

Dynamics of populations on the verge of extinction

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Theoretical considerations suggest that extinction in dispersal-limited populations is necessarily a threshold-like process that is analogous to a critical phase transition in physics. We use this analogy to find robust, common features in the dynamics of extinctions, and suggest early warning signals which may indicate that a population is endangered. As the critical threshold of extinction is approached, the population spontaneously fragments into discrete subpopulations and, consequently, density regulation fails. The population size declines and its spatial variance diverges according to scaling laws. Therefore, we can make robust predictions exactly in the range where prognosis is vital, on the verge of extinction.

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Ecologists are aware of several factors that can cause extinction in natural populations (man-made disturbance, pests, etc.). In the fortunate case, the areas of extinction are smaller than the total area where the species occurs, thus, local extinctions can be compensated by the colonization of empty sites. How should the rate of colonization relate to the rate of extinction to ensure a persistent population? This question has been in the focus of spatial ecology for decades (Durrett and Levin 1994, Tilman and Kareiva 1997, Czárán 1998). Studies on metapopulation dynamics have paid particular attention to the extinction–colonization equilibrium (Levins 1969, Keymer et al. 1998, Hanski 1999). In this paper, we review how contact processes may contribute to understanding population persistence by deducing the biological problem to a well-studied phenomenon in statistical physics, directed percolation. Then we suggest extensions to more complex systems.

To start from a simple model, let us assume that the area over which the colonization–extinction processes

take place is very large, so that a single, local colonization or extinction event causes only an infinitesimally small change in the occupancy of the total area. The area is divided into discrete sites (e.g. cells of a square lattice; Fig. 1). Only two types of sites are distinguished: empty or occupied. Occupied sites become empty by extinction with a constant rate e . Empty sites become occupied by colonization from neighbouring occupied sites with rate c . Neighbourhood can be defined in various ways according to the assumption about the ability of the species to disperse propagula. We compare two dispersal modes.

In the first case, the species has extremely far-dispersing propagula so that any empty site can be colonized from any occupied site (mean field model). This is equivalent with the classical patch occupancy model of Levins (Levins 1969, Keymer et al. 1998, Hanski 1999). Changes in the density of the occupied sites n over time t can be described by a basic equation in metapopulation dynamics,

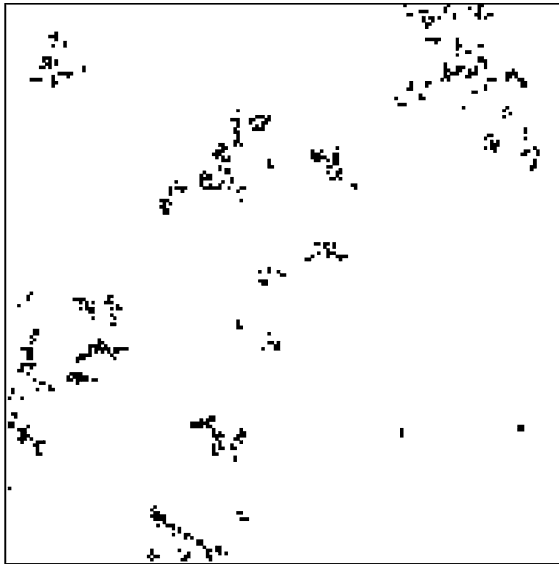


Fig. 1. Snapshot from a contact process, showing fragmentation of a population. The fragments are known to move by branching-annihilating random walk (Hinrichsen 2000a).

$$\frac{dn(t)}{dt} = cn(t)[1 - n(t)] - en(t) \quad (1)$$

The term in square brackets [...] expresses that only empty sites can be colonized. Note that the equation is formally equivalent with the classical, logistic equation of population growth, 'occupied sites' replaced by 'individuals'.

In the second case, dispersal is limited to a finite distance. This is a plausible assumption, since dispersal in most species is constrained in space (Begon et al. 1996). The simplest way to introduce dispersal limitation in the square lattice is to restrict colonisation to the four neighbouring cells. Interestingly, this basic population dynamic model is exactly the same as a contact process (CP) model (Levin and Pacala 1997, Snyder and Nisbet 2000, Ovaskainen et al. 2002), which has been studied thoroughly in statistical physics (Marro and Dickman 1999, Hinrichsen 2000a). (See the Appendix about Monte Carlo simulations of the CP.)

The CP was originally introduced for a general purpose to investigate the spreading of localized effects through neighbourhood contacts (Harris 1974). It has been applied in epidemiology (Harris 1974, Anderson and May 1991, Levin and Durrett 1996, Holmes 1997) and in ecology, too, for modelling the spatial dynamics of perennial plant species (Barkham and Hance 1982, Crawley and May 1987, reviewed by Durrett and Levin 1994). In spite of its sporadic application so far, the CP is a very basic model in ecology (Durrett and Levin 1994, Levin and Pacala 1997, Snyder and Nisbet 2000): this is the simplest spatial extension of the patch-occupancy model and of the logistic model of population growth.

Vice versa, these well known ecological models are equivalent with the mean field (MF) approximation of the CP.

A comparison between the MF and the CP reveals important messages about the importance of dispersal limitation in population extinctions (Durrett and Levin 1994, Snyder and Nisbet 2000, Ovaskainen et al. 2002, Franc 2003). Suppose that the conditions for living worsen for any external reason (climate change, etc.) and, consequently, c decreases and/or e increases. It is convenient to use a single parameter, the spreading rate $\lambda = c/e$ that expresses the relative strength of two competing processes, colonization vs extinction. As λ decreases, the equilibrium density of occupied sites, n , declines. The MF and the CP show important differences in $n(\lambda)$, and thus, in the dynamics of extinction (Fig. 2a). The extinction threshold is considerably higher in the CP: only a relatively high rate of colonisation can compensate for local extinctions. The behaviours before extinction also differ. In the MF, n reaches zero by a slow, linear decrease (Eq. 1). In the CP, extinction is an abrupt change that is analogous to a critical phase transition in physics (Stanley 1971, Marro and Dickman 1999, Hinrichsen 2000a). As the extinction threshold λ_c is approached, the equilibrium density n declines according to a power law:

$$n \propto (\lambda - \lambda_c)^\beta \quad (2)$$

Monte Carlo simulations (Broadbent and Hammersley 1957, Marro and Dickman 1999, Hinrichsen 2000a) have estimated that $\beta = 0.583(4)$ in two dimensions (Fig. 2b). The characteristic differences between the MF and the CP suggest that dispersal limitation can seriously threaten the viability of a low-density population.

The difference originates from the way of density regulation. When λ decreases, the number of empty sites increases and, therefore, new sites become open for colonization. In the MF, the empty sites are freely available by dispersal; it is only the average density of occupied sites that limits population growth (see the term in square brackets in Eq. 1). In the CP, the colonized site must be in the neighbourhood of the colonizer, therefore, it is the local density around each occupied site that matters. Local densities are statistically higher than the global density, because neighbourhood colonization causes clumping. The discrepancy between local and global densities becomes especially serious as extinction is approached (Snyder and Nisbet 2000). In the population in Fig. 1, the local densities within the population fragments are still rather high, whereas the population inhabits only a small part of the area, exploiting only a small proportion of its carrying capacity.

Vacant areas can be colonized only from the edges of existing population fragments, which become more and more scattered as extinction is getting near. The occur-

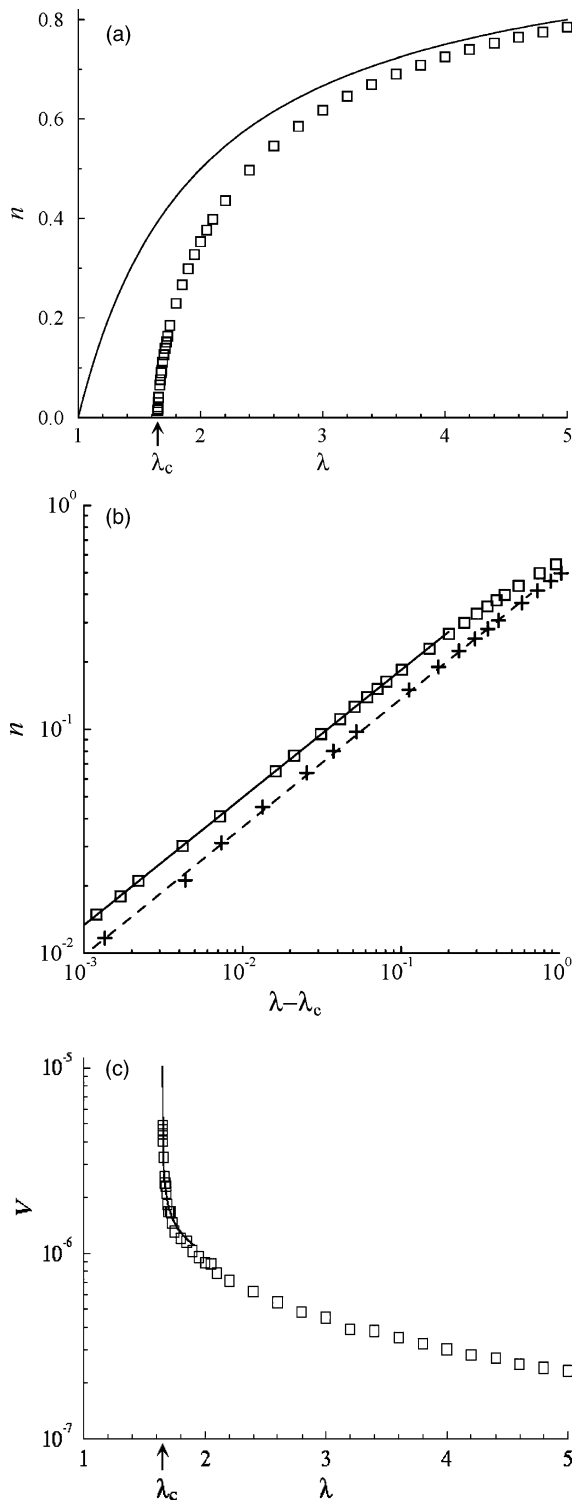


Fig. 2. Survival of a population critically depends on the spreading rate (λ). Averages from Monte Carlo simulations are plotted by squares (basic contact process) or crosses (heterogeneous environment contact process). Data in the basic CP are reproduced from the literature (Marro and Dickman 1999, Hinrichsen 2000a); the results in the heterogeneous

environment CP are obtained from our model (Szabó et al. 2002). (a) The equilibrium density (n) declines as λ decreases. In the CP, extinction is a critical transition: there is a sharp threshold, $\lambda_c = 1.6488(1)$, where the derivative of $n(\lambda)$ is infinite. In the corresponding Mean Field model (solid line), extinction is a gradual process. The population density declines

$$\xi \propto (\lambda - \lambda_c)^{-\nu} \quad (3)$$

as $n(\lambda) = \frac{\lambda - 1}{\lambda}$; extinction starts at $\lambda = 1$. (b) The decrease of n at λ_c follows a power law, as demonstrated by a fitted straight line on a log-log plot. In the basic CP (squares), the environment was homogeneous. In the heterogeneous environment CP (crosses), the habitat consisted of good and bad patches, which differed in the local rate of spreading ($\lambda_g = 4$; $\lambda_b = 1$, respectively). We varied the proportion of good patches (p), and thus, changed the average $\lambda = p\lambda_g + (1-p)\lambda_b$. Some fluctuation in site qualities was permitted (good lattice cells turning into bad or vice versa at random, with a rate 0.02). The simulations yielded $\lambda_c = 1.84765(5)$ for the critical threshold. The slopes of both fitted straight lines are consistent with the theoretically predicted scaling exponent of directed percolation, $\beta = 0.583(4)$, indicating that rather different population models may show the same, universal behaviour at low population densities. (c) The spatial variance of population density (V) goes to infinity as λ_c is approached. The solid line shows the theoretically predicted power law function.

ence of large, unchanging, empty regions can be detected by measuring autocorrelation distances in space and time. Detailed analyses (Marro and Dickman 1999, Hinrichsen 2000a) have shown that these quantities also follow power-law behaviour:

The same problem becomes even more apparent when we zoom in from the global population density to regional densities in finite areas. Let us consider an area A which is larger in linear extension than the autocorrelation distance in space, and observe it for a period of time that is longer than the autocorrelation distance in time. Since the interdependence of sites is negligible on this scale, we can apply the above-mentioned power law for estimating the mean population density: $\bar{N} \propto (\lambda - \lambda_c)^\beta$. A remarkable result is that the variance of population density also follows a power

environment CP are obtained from our model (Szabó et al. 2002). (a) The equilibrium density (n) declines as λ decreases. In the CP, extinction is a critical transition: there is a sharp threshold, $\lambda_c = 1.6488(1)$, where the derivative of $n(\lambda)$ is infinite. In the corresponding Mean Field model (solid line), extinction is a gradual process. The population density declines as $n(\lambda) = \frac{\lambda - 1}{\lambda}$; extinction starts at $\lambda = 1$. (b) The decrease of n at λ_c follows a power law, as demonstrated by a fitted straight line on a log-log plot. In the basic CP (squares), the environment was homogeneous. In the heterogeneous environment CP (crosses), the habitat consisted of good and bad patches, which differed in the local rate of spreading ($\lambda_g = 4$; $\lambda_b = 1$, respectively). We varied the proportion of good patches (p), and thus, changed the average $\lambda = p\lambda_g + (1-p)\lambda_b$. Some fluctuation in site qualities was permitted (good lattice cells turning into bad or vice versa at random, with a rate 0.02). The simulations yielded $\lambda_c = 1.84765(5)$ for the critical threshold. The slopes of both fitted straight lines are consistent with the theoretically predicted scaling exponent of directed percolation, $\beta = 0.583(4)$, indicating that rather different population models may show the same, universal behaviour at low population densities. (c) The spatial variance of population density (V) goes to infinity as λ_c is approached. The solid line shows the theoretically predicted power law function.

law (Broadabent and Hammersley 1957, Stanley 1971, Harris 1974),

$$V \propto (\lambda - \lambda_c)^{-\gamma}/A \quad (4)$$

where $\gamma=0.35(1)$ (Fig. 2c; the area in the simulations was $A=10^6$). This sheds light on the very mechanism of extinction. As the critical threshold is approached, the population density declines, and at the same time, its variance diverges. Thus, stochastic extinction becomes increasingly probable. For any actual value of $\lambda > \lambda_c$, we can find an area A that could provide a statistically good chance for survival. But this area is increasing rapidly with the decrease of λ . An important message from the theory is that even an infinitely large habitat cannot maintain any persistent population at $\lambda \leq \lambda_c$.

These results suggest that estimating a population size becomes increasingly difficult as the population is getting near to extinction. Endangered populations should be monitored for long periods of time because of the divergence of V .

Equation 3 predicts that a dispersal-limited population near to extinction consists of small subpopulations fragmented in a fractal structure. The fractal dimension is rather low, $v_s = 0.733(4)$. The fragments are mobile in space, split and merge in a random fashion, and do not show any distinguished direction of motion (branching-annihilating random walk; Hinrichsen 2000a). This property may help to detect that a population is endangered. Fractal structure, by itself, is not an unequivocal indicator of the danger of extinction, because it may also be caused by a fractal structure in the environment (e.g. in the topography; Turner et al. 2001). In that case, however, the clumps of the population do not tend to move away from suitable habitat patches. Random motion can be clearly distinguished from this situation.

Repeated mapping of a population can detect the danger of extinction (λ approaching λ_c) by the following symptoms: 1) the spatial structure can be described by a low-dimensional fractal of randomly moving clumps, 2) there are large fluctuations in the population density, and 3) the equilibrium is re-attained slowly after perturbation. Power laws predict that symptoms 2 and 3 worsen rapidly as λ_c is approached. Provided that the time of observation is sufficiently long for measuring multiple points on an extinction curve (Eq. 2, 3 or 4), even the exact distance from the threshold can be determined by a linear regression on a log-log plot (Fig. 2b).

If the system passes beyond the extinction threshold λ_c the probability of extinction becomes 1. Starting from any initial value, the population density declines exponentially to zero. The half-life-time of the population during the extinction process depends on λ . This dependence can also be described by a power law in the vicinity of λ_c (Hinrichsen 2000a),

$$t_{1/2} \propto |\lambda - \lambda_c|^{v_t} \quad (5)$$

Note that the exponent is the same as in Eq. 3, $v_t = 1.295(6)$. Relaxation to an equilibrium state is the same exponential process above and below the threshold; the only difference is that the equilibrium is $n > 0$ above the threshold, and $n = 0$ below. The relaxation time is infinite on the threshold: this is the borderline between extinction and survival.

The power-law scaling of a suite of important quantities indicates that dispersal-limited extinction is a critical transition. The concept of critical transitions originated from equilibrium thermodynamics to describe liquid-gas, ferromagnetic and other continuous phase transitions (Stanley 1971). A common feature in these systems is that a continuous decrease of a control parameter (now λ) leads to a continuous, power-law vanishment of an order parameter (now n); and fluctuation (χ), correlation length (ξ) and correlation time (τ) diverge at the critical point. The CP belongs to a well defined universality class of critical phenomena: directed percolation (Broadabent and Hammersley 1957, Hinrichsen 2000a). Note that directed percolation differs from isotropic percolation (Stanley 1971). The latter has been used frequently for modelling habitat fragmentation in landscape ecology (Turner et al. 2001). 'Directed' in the context of the CP refers to percolation in the time direction (i.e. we are interested in long term survival).

'Universality' is not an exaggeration: analyses have shown (Broadabent and Hammersley 1957, Hinrichsen 2000b) that the values of the critical exponents do not depend on the details of the model, only on the dimensionality (which is $D=2$ now). Geometry of the lattice (square, triangle, honeycomb, etc.) can be freely varied; even continuous space can be assumed without any change in the values of exponents. The representation of states can also be extended from binary (empty vs occupied) to other discrete or continuous variables (Lande et al. 1998 and Foley 1997 extensions of the Levins model). Details of the local interaction can also be varied: assumptions about the finite neighborhood (four cells, eight cells, etc.) or the introduction of diffusion or any other short range random noise does not influence the values of exponents. Only serious modifications in the model structure can violate the assumptions of the universality class, for example, if special symmetries or pairs of occupied sites are needed for the colonization (Hinrichsen 2000b, Henkel and Hinrichsen 2004). Noest (1986) and later Dickman and Moreira (1998) have warned that quenched disorder crucially disturbs the critical transition. Quenched disorder means biologically that the habitat is patchy, and the spatial pattern of patches does not change over time. We have shown (Szabó et al. 2002) that even a small rate of change drives the system back to the universality class of the CP, producing the exact values of its characteristic

exponents. Fig. 2b shows an example from the simulations (unpublished so far).

In summary, the predictions of the CP at extremely low densities are likely to apply for a broad range of spatial population dynamic models. In the proximity of extinction, various types of population dynamics can converge into a single, robust process. A common feature of these dynamics is that local extinction is competing with local, finite-distance colonization, and the environment is either homogeneous, or it is heterogeneous but can be characterized by random fluctuations in the quality of sites.

Universality can be explained by the fact that near to the threshold, the behavior of the system is dominated by long-range correlations (see ξ and τ ; Sato and Iwasa 2000). Microscopic details become irrelevant: several kinds of processes that share some basic properties show the same macroscopic behaviour.

The importance of scaling laws (power laws) has been emphasized in a number of biological systems (Enquist et al. 1998, Ferrière and Cazes 1999, Brown and West 2000, Allen et al. 2002, West et al. 2002). For example, critical transitions have been detected in the collapse of food webs and in the pattern of mass extinctions in paleontological data (Solé et al. 1999, Brown and West 2000, Newman and Palmer 2003). Spatial population dynamics adds another example: critical transitions are likely to occur whenever local colonization and extinction processes compete in space.

The CP implies some important messages to nature conservation:

[1] Classical (non-spatial) models of population dynamics can easily underestimate the danger of extinction. The MF showed a steady, slow decline; the CP predicted a sudden, threshold-like extinction.

[2] Several studies in conservation biology have warned about the dangers of small population size (genetic drift, demographic finite-size effects, etc; Primack 1998). We wish to emphasize that not only small size but also low density can be dangerous. The phenomena described here are present even in infinite-sized populations. Adverse effects of low density are not unknown in the ecological literature. For example, a member of a low-density group may have difficulties in finding a mating partner, or may be weak in defending itself against predators (Allee 1931, Stephens and Sutherland 1999). However, the phenomenon studied in our paper differs from an Allee effect in a fundamental feature: the per capita rate of birth does not decrease with the decline of population density to zero (c being constant). We show that even if a population is not threatened by an Allee effect, it can get into a vortex of extinction because of limited dispersal, and a consequent failure in the regulation of population density.

[3] Finite-sized populations suffer from an additional problem. As λ is decreasing, the amplitude of fluctua-

tions in the population density becomes comparable to the average. Thus, global extinction is likely to occur well before reaching the theoretical λ_c . The CP model, which assumes very large (virtually infinite) population size, represents an optimistic estimation compared to the real danger of extinction in a smaller population.

[4] A practical problem associated with the rapid increase of fluctuation is that it becomes difficult to estimate the population size near to extinction. So, exactly the endangered species, for which we need reliable estimations, may lack the sufficient amount of data.

[5] The CP shows that fragmentation of a population is not necessarily a consequence of fragmented habitat structure, but an inevitable consequence of low spreading rate (λ) even in a homogeneous habitat. A direct consequence of spontaneous fragmentation is that local fluctuations cannot be damped by local compensatory processes, and thus, the global fluctuation increases non-linearly, according to a power law. The power law scaling of some key parameters of the population may help to predict the vicinity of the threshold well before the actual danger of extinction would emerge.

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Appendix

Monte Carlo simulations of the CP

The behavior of the CP is usually studied by Monte Carlo simulations on finite but large lattices under periodic boundary conditions. Cells of the lattice are updated asynchronously. If a cell is occupied, it becomes empty (i.e. local extinction occurs) with probability e . If a cell is empty, it becomes occupied (i.e. colonization occurs) with probability $c \frac{k}{4}$, where k is the number of occupied cells out of the four nearest neighbors. The initial state of the lattice can be chosen arbitrarily. It is customary to study spreading from a single occupied cell ('seed'), or start from a maximally high density population, in which every cell is occupied.