main text).

depends on the local configuration of spins. This model can be viewed as a template for well-mixed disturbance where the local configuration of individuals defines susceptibility. As for any disturbance model, local processes are influenced by forcing parameters (e.g. wind speed in forests or magnetic field in ferromagnets). As a consequence, all models comparable to the Ising model exhibit criticality only at the phase transition, which corresponds to a restricted range of forcing parameter values (Figure 1a,c). In the SI model, the transition is from a state in which the infection cannot invade to the sudden establishment of the disease, when the transmission rate crosses a critical value (e.g. [20]). Thus, for well-mixed disturbance regimes, the observation of criticality and associated scale invariance implies that the forcing parameters are at, or very close to, their critical value. This property was argued to be the case for wind-disturbed tropical forests [6], where a sudden collapse is predicted to occur over a narrow range of disturbance intensity, and for predator–prey intertidal systems [3], where a similar change is predicted for small changes in predator efficiency [3].

It follows that criticality in these systems implies a high sensitivity to perturbations, or low resilience, with small changes in parameters leading to the complete collapse of the susceptible state. Furthermore, because disturbance can always spread into susceptible clusters, no cluster can temporarily escape from disturbance. Thus, abundances are unable to accumulate slowly in times between disturbances, precluding the slow build up of high abundances that would make the system susceptible to large disturbance events. Thus, large intermittent temporal fluctuations do not occur. Furthermore, spatial power laws are observed only at the critical point, for an extremely narrow range of parameters, and should therefore be rare. Only if parameters are under selection pressure can two-state models explain the observation of power laws in systems where such patterns have an adaptive value for individuals. Finally, along spatial gradients, sharp boundaries between regions of full occupancy and extinction would arise, with patchiness in the distribution of individuals observable only at the boundary itself for a restricted range of environmental parameters (Figure 1e).

**Box 2. Disturbance regimes in lattice models**

Spatially explicit dynamics can be implemented as lattice models with space represented as a grid comprising discrete locations or cells. Each cell is in one of a set of possible states representing local space occupancy. Lattice models for disturbance–recovery systems differ in the number of states, reflecting different assumptions about these processes and implying fundamentally different dynamics. Well-mixed disturbance dynamics can be implemented as a two-state model in which susceptibility to disturbance is determined by the local density of individuals. For example, susceptibility can be inversely proportional to the density of neighbors, as in models of wind-disturbed tropical forests illustrated in [24].

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**Figure I.**
slow migration of infecteds providing the spark to fuel the epidemics. With the consideration of a recovered state, this disease system is now similar to forest-fire models with at least three states (Box 2). Thus, the change from well-mixed to distributed disturbance is caused by the key assumption of disturbance having a limited lifespan before a new collapse. Under these conditions, tree clusters of all sizes are observed, which follow a power-law frequency distribution. Intermittent temporal fluctuations result from the slow accumulation and quick release of abundance (or energy). The slow accumulation of susceptible individuals through growth leads to enhanced connectedness among clusters and therefore, to a higher susceptibility to disturbance at the whole-system level.

By contrast to wind disturbance, fire disturbance cannot be assumed to be well mixed over the forest. Rather, the susceptibility to disturbance of any tree depends on its proximity to a recently disturbed (burning) tree. A burning tree has a limited burning time, and is replaced by a gap after it is completely disturbed. Thus, in this second class of critical systems, the disturbance agent (or infective stage) has a limited lifespan and spatial distribution, which are independent from its neighborhood configuration. Susceptibility then depends not only on the local density of the susceptible state, but also on the local density of the infective. In this case, disturbance is spatially distributed or heterogeneous, and needs to be represented explicitly as a state, resulting in a system with at least three states (Box 2). Thus, the change from well-mixed to distributed disturbance is caused by the key assumption of disturbance having a limited lifespan at any location, independent from the transition to the susceptible state. The end of the disturbance does not lead directly to susceptibility but to a state refractory to further disturbance, such as empty sites in forest-fire models that must be re-colonized before fire is able to spread again. A three-state system is one way to represent this delay in the return to the susceptible state. Similarly in SIR models, infectives recover to immune individuals or die (the recovered state in SIR models) [10]. This limited lifespan of the infected state is independent from the recovery to the susceptible state through the loss of immunity or birth.

Because no fine-tuning of parameters is required for SOC, perturbations modifying these parameters should not cause a drastic shift in system state. Instead, large and intermittent temporal fluctuations reflect the fast propagation of a disturbance through the system once sufficient susceptibility has been rebuilt through growth. Key

Figure 1. Comparison between the well-mixed disturbance (left, first class), and the distributed disturbance with local recovery (right, third class) applied to wave disturbed mussel dynamics (see main text, and [4,5] for details). Results for the second class, distributed disturbance and well-mixed recovery leading to self-organized criticality, are not shown because the explicit separation of temporal scales between disturbance and recovery prevents the study of the full parameter space. (a,b) Mean mussel cover as a function of disturbance and recovery rates. (c,d) Scale invariance in mussel cluster size distribution at criticality. With well-mixed disturbance (a,e), scale invariance is observed at the phase transition, along the shaded area in (a). At the phase transition, the mussel cluster size distribution is a power law (c). The addition of an explicit state for disturbance in the distributed disturbance regime (b,d,f) results in a switch from a phase transition to a broad region of scale invariance in the parameter region of high disturbance delimited by the shaded area in (b). In this broad region, cluster size distribution follows a power-law relationship (d) with a scaling exponent weakly influenced by parameter values for disturbance and recovery rates (d). The particular parameters used to illustrate cluster size distributions [frequency \( f(S) \) of clusters of size \( S \)] are shown by asterisks in (a) and (b). (e,f) Mussel bed distributions (black pixels) over a lattice characterized by a gradient in disturbance and recovery rates for the well-mixed (e) and distributed (f) disturbance regimes. Each cell is submitted to a different combination of disturbance (horizontal axis) and recovery (vertical axis) rates varying from 0 to 1. The properties of the local disturbance regime influence large-scale patterns along environmental gradients. Whereas well-mixed disturbance results in a sharp boundary between two absorbing states, the distributed disturbance (three states) with local recovery and disturbance maintains spatial variability across both gradients. Adapted with permission from [4] (a,e) and [5] (b,d).
ingredients are the limited lifespan of disturbance, associated with the existence of a refractory state, and the double separation of timescales. To address whether the double separation of timescales is always realistic in ecological systems, we turn our attention to the properties of growth processes in disturbed systems.

Distributed disturbance and local recovery

Is criticality always associated with drastic changes, either in the form of the large temporal fluctuations of self-organized criticality or the high sensitivity to parameters of classical phase transitions? To address this question, we begin with an example of wave disturbance in intertidal mussel beds [5,34].

In marine rocky intertidal zones, mussels are often the dominant competitors for space, a key limiting resource. Gap formation resulting from wave disturbance and recovery through mussel recruitment into gaps can constitute the dominant dynamical processes in high-energy environments [13]. The recovery of the disturbed population is often a local process, limited by the reproduction and dispersal ability of susceptible individuals, or by local density dependence in the success of re-colonization. Localized recovery contrasts with tree growth in the forest-fire model, a density-independent and non-spatial process in which individuals recolonize empty areas at random locations. A recent model for the intertidal zone assumes that disturbance spreads as long as mussels on the edge of the newly formed gap have not reattached to the substratum and to conspecifics, a process that turns the disturbed state into a stable edge. This simple modification from earlier mussel disturbance models [4] limits the lifespan of the disturbed state, which is now restricted to the stabilization time of recently disturbed edges. Thus, the mussel bed model of [5] is a version of the forest-fire model, where the growth rate of trees is replaced by the local spread of mussels into empty neighbors, through (positive density-dependent) local recruitment and growth. Both disturbance and recovery are now local processes. The separation of timescales for growth and disturbance propagation is also absent.

Whereas the original forest-fire model quickly loses its critical state as the growth rate of trees increases [30], the mussel disturbance dynamics maintains properties of criticality when recovery and disturbance rates are comparable. Specifically, the power-law scaling of the cluster size distribution and the long-range correlations of the mussel bed persist broadly in parameter space (Figure 1b,d). A similar behavior was described for other lattice models in which both disturbance propagation and recovery are local processes, including predator–prey and food-web dynamics [21]. For the predator–prey lattice model, a ‘percolation-type’ transition was described at which connectedness, measured as the size of the largest cluster or patch, changes abruptly [22]. At this point in parameter space, long-range correlations form and power laws characterize the size distribution of clusters. Surprisingly, there is no concurrent abrupt change in the state of the system for the biological variables of interest, namely species densities and coexistence. Furthermore, the spatial power laws persist in a wide region around this point, in the sense that the scaling holds for a significant range of scales even if this range diminishes as one moves away from the critical point.

One general implication of this type of system is that scale invariance and spatial correlations can be generated by local processes under broad environmental conditions, in direct contrast to what is observed in the original two-state systems. In particular, spatial patterns are now expected to show a signature of local interactions along environmental gradients, with the sharp boundaries of two-state systems replaced by a smoother transition to scale-invariant patterns (Figure 1e,f). Moreover, the temporal dynamics differ significantly from those of SOC: intermittent fluctuations are no longer present and are replaced by smoother cycles, whose amplitude decreases with sampling scale [21,35,36]. Table 1 summarizes the assumptions and consequences of the three classes of system that we have described.

Some evolutionary considerations

Evolutionary processes have also been invoked to explain the ubiquity of criticality in biological systems showing phase transitions [20,37]. Rand et al. [38] and Keeling [39] studied a three-state epidemic model in which the local spread of infected individuals (transmissibility) is allowed to mutate. They showed that transmissibility evolves to its critical value associated with scale invariance. Similarly, in models of epidemics where a separation of temporal scales between transmission and recovery is imposed,

Table 1. Types of criticality and associated consequences

<table>
<thead>
<tr>
<th>Class</th>
<th>Criticality</th>
<th>Spatial patterns</th>
<th>Temporal dynamics</th>
<th>Threshold behavior*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Well-mixed disturbance (two states)</td>
<td>Phase transition</td>
<td>Scale invariance only at critical point.</td>
<td>High sensitivity to perturbations; drastic shifts between states across a critical parameter</td>
<td>Yes (shift in state)</td>
</tr>
<tr>
<td>Distributed disturbance, separation of timescales (at least three states)</td>
<td>Self-organized criticality</td>
<td>Scale invariance without tuning of parameters</td>
<td>No high sensitivity to parameter changes, but large intermittent temporal fluctuations</td>
<td>Yes (large temporal fluctuations)</td>
</tr>
<tr>
<td>Distributed disturbance and recovery, no separation of timescales (at least three states)</td>
<td>‘Robust’ criticality (‘percolation-type’ transition with broad scaling region)</td>
<td>Scale invariance without tuning of parameters</td>
<td>No high sensitivity; no large intermittent temporal fluctuations</td>
<td>No</td>
</tr>
</tbody>
</table>

*Threshold behavior refers to the rapid change in the density or coexistence of the states of the system (e.g. different species, susceptible-infected-recovered individuals, gap and non-gap patches). The last column indicates whether such behavior is seen when connectedness becomes large; that is, when a large cluster or patch has formed in the system.

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evolution in the mortality of susceptibles (independent from infection) can drive the system to criticality [40]. These results show that different parameters affecting the local dynamics of distributed disturbance models can evolve to their critical values, thus suggesting that emergent properties associated with scale invariance have an adaptive value for the disease [38] or for the host [40]. However, in two-state disease models, the absence of a distributed disturbance agent results in no difference between the evolution of the spatial and nonspatial systems [41], and evolution is not associated with criticality. Thus, the adaptive value of long-range correlations in disturbed systems appears to be sensitive to assumptions about local processes. As for the above ecological examples, these assumptions matter and reflect real biological properties.

Conclusions
Criticality has been an appealing ecological concept from two different perspectives: first, as an explanation for scale-invariant patterns in nature, and second, as a mechanism underlying drastic change, in the form of either large unpredictable temporal fluctuations (SOC) or sudden state shifts driven by small perturbations (classical phase transitions). We have argued that these two perspectives are not necessarily linked: properties of the spatial patterns, including power laws and high connectedness, do not necessarily imply drastic shifts of state or large temporal fluctuations. There are, however, distinct properties of the processes of disturbance and recovery themselves that enable us to differentiate three main classes of critical system with clear implications for both resilience and temporal dynamics.

Although our focus has been on spatial systems, ecological examples of criticality are not restricted to spatiotemporal dynamics [10]. The types of behavior that we have outlined here are also relevant in a temporal context, but the specific mechanisms that underlie the differences would need to be examined. For example, broad scaling regions have also been recently described in a non-spatial model for (SIR) disease dynamics when there is a distribution of susceptibility in the population [42].

As one of the simplest spatial implementations of disturbance and recovery, lattice models provided us with a tool with which to identify and compare different classes of critical behavior in spatial systems. Because the third type of system has only been recently described, it is too early to tell whether further analysis will interpret it within either the framework of SOC or classical phase transitions. So far, the existence of a broad scaling region does not appear to be an artifact of (finite) system size [22]. Although those detailed considerations are relevant to the theory of criticality, they are, in our opinion, of little consequence for ecology. More importantly, future work should address whether more realistic spatiotemporal systems with higher levels of detail conform to the classes and dynamical consequences that we have outlined here. Comparisons with models in landscape ecology should be particularly interesting given that disturbance–recovery models are a natural tool with which to address the consequences of habitat destruction and/or restoration (e.g. [14]). Consideration of the different classes of behavior is likely to be important in establishing the generality of results obtained for example in community ecology using dynamical landscapes (e.g. [43]).

Finally, consideration of the different types of criticality described here should be relevant to extend to a spatial context, conceptual models for the temporal collapse and reorganization of ecosystems [2]. A recent attempt [8] to link particular patterns of patchiness (spots, bands, labyrinths and stripes) to catastrophic shifts in ecosystems considers deterministic spatial models with mechanisms of short-range facilitation and long-range inhibition that are well known to generate a variety of smooth spatial patterns in other models of mathematical biology [44]. The additional consideration of stochastic effects and the scaling properties of the resulting spatial patterns is warranted. For patterns of patchiness lacking a characteristic scale, such as the ones that we have considered here, it is clear that spatial snapshots alone will not be sufficient to identify the likelihood of impending catastrophic shifts. Although this conclusion remains to be examined more fully for other patterns in ecosystems, it is likely that additional information about underlying processes will be required. As shown here, the temporal and spatial scales of recovery and disturbance (activation and inhibition) are likely to be critical.

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References


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**AGORA initiative provides free agriculture journals to developing countries**

The Health Internetwork Access to Research Initiative (HINARI) of the WHO has launched a new community scheme with the UN Food and Agriculture Organization.

As part of this enterprise, Elsevier has given 185 journals to institutions are now registered for the scheme, which aims to provide developing countries with free access to vital research that will ultimately help increase crop yields and encourage agricultural self-sufficiency.

According to the Africa University in Zimbabwe, AGORA has been welcomed by both students and staff. "It has brought a wealth of information to our fingertips" says Vimbai Hungwe. "The information made available goes a long way in helping the learning, teaching and research activities within the University. Given the economic hardships we are going through, it couldn’t have come at a better time."

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