

Changes in the gradient percolation transition caused by an Allee effect

Michael T. Gastner,^{1,2} Beata Oborny,³ Alexey B. Ryabov,¹ and Bernd Blasius¹

¹*Institute for the Chemistry and Biology of the Marine Environment,
Carl von Ossietzky Universität, Carl-von-Ossietzky Str. 9-11, 26111 Oldenburg, Germany*

²*Institute for Mathematical Sciences and Department of Mathematics,
Imperial College London, 53 Prince's Gate, London SW7 2PG, United Kingdom*

³*Department of Plant Taxonomy and Ecology, Loránd Eötvös University,
Pázmány Péter sny. 1/C, H-1117, Budapest, Hungary*

The establishment and spreading of biological populations depends crucially on population growth at low densities. The Allee effect is a problem in those populations where the per-capita growth rate at low densities is reduced. We examine stochastic spatial models in which the reproduction rate changes across a gradient g so that the population undergoes a gradient percolation transition. Without Allee effect, the transition is continuous and the width w of the hull scales as in conventional (i.e., uncorrelated) gradient percolation, $w \propto g^{-0.57}$. However, with a strong Allee effect the transition is first-order and $w \propto g^{-0.26}$.

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Not only human relationships frequently obey the rule “two’s company, three’s a crowd.” Negative density dependence, defined as a decrease of the per-capita growth rate with increasing population density, is common among almost all species at high densities, where overcrowding and the depletion of resources limit further growth. The most common model for negative density dependence is the logistic equation which assumes that the per-capita growth rate decreases linearly with the population size n ,

$$\frac{1}{n} \frac{dn}{dt} = r \left(1 - \frac{n}{K}\right), \quad (1)$$

where t is time, r is the intrinsic rate of increase, and K the carrying capacity.

If $r, K > 0$, Eq. 1 is characterized by a negative density dependence for all population sizes n . For some small populations, however, a positive density dependence can be observed. The latter is called a demographic Allee effect, named after Warder Clyde Allee, who described it first, and supported the theory with examples from various animal species from insects to mammals [1]. Small populations can suffer from reduced growth rates for various reasons. Frequently, a collective behavior (e.g., defense against predators) becomes inefficient when the group is small. Additionally, small populations are less efficient in modifying the environment to their own benefit. For example, plant individuals in aggregations can reduce frost or desiccation, but only when the density in the clump is sufficiently high [2]. To generalize density dependence, Volterra proposed to replace the right-hand side of Eq. 1 with a quadratic function of n [3],

$$\frac{1}{n} \frac{dn}{dt} = -A + Bn - Cn^2, \quad A, B, C > 0. \quad (2)$$

If $B^2 - 4AC > 0$, Eq. 2 has two stable fixed points, unlike Eq. 1, which has only one, so that the long-term behavior of Eq. 2 depends on the initial population density. If

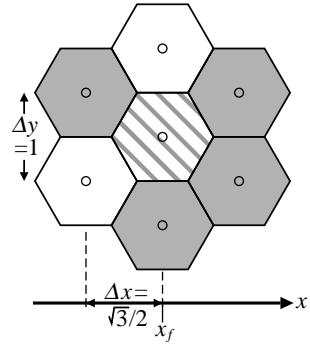


FIG. 1: Sites in the spatial models are placed in the centers of the hexagons in a honeycomb lattice. Gray cells represent populated (A), white cells vacant (\emptyset) sites. In this example, the focal site in the center has $n = 4$ populated neighbors. If this site is populated, it will die during a small time interval dt with probability equal to dt . If, on the other hand, this site is vacant, it will become populated with probability $n/6 \cdot b(x_f) \cdot dt$ in the GCP or $\frac{1}{2}n(n-1)/15 \cdot b(x_f) \cdot dt$ in the GAP, where $b(x_f)$ is the local birth attempt rate.

$n > (B - \sqrt{B^2 - 4AC})/2C$ at $t = 0$, the population will approach a positive limit, whereas a smaller initial population will become extinct. Several other formulations of the Allee effect have been suggested in the past decades, some including stochastic and spatial effects [4, 5] (see chapter 3.5 in Ref. 6 for a review). They all have in common that a strongly positive density dependence accelerates the extinction of small populations.

The work described here is motivated by the question: what are the consequences of an Allee effect on populations that live at a margin of a geographic range? Because such populations usually have low densities, one can expect that it matters greatly for the success of establishment and spreading if an Allee effect is present or not [5, 7]. In this letter, we investigate the situation near

a geographic margin with two models where the density changes across space from low to high values. We show that a strong Allee effect makes the percolation transition at the margin discontinuous, causing scaling behavior different from previously studied types of gradient percolation [8, 9].

Our models are stochastic cellular automata whose local rules correspond to discretized versions of Eq. 1 or 2. Both cellular automata operate on a two-dimensional honeycomb lattice where the sites are either populated (A) or vacant (\emptyset , Fig. 1). They can change their state by local death and birth events. In both models, deaths are Poisson processes:

- $A \rightarrow \emptyset$: A populated site becomes vacant with rate 1.

In our first model, the rate, with which a vacant site becomes populated by a local birth event, is exactly proportional to the number of neighbors:

- $A \rightarrow 2A$: A vacant site at position (x, y) with n populated adjacent sites becomes itself populated with rate $b(x) \cdot n/6$.

The second model implements a local Allee effect by requiring at least one pair of neighbors for successful births. The rule $A \rightarrow 2A$ is replaced with:

- $2A \rightarrow 3A$: A vacant site at (x, y) with n neighbors (i.e., $\frac{1}{2}n(n - 1)$ pairs of neighbors) becomes populated with rate $b(x) \cdot \frac{1}{2}n(n - 1)/15$.

The denominators 6 and 15 are the maximum number of neighbors and the maximum number of neighbor pairs, respectively. Sites are updated in a random order with the rates stated above following the algorithm of Ref. 10.

The function $b(x)$ can be interpreted as the rate with which an individual in column x attempts to produce offspring on an adjacent site. A birth attempt succeeds only if that site is vacant. In the case of $2A \rightarrow 3A$, success further depends on a second neighbor adjacent to the newly born individual. If $b(x) = \text{const.}$, then the first model is equivalent to a contact process [11], and our second model becomes a special case of “Schlögl’s second model” [12, 13]. Neglecting spatial correlations (i.e., by replacing the local n with its global mean), one can easily calculate the mean-field equations for these two processes [14] which are Eq. 1 and 2 with $r = b - 1$, $k = 1 - 1/b$, $A = 1$, $B = C = b$.

Our work differs from the usual contact process and Schrögl’s second model by assuming a constant gradient $g > 0$ in the birth attempt rate, $b(x) = gx$. Long-range gradients are important in ecology because the environmental conditions can change gradually over distances larger than the distance of dispersal within one generation (e.g., along a hillside or across geographic latitudes). We call $A \rightarrow 2A$ a gradient contact process (GCP) [10] and $2A \rightarrow 3A$ a gradient Allee process (GAP).

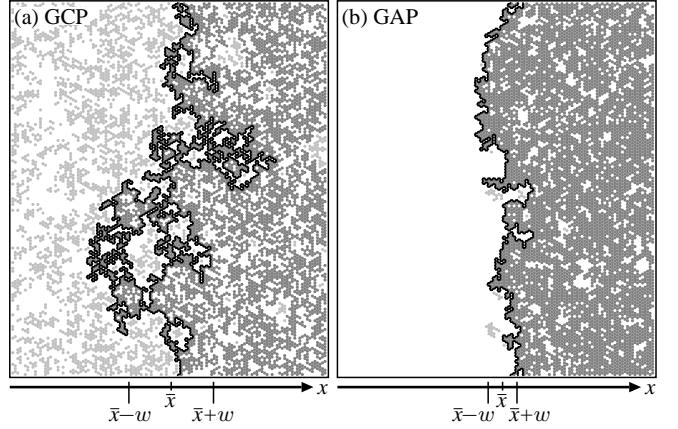


FIG. 2: Typical snapshots of (a) the GCP and (b) the GAP. Dark gray: the largest populated cluster. Light gray: all other populated sites. Black curve: percolation hull. The mean hull position \bar{x} and the width of the fluctuations w are indicated at the bottom.

Because $g > 0$, the steady-state density [22] of populated sites grows in both the GCP and the GAP as x , and hence b , increases. At small x , the populated sites form small isolated patches (light gray sites in Fig. 2) whereas at large x most populated sites belong to one and the same large cluster (dark gray sites). The curve along which the largest cluster touches the largest contiguous vacant area (black curve in Fig. 2) is the so-called percolation hull [8, 15]. If the studied species provides habitat or food for another species, the hull marks the borderline between the connected and fragmented occurrence of this resource. An example is a treeline across an altitudinal or latitudinal gradient. Births and deaths cause the position and shape of the percolation hull to fluctuate. The average position of the hull \bar{x} and the characteristic width of the fluctuations w depend on g and the model (GCP vs. GAP, Fig. 2). We compute \bar{x} and w as the mean and the standard deviation of the distribution of x -coordinates along the hull during several independent runs.

In Fig. 2, the number of sites in the GCP’s largest cluster increases gradually from left to right. The increase is much more abrupt in the GAP which generates only few isolated clusters to the left of the hull. This visual impression can be confirmed by looking at local densities in the transition region near \bar{x} . Because w is the relevant length scale in this region, we investigate circular subsystems of radius w centered at \bar{x} (Fig. 3a). We define the local density ρ as the number of those sites inside the circle that belong to the largest cluster (dark gray in Fig. 3a) divided by the number of all sites in the circle (white, light and dark gray). The distributions of ρ , aggregated over independent runs of the GCP and the GAP, at different y -coordinates and at different times, are represented as

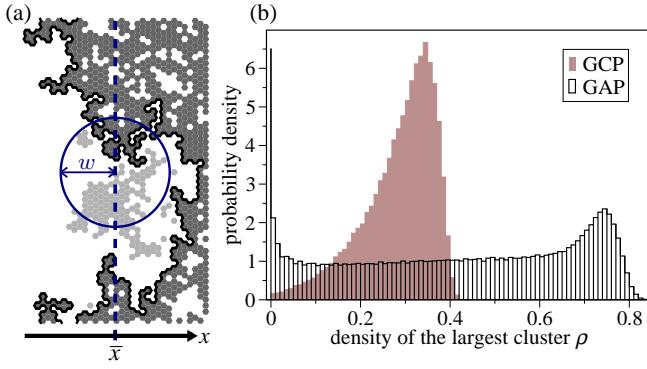


FIG. 3: (a) To distinguish between a continuous and a first-order transition at the mean hull position \bar{x} , we investigate circular subsystems with radius equal to the hull width w . We measure the fraction of sites ρ inside the circle that belong to the largest cluster (i.e., the dark gray area inside the circle divided by the total area of the circle). (b) From data of several independent runs, we obtain the probability distribution for ρ , represented as a histogram. The GCP distribution is uni-, the GAP distribution bimodal. Plotted are the distributions for $g = 2 \cdot 10^{-4}$. The smaller the gradient, the more weight is concentrated in the two peaks of the GAP distribution.

histograms in Fig. 3b. The GCP distribution has one single sharp peak at intermediate densities whereas the GAP has two local maxima, one at zero and another one at high density. In analogy to thermodynamics, where a bimodal probability distribution of an order parameter is an indication of a first-order phase transition [16], percolation in the GAP can be interpreted as a first-order transition between two steady states of either zero or of a positive density. Thus only a population larger than a critical density (i.e., on the right of the hull) is able to grow and, when this density is exceeded, the cluster size grows abruptly, distantly reminiscent of percolation in an Achlioptas process [17]. This behavior is in sharp contrast to the GCP which, like gradient percolation on uncorrelated lattices [8], exhibits a continuous transition.

Our results shed new light on the controversy about the order of the transition in Schlögl's second model. The mean-field equation, Eq. 2, predicts a saddle-node bifurcation at $B = 2\sqrt{AC}$ so that the largest stable population undergoes a first-order transition, jumping discontinuously from zero to a finite positive value. However, Grassberger [13] found signs of a continuous transition in two dimensions. Results by Liu et al. [18] might suggest that, instead of a clearly defined transition, there could be a finite interval of birth rates where high- and low-density phases coexist. Our data, however, strongly support previous reports of a first-order transition [19]. We find no indication of a broad coexistence interval; the position \bar{x} is independent of the initial condition, thus sharply defining the critical birth rate. The smaller g in the GAP, the deeper the valley between the two peaks

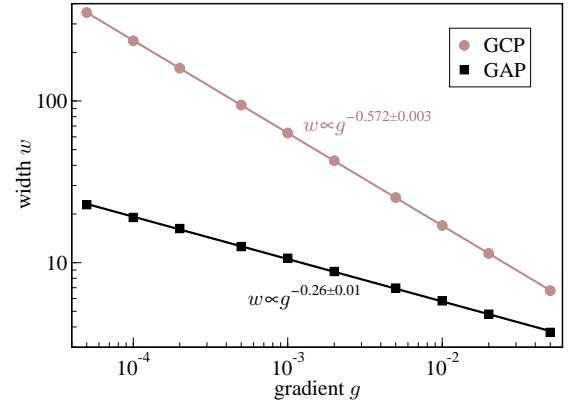


FIG. 4: The hull width w as a function of the gradient g . The lines are least-squares fits to the data. Error bars are smaller than the symbol sizes.

in the distribution of ρ , consistent with a discontinuous transition in the limit $g \rightarrow 0$.

The low frequency of intermediate densities in the GAP does not only reduce the hull width compared to the GCP (Fig. 2), but also leads to a different scaling relation between w and g (Fig. 4). For the GCP, we find $w \propto g^{-a_{GCP}}$, $a_{GCP} = 0.572(3)$ (95% CI), in excellent agreement with the scaling $w \propto g^{-4/7}$ in uncorrelated gradient percolation [8]. The GAP width also follows a power law, but with a smaller exponent $a_{GAP} = 0.26(1)$. The exponent $a_{GCP} = 4/7$ is related to the divergence of the correlation length in two-dimensional percolation with the critical exponent $\nu = 4/3$ via $a_{GCP} = \nu/(\nu+1)$ [8]. There is no analogous relation for a_{GAP} , because the correlation length is finite at a first-order transition. The result that w , nevertheless, scales with g in the GAP is surprising, considering that scaling in stochastic gradient models has so far been linked to divergent correlation lengths [9]. An exponent $a_{GAP} = 1/4$ is within the error bounds, and in this respect the GAP scaling resembles 3D wedge wetting, where the interfacial roughness scales as $t^{-1/4}$, t being the difference from the filling temperature [20].

Although the spatial width of the hull increases with decreasing g , the transition zone becomes, in terms of the birth rate b , more confined. This slightly counterintuitive fact becomes clear by plotting $p(b)$, the probability that a site with birth rate b belongs to the largest cluster (Fig. 5). In both models, $p(b)$ approaches a limiting function as $g \rightarrow 0$ with a sharp increase at the percolation thresholds $b_{p,GCP} = 2.260(1)$ and $b_{p,GAP} = 7.7340(3)$. For finite g , $p(b)$ obeys the finite-size scaling

$$p(b, g) = g^c f(|b - b_p| g^{a-1}), \quad (3)$$

where a is the hull width exponent a_{GCP} or a_{GAP} , respectively, and f is a model-dependent scaling function. In the GCP, we expect $c = \beta/(\nu + 1)$, where the critical exponents are those of homogeneous percolation (i.e.,

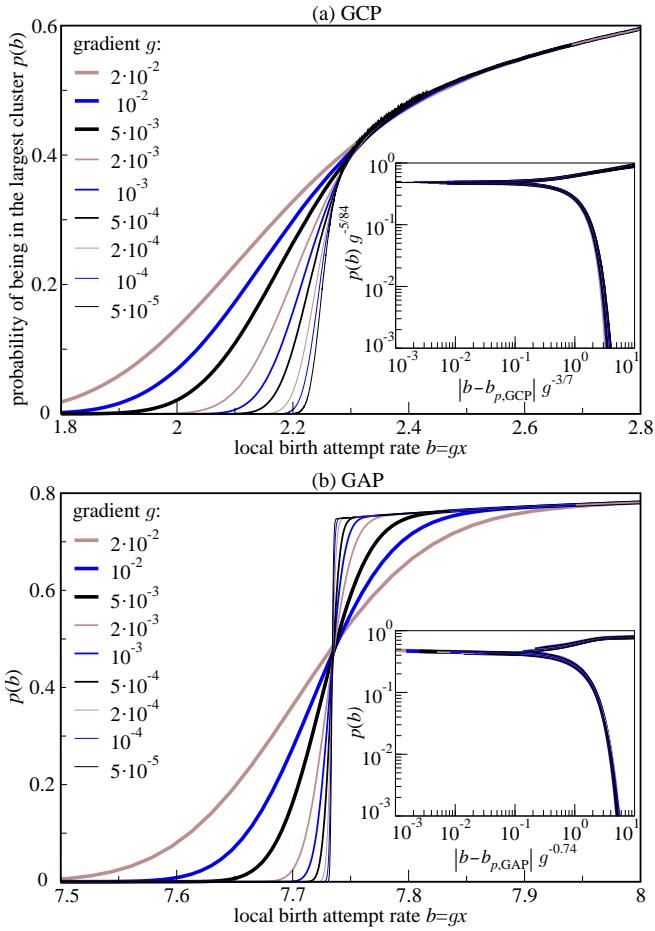


FIG. 5: The probability p that a site belongs to the largest cluster as a function of the site's birth attempt rate b in (a) the GCP, (b) the GAP for various gradients g . Insets: The functions collapse if the coordinates are rescaled in accordance with Eq. 3. In both insets, the same nine data sets are shown as in the main panels.

$g = 0$), $\beta = 5/36$ and $\nu = 4/3$ [21]. The denominator $\nu + 1$ is explained by the non-zero gradient, thus $c_{\text{GCP}} = 5/84$. For the GAP, however, the first-order transition demands that p has a discontinuity in the limit $g \rightarrow 0$ and therefore $c_{\text{GAP}} = 0$. The insets of Fig. 5 show a remarkable data collapse for the anticipated exponents.

In summary, the GCP and the GAP behave fundamentally differently near the margin of the populated range. The GCP, a model without any Allee effect, possesses the same characteristic features as previously reported for uncorrelated gradient percolation. The Allee effect in the GAP changes the situation drastically: the percolation transition is first-order and the hull width diverges more slowly for $g \rightarrow 0$.

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 - [22] We started all simulations from initial conditions where sites (x, y) are vacant if $x < x_0$ and populated if $x \geq x_0$ for different thresholds x_0 . We monitored how the mean hull position \bar{x} changes over time and observed that, after a transient, \bar{x} fluctuates around the same value regardless of the choice of x_0 . Additional simulations, where the initial border between the populated and the vacant region was parallel instead of perpendicular to the gradient, resulted in the same \bar{x} . The transient time and \bar{x} depend on g and the model (GCP or GAP). All numerical data

presented in this paper were taken in the steady state, (i.e., long after the transient). All lattices had 1024 sites per x -column. Periodic boundary conditions were applied

in the y -direction.