

# Pair statistics clarify percolation properties of spatially explicit simulations

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**Abstract**

Dispersal is a fundamental control on the spatial structure of a population. We investigate the precise mechanism by which a mixed strategy of short- and long-distance dispersal affects spatial patterning. Using techniques from pair approximation and percolation theory, we demonstrate that dispersal controls the extent to which a population is completely connected by modulating the proportion of neighboring sites which are simultaneously occupied. We show that near the percolation threshold this pair statistic, rather than other metrics proposed earlier, best explains clustering, and we suggest more general circumstances under which this may hold.

*Key words:* dispersal, percolation, pair approximation, aggregation, spatial models, connectivity

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Understanding the sources and consequences of spatial heterogeneity is a fundamental task in ecology (Levin, 1992). Both in terrestrial (Cain et al., 2000) and marine (Carlson and Olson, 1993) systems, dispersal is one of the basic forces which shapes the spatial structure of a population (Levin and Muller-Landau, 2000; Tilman and Kareiva, 1997). A poorly-dispersing species shows spatial autocorrelation, whereas long-distance dispersal contributes to the spatial mixing of a population (Reed et al., 2000). This spatial patterning has important consequences for phenomena such as species coexistence (Bolker and Pacala, 1999), vulnerability to and recovery from disturbance (Etter and Caswell, 1994; Hiebeler, 2004), and other aspects of ecosystem function (Pacala and Deutschman, 1995). Through such mechanisms, whether dispersal is highly localized, long-distance, or a mixture of the two can affect the spatiotemporal dynamics of a population.

In this paper, we examine the effects of mixed dispersal strategies on the spatial structure of a population. To this end we consider a spatially explicit birth-death model, in which organisms have a mixed strategy of local and global dispersal. We will see that the exact strategy – that is, the relative frequency of local and global dispersal – has important consequences for the spatial structure of a population. Specifically, we show that whether a population is completely connected depends on the proportion of pairs of neighboring sites which are simultaneously occupied, and that dispersal influences patterns of aggregation by changing this pair statistic. (Earlier statements in the literature (Iwasa, 2000; Kubo et al., 1996) imply that clustering is determined by a conditional site occupation probability which is related to, but distinct from, the pair statistic.) Briefly, *local* density controls *global* connectedness.

Much prior work on spatially-explicit, single-species systems has focused on the special case of either purely local (de Aguiar et al., 2004; Haraguchi and Sasaki, 2000) or purely global (Derebec and Courchamp, 2003; Tilman, 1994) dispersal. Other researchers have examined both cases simultaneously (Boots and Sasaki, 2000; Socolar et al., 2001), without considering intermediate or mixed strategies.

A class of models which explicitly addresses mixed dispersal strategies arises in the original work of Harada and Iwasa (1994) (see also Etter and Caswell (1994) for a model of marine invertebrates, and Kubo et al. (1996) for forest gap dynamics), in which a linear resource trade-off between local and global dispersal is assumed and an optimum is calculated. In contrast to Harada and Iwasa (1994), our goal is to investigate the direct effects of dispersal strategy on spatial structure, rather than to optimize a productivity function. Because of this, we investigate a higher-resolution lattice and a broader range of parameters, so that we can discern more subtle effects in spatial patterning.

One way spatial structure, and thus dispersal strategy, affects the dynamics

of a population is by modulating the effect of “contagious” (Peterson, 2002) disturbances such as fire, disease or fluid shear. Whether such a disturbance can propagate throughout a population depends on whether that population is connected, in the sense that each individual is linked to any other by a sequence of adjacent individuals. This gives biological meaning (O’Neill et al., 1999; Plotnick and Gardner, 1993) to a fundamental attribute of a lattice-based model, namely, the proportion of individuals which are members of the largest cluster. We determine the region of parameter space in which the population coalesces into a single, large cluster. The boundary of this region is an important threshold, for it determines the extent to which the entire population is placed at risk from a disturbance which spreads from an initial focal individual. We show (Figure 1) that the exact dispersal strategy determines the threshold population density at which the population aggregates into a single cluster. For a given population density, a higher proportion of local dispersal means that more individuals will be in the largest cluster.

The presence of this threshold parallels results in landscape ecology (With et al., 1997). Suppose that a landscape is divided into patches, each of which is either suitable habitat for a given organism or completely impermeable to that organism. If most patches are habitat, then the organism experiences the landscape as connected. If, conversely, most patches are impermeable, then from the organism’s perspective the landscape is a collection of isolated clusters of habitat. It turns out that there is a sharp threshold of habitat density distinguishing essentially connected from essentially isolated landscapes (Flather and Bevers, 2002; With et al., 1997).

Population clustering and landscape connectivity are two biological interpretations of the same mathematical abstraction: percolation theory (Grimmett, 1999; Stauffer and Aharony, 1991). This formalism studies the random structures created by deleting vertices or edges from networks with fixed, independent probability. While this process makes sense on any graph, the most familiar formulation is site percolation on the square lattice. Consider an infinite, two-dimensional grid. Suppose that each lattice point, or crossing, is deleted with some fixed probability  $1 - s$  (or, equivalently, preserved with probability  $s$ ). Much is known about the behavior of the typical resulting configuration. Most fundamental is the phenomenon of criticality. There is a number  $s_{\text{crit}}$  so that, if  $s < s_{\text{crit}}$ , then every cluster is almost surely finite. Conversely, if  $s > s_{\text{crit}}$ , then there is almost surely a unique infinite cluster.

In the special case of our model where all dispersal is global, at equilibrium each site is occupied with independent probability equal to the steady-state density of the population; the analogy between the model and that studied in percolation theory is, except for finite-size effects, exact. In contrast, the arrangement of a population with a mixed dispersal strategy does not correspond, at least naively, to site percolation on the grid. The fundamental fact

that local dispersal causes spatial autocorrelation is echoed in the shift (Figure 1) of the threshold of aggregation as a function of dispersal strategy.

Aiming to make this intuition precise, we explain the mechanism for this shift in two stages. In the first, we derive a simple system of differential equations for density  $\rho$  and pair-density  $\sigma$  to approximate the dynamics of our model. We use the pair approximation (Harada and Iwasa, 1994; Matsuda et al., 1992) as a framework for understanding dynamics of a lattice-based model. Our model is quite similar to that of Iwasa (2000), and the equations we derive are essentially the same.

In the second stage, we use the derivation to understand the region of parameter space in which almost all individuals aggregate into a single cluster. Since our differential equations capture the dynamics of our model quite well (Figure 2), we are led to seek an explanation for clustering which depends only on  $\rho$  and  $\sigma$ .

The analogy (Plotnick and Gardner, 1993) between random patterns of patch occupancy and site percolation on a lattice is tantalizing, but not transparent. Earlier assertions (Iwasa, 2000; Kubo et al., 1996) in the literature suggest that site percolation explains patterns of aggregations in models such as that considered here. Empirically (Figure 4) we find such an explanation inadequate. Guided by our derivation, we propose an alternative mathematical mechanism for coalescence. We show that model parameters in general, and levels of long-distance dispersal in particular, affect the aggregation of the population by means of their effect on the steady-state value of  $\sigma$ .

We start by defining our model and presenting data from simulations. In the second section, we use pair-approximation techniques to derive a pair of differential equations which captures part of the information in our model, and compare its predictions to empirical results. In the third section, we use the methods of section two to explore and explain the patterns of aggregation observed in the first section. We close by examining some consequences of this more detailed understanding of coalescence.

## 1 A spatial birth-death process

### 1.1 *The basic model*

Consider a lattice in which each site is connected to exactly  $N$  (typically 4 or 8) neighbors. At any given time, each site may be empty or occupied. Parameters  $\beta$ ,  $\mu$  and  $p$  are fixed, and dynamics unfold in the following way.

- *death* An occupied site becomes empty at rate  $\mu$ .
- *birth* An occupied site gives birth at rate  $\beta$ .
  - *global* With probability  $p$ , dispersal of the new propagule is global. A site is chosen at random among all lattice sites; if empty, it becomes occupied.
  - *local* With probability  $\bar{p} = 1 - p$ , dispersal of the new propagule is local. A neighboring site is chosen at random; if empty, it becomes occupied.

Model parameters are summarized in Table 1. Unless otherwise specified, all random variables are distributed uniformly over their range. Note that simultaneously rescaling  $\beta$  and  $\mu$  has the effect of changing the time scale of the process, but not the proportion of births to deaths in any given configuration. Therefore, while the values of  $\beta$  and  $\mu$  control how fast the system approaches equilibrium, only their *ratio* affects the steady state of the system; we interpret  $\beta/\mu$  as a measure of the growth rate of the population, and call it the relative birth rate (cf. Bolker (1999, p.853)). The process described here naturally gives rise to patterns of population clustering potentially important for disturbance spread. This class of patterns is also similar to those studied in landscape ecology, if occupied sites are interpreted as patches of good habitat and empty sites as unsuitable habitat.

Although this model is relatively simple, minor variants of it explain gaps in forest canopy (Kubo et al., 1996) and the distribution of phytoplankton (Etter and Caswell, 1994). Moreover, this model is already rich enough to allow us to explore questions of aggregation and connectivity.

When  $p = 1$ , all reproduction is global, and one recovers a mean-field model. Space is a component of the model only insofar as there are finitely many patches, each of which can be empty or occupied; distance between patches is effectively erased. The probability that a birth event is successful is equal to the proportion of empty sites in the lattice, and the population satisfies a logistic growth equation.

When  $p = 0$ , all reproduction is local, and the model degenerates to a contact process. Such stochastic systems have been intensively studied since their introduction by Harris (1974); we refer the reader to the surveys of Durrett (1991) and of Liggett (2004). Contact processes are common in spatially explicit epidemiological models. Indeed, if we relabel the model by interpreting empty sites as susceptible individuals (or hosts), and occupied sites as infected hosts (or parasites), then the birth process represents the spread of a pathogen, while the death process is the recovery of a host. In this way, the special case  $p = 0$  of our model supports an interpretation as a spatially explicit S-I model.

Values of  $p$  between 0 and 1 correspond to mixed dispersal strategies. Such intermediate levels of dispersal arise in a wide variety of settings, including plants in which seeds are occasionally carried far away (Nathan et al., 2002;

Cain et al., 2000); plants which reproduce vegetatively as well as sexually (van Groenendael et al., 1997); and communities of plankton in which individuals of different species disperse near or far from the natal site (Shanks et al., 2003). In our model, a birth happens either next to the parent or at a site chosen at random from the entire lattice. Still, the argument of Bolker (1999, Appendix A) describes a parallel between the *mixed dispersal strategy* used here and an *intermediate dispersal strategy*, in which dispersal follows a kernel which decays at some intermediate distance from the parent.

We wrote our simulator in Java. It is available for experimentation (Achter, 2004), and source code is available upon request. The simulation was run on a  $400 \times 400$  grid with periodic boundaries, in which every site has exactly four neighbors, for one thousand time units. (Varying the grid size from  $200 \times 200$  to  $800 \times 800$  does not appear to affect equilibrium densities. Moreover, the system reaches steady state well before time one thousand.) Rates  $\beta$  and  $\mu$  are interpreted and implemented as parameters for Poisson processes; the simulation runs in continuous time. Simulation results are shown in Figure 2.

## 1.2 Aggregation

A population of global dispersers spreads uniformly throughout its range, while a population of short-range dispersers may well exhibit aggregation. We study spatial patterning in our model by focusing on one aspect of clustering. The cluster containing an individual consists of all neighbors of that individual, all neighbors of *those* individuals, and so on. Understanding the distribution of cluster sizes is necessary for investigating the propagation of disturbance through a population (Pascual et al., 2002). A coarse but crucial aspect of this distribution (Plotnick and Gardner, 1993) is  $B = B(\beta, \mu, p)$ , the proportion of individuals which are in the largest cluster. We would expect that, if the steady-state population density  $\rho$  is sufficiently high, then most individuals will be members of the largest cluster. This prediction is borne out in Figure 1. For a fixed level  $p$  of global dispersal, a threshold emerges. If the population is above this threshold, then almost the entire population aggregates into a single, giant cluster, while if the population is even slightly below that threshold, each cluster accounts for a very small fraction of the entire population. (The connection between this thresholding and percolation theory, already mentioned in the introduction, is discussed at greater length in Section 3.)

Moreover, we see in Figure 1 that the mixture of local and global dispersal systematically influences the location of this threshold. For fixed density  $\rho$ , a smaller value of  $p$  means that more organisms are in the largest cluster. In the remainder of this paper we explore this phenomenon.

## 2 Analytic approximation

Over ten years ago, Matsuda et al. (1992) translated from statistical physics to ecology the first of a class of methods, called pair-approximation techniques, for distilling a lattice-based model down to a small collection of differential equations. Suppose that each site can be in one of finitely many states (e.g., *empty* or *occupied*). Typically, for each state  $\chi$  one tries to derive equations for the rate of change of  $\rho_\chi$ , the density of sites in state  $\chi$ , and for  $\sigma_\chi$ , the density of *pairs* of neighboring sites which are both in state  $\chi$ . While an exact solution must account for higher-order interactions between next-nearest neighbors and so on, in practice one can often truncate these higher moments and still obtain reasonable results.

Following Harada and Iwasa (1994), we can attempt to understand our model analytically. The goal here is not to simply reproduce the dynamics of simulations. Rather, the lessons we learn in the process of deriving such equations can help us explain the relation in Figure 1 between dispersal strategy and clustering. Specifically, we will try to forge a connection between the clustering thresholds in Figure 1 and percolation theory.

Let  $\rho = \rho(t)$  be the proportion of sites which are expected to be occupied, and let  $\sigma = \sigma(t)$  be the expected proportion of neighboring sites which are both occupied. Finally, let  $\tau_{0/+}(t)$  be the probability that a site is empty, *given* that a neighboring site is occupied, and similarly define  $\tau_{+/+}$ , etc. These variables are summarized in Table 1. Note that if occupied sites are aggregated, then  $\sigma(t) > \rho(t) \cdot \rho(t)$ , while if occupied sites are overdispersed then the reverse is true. Quantities such as  $\sigma$  and  $\tau_{+/+}$  measure the local density of the population. Indeed, Harada and Iwasa (1994) show that  $\tau_{+/+}$  is exactly the mean crowding index, if the latter is measured using only nearest-neighbor pairs (Lloyd, 1967).

Suppose that the (finite) lattice contains  $L$  sites; by definition,  $L\rho(t)$  sites are occupied. At each occupied site, the death process is a Poisson process with parameter  $\mu$ . Since the processes at distinct sites are independent, the expected number of deaths during a small time interval  $\Delta t$  is  $\mu L\rho(t)\Delta t + o(\Delta t)$ . After dividing by  $\Delta t$  and taking the limit as  $\Delta t$  gets arbitrarily small, we find that the instantaneous rate of change in the population due to the death process is  $-\mu L\rho(t)$ . Normalizing by lattice size, we find that the instantaneous rate of change in expected population *density* due to death is  $-\mu\rho(t)$ .

The birth process at each occupied site is independent of the death process, so that the overall instantaneous rate of change of  $\rho$  is the sum of the effects due to death and to birth. After normalizing by lattice size, the expected number of attempted births is  $\beta\rho(t)\Delta t$ . (Now and henceforth we suppress terms of size

$o(\Delta t)$ .) A birth event increases the population only if the chosen site is empty.

Now, the probability that a site chosen uniformly from the lattice is empty is  $1 - \rho(t)$ . Therefore, during a time interval of length  $\Delta t$  the expected increase in population density due to global reproduction is  $\beta\rho(t)p(1 - \rho(t))\Delta t$ . We similarly address local reproduction. The probability that a site is empty, *given* that the neighboring parent site is occupied, is by definition  $\tau_{0/+}(t)$ . The contribution of the local birth process to population density is therefore  $\beta\rho(t)\bar{p}\tau_{0/+}\Delta t$ , and the rate of change of the expected value of  $\rho$  is

$$\frac{\partial}{\partial t}\rho(t) = \beta\rho(t)(p(1 - \rho(t)) + \bar{p}\tau_{0/+}(t)) - \mu\rho(t). \quad (1)$$

We will see below (equation (3)) that it is possible to eliminate  $\tau_{0/+}$  from equation (1), and thus to express the right-hand side as a function of  $\rho$ ,  $\sigma$  and the model parameters.

It remains to derive a similar expression for the dynamics of  $\sigma(t)$ . An occupied site is expected to have  $N\tau_{+/+}$  occupied neighbors. Therefore, the death process contributes  $-\mu\rho(t)N\tau_{+/+}\Delta t$  to  $\sigma(t)$ .

We now turn to the effect of the birth process on  $\sigma(t)$ . The probability that a given neighbor of a randomly chosen empty cell is occupied is  $\tau_{+/0}(t)$ . The expected number of occupied neighbors of a given empty cell is  $N\tau_{+/0}(t)$ ; this is the expected contribution of a global birth event to  $\sigma(t)$ .

The local process is more subtle. Each local birth event necessarily contributes at least one pair to the value of  $\sigma$ ; the parent and daughter are, by definition, neighbors. The extent to which a birth increases  $\sigma$  depends on how many (other) occupied neighbors the daughter site has. The pair approximation *assumes* that the expected number of occupied neighbors of the daughter site depends *only* on the fact that it was unoccupied, and in particular is independent of the parent site's status. (We revisit this assumption at the end of this section.) Thus, each birth is expected to contribute  $(1 + (N - 1)\tau_{+/0})$  to  $\sigma$ , and our assumption yields the approximation:

$$\frac{\partial}{\partial t}\sigma(t) = \beta\rho(t) \left( p(1 - \rho(t))N\tau_{+/0}(t) + \bar{p}\tau_{0/+}(t)(1 + (N - 1)\tau_{+/0}(t)) \right) - \mu\rho(t)N\tau_{+/+}(t). \quad (2)$$

We can rewrite equations (1) and (2) as a closed system involving only  $\rho$ ,  $\sigma$  and model parameters. Indeed,  $\tau_{0/+} = 1 - \tau_{+/+}$ , while the conditional probabilities  $\tau$  satisfy  $\tau_{+/+} \cdot \rho = \sigma$  and  $\tau_{0/+} \cdot \rho = \tau_{+/0} \cdot (1 - \rho)$ . Therefore, the system is

equivalent to

$$\frac{\partial}{\partial t}\rho(t) = (\beta(\bar{p}(1 - \frac{\sigma(t)}{\rho(t)}) + p(1 - \rho(t))) - \mu)\rho(t) \quad (3)$$

$$\begin{aligned} \frac{\partial}{\partial t}\sigma(t) = & \beta\rho(t) \left( p(1 - \rho(t))N\frac{\rho(t) - \sigma(t)}{1 - \rho(t)} + \bar{p}(1 - \frac{\sigma(t)}{\rho(t)})(1 + (N - 1)\frac{\rho(t) - \sigma(t)}{1 - \rho(t)}) \right) \\ & - \mu\rho(t)N\frac{\sigma(t)}{\rho(t)}. \end{aligned} \quad (4)$$

One can use these equations to calculate equilibrium values  $\rho(\beta, \mu, p)$  and  $\sigma(\beta, \mu, p)$ . In Figure 2 we plot the steady-state population density as a function of  $\beta/\mu$  and  $p$ . We see that equations (3) and (4) predict the equilibrium state of our model, at least in the region of parameter space where the population empirically persists.

In the special case where all dispersal is global, we set  $p = 1$  in equations (3) and (4), and find that the equilibrium values are  $\hat{\rho} = (\beta - \mu)/\beta$  and  $\hat{\sigma} = (\hat{\rho})^2$ ; we interpret the former value as the carrying capacity of the system. Indeed, if we let  $K = (\beta - \mu)/\mu$ , then equation (3) becomes the usual logistic equation

$$\frac{\partial}{\partial t}\rho(t) = \rho \cdot (1 - \frac{\rho}{K}). \quad (5)$$

We have used the approximation  $\tau_{+/0+} \approx \tau_{+/+}$  in order to obtain the closed system of equations (3)-(4). Approximating triplet densities by pair densities is a discrete analogue of approximating the third moment of a spatial distribution by its second moment, as in the work of Bolker (1999). Other choices of approximation are available, such as the ‘‘improved pair approximation’’ in which one selects constants  $\epsilon_{l,m}^{(i,j,k)}$  and assumes  $\tau_{i/jk} \approx \sum_{l,m} \epsilon_{l,m}^{(i,j,k)} \tau_{l/m}$ . (Here,  $i, j, k, l$  and  $m$  are possible states for a site; refer to Sato et al. (1994) for more details.) One can also keep track of higher moments, by (for example) explicitly maintaining expected values of various triplet densities. In the process of doing so, quartet statistics arise. One then must choose whether to model quartets directly or to make a ‘‘triplet approximation’’ (Matsuda et al., 1992, Appendix). We have actually carried out the latter procedure, and thereby derived a system of equations for triplet densities, for our model on a triangular lattice. We found that, as expected, tracking triplets expanded the region of parameter space in which our approximation closely matched simulation results. However, a small region of relatively poor performance persisted.

### 3 Percolation Theories

We have seen in Section 1.2 that  $p$ , the amount of birth via global dispersal, affects the spatial configuration of the population. Specifically, at a given level of population density, a smaller value of  $p$  means that more individuals are members of the largest cluster. This is not surprising; it is one manifestation of the general fact that, after controlling for carrying capacity, a population whose dispersal mode is purely local is more clustered.

In this section, we attempt to quantify and explain the effect of  $p$  on aggregation by tracing through the consequences of our pair-approximation assumption. In Section 2, we saw that when the proportion of global dispersal is nonzero, or when the birth rate is at least moderately high, the dynamics of the system depend only on density ( $\rho$ ) and nearest-neighbor ( $\sigma$ ) statistics. Given this, at least in the region of parameter space where the pair approximation agrees well with simulation, we expect to successfully predict any higher-order property, such as degree of aggregation, by means of  $\rho$  and  $\sigma$ . (Note that, because of the relation  $\sigma = \rho \cdot \tau$ , the knowledge of any two of  $\rho$ ,  $\sigma$  and  $\tau$  is sufficient to recover the third parameter. Therefore, we might equivalently ask for a description of aggregation which depends only on  $\rho$  and  $\tau$ .)

We first consider the case where  $p = 1$ , in which all dispersal is global. The analysis culminating in equation (5) shows that this corresponds to logistic growth with carrying capacity  $K = (\beta - \mu)/\mu$ . For a set of parameters  $\beta$ ,  $\mu$  and  $p$ , let  $B(\beta, \mu, p)$  be the proportion of individuals in the largest cluster at equilibrium. Recall that  $\rho(\beta, \mu, p)$  is the equilibrium density;  $\sigma(\beta, \mu, p)$  is the proportion of neighboring sites which are both occupied; and  $\tau(\beta, \mu, p) = \tau_{+/+}(\beta, \mu, p)$  is the conditional probability that a site is occupied, given that a neighboring site is occupied. We have fixed  $p = 1$ , varied  $\beta/\mu$ , and plotted  $B(\beta, \mu, 1)$  as a function of  $\rho$ ,  $\sigma$  and  $\tau$  in Figures 1, 3, and 4.

These graphs share a sigmoidal shape which signals the presence of a threshold. There is a critical value so that almost the entire population aggregates into a single large cluster if and only if the independent variable is larger than that critical value. To determine the threshold, we fit a logistic function  $y \sim a/(1 + \exp(b \cdot (x - c)))$  to data from five hundred runs, and interpret  $c$  as the threshold value. To enhance precision, all runs were executed on a fine,  $800 \times 800$  grid. Our method is validated below.

When  $p = 1$ , we estimate the three thresholds as  $\rho_{\text{crit}}(1) = 0.5932$ ,  $\sigma_{\text{crit}}(1) = 0.3519$ , and  $\tau_{\text{crit}}(1) = 0.5931$ , respectively. (In general, we define  $\rho_{\text{crit}}(p_0)$  as the threshold for aggregation as a function of  $\rho$  when  $p$  is fixed at  $p_0$ , and define  $\sigma_{\text{crit}}(p_0)$  and  $\tau_{\text{crit}}(p_0)$  analogously.) Such critical values can control

whether a spreading disturbance affects an entire population (Guichard et al., 2003). Thresholds arising from similar patterns are a pervasive and important phenomenon in the way populations interact with heterogeneous landscapes (Flather and Bevers, 2002; With et al., 1997). Indeed, from the perspective of an organism trying to traverse a landscape composed of patches of suitable habitat or host, especially a poorly dispersing one (King and With, 2002), whether the landscape is past the threshold of total clustering controls whether that organism experiences the entire landscape as connected.

We interpret these initial results in the framework of percolation theory. The most familiar version of percolation theory is site percolation on the square lattice, in which nodes of a lattice are preserved or deleted. We emphasize that this situation is just one instance of a family of such problems. For instance, one can instead consider *bond* percolation on the lattice, in which it is the edges between nodes, rather than the nodes themselves, which are deleted. Moreover, one can also apply this probabilistic thinning to any graph, rather than just the square lattice. In each setting, a threshold exists, but the numeric value of this threshold depends on the topology of the graph and on whether one deletes edges or vertices. Known (and estimated) values for various percolation problems are summarized in Stauffer and Aharony (1991, p.17) and Hughes (1996, p.182).

It is, of course, difficult to simulate an infinite lattice on a finite computer. In empirical (as opposed to purely mathematical) percolation theory, one simulates a percolation model on a finite grid, typically with periodic boundary conditions. For site percolation, one finds (Amritkar and Roy, 1998) that the system is past the percolation threshold when the proportion of occupied sites which are in the largest cluster is close to one. One can also declare that a finite simulation percolates if there exists a cluster connecting opposite sides of a grid without periodic boundaries. These two notions are compatible, in the sense that either definition of the onset of percolation leads to the same critical value. Moreover, Stauffer and Aharony (1991, p. 74) show that the error associated with estimating the percolation threshold from a finite simulation scales with lattice size in the same way.

Now, von Niessen and Blumen (1988) simulate the spread of a forest fire over a lattice. They show that different choices for the mechanism by which fire spreads link their basic model to different variants of percolation theory. This is part of a more general phenomenon (Wiens et al., 1997); there is no canonical identification between ecological models and a choice of percolation model. Given this, any proposed analogy between ecology and percolation theory must be probed and refined in order for it to be a quantitative tool.

When dispersal is purely global, all spatial correlations are erased. Therefore, each site is occupied with probability  $\rho$ , where  $\rho$  is the overall density of the

population. This is *literally* the same process as site percolation on the square lattice with parameter  $\rho$ . Our computed threshold  $\rho_{\text{crit}}(1) = 0.5932$  is within 0.1% of 0.592746, the best available estimate of the threshold for site percolation on the square lattice (Newman and Ziff, 2000). We note that while the technique used here for estimating percolation thresholds is relatively naïve, the work summarized in Stauffer and Aharony (1991) and Hughes (1996) involves extensive series expansions and more delicate Monte Carlo simulations. We view the excellent agreement between our statistically estimated threshold and the much more rigorous published estimates as validating our method for computing thresholds.

When  $p = 1$ , the absence of spatial correlation means that we should have  $\tau = \rho$  and  $\sigma = (\rho)^2$ . The values of  $\rho_{\text{crit}}(1)$ ,  $\sigma_{\text{crit}}(1)$  and  $\tau_{\text{crit}}(1)$  reported above enjoy this relation. While the equality  $\sigma = \tau \cdot \rho$  is tautologically true for any particular realization of the simulation (regardless of  $p$ ), we see here that it is preserved both by averaging over multiple realizations and by our statistical technique, which yields the properties of a hypothetical “critical realization” of our model.

When  $p = 0$ , all dispersal is purely local, and certain thresholds shift dramatically. Consider the graph in Figure 1, which plots the proportion of individuals in the largest cluster as a function of steady-state density,  $\rho$ . Visually, we see that the threshold appears to have shifted to the left. Numerically, the estimation technique used before shows that the threshold occurs at  $\rho_{\text{crit}}(0) = 0.5597$ . We can explain this qualitative behavior in terms of the model. For a given equilibrium density, a population which disperses locally aggregates into a larger cluster than a population in which dispersal is global. Mathematically, this reflects the fact that for  $p < 1$  the random process on the lattice is no longer independent at each site, but rather correlated (Weinrib, 1984); this effect is strongest when  $p = 0$ .

Following suggestions in the literature (see Iwasa (2000) and Kubo et al. (1996); we return to this point in Section 4 below), one might expect that  $\tau$  explains aggregation. In fact, we see in Figure 4 that the variation of  $\tau_{\text{crit}}(p)$  for varying  $p$  is just as large as that of  $\rho_{\text{crit}}(p)$ .

Figure 5 shows that varying the parameter  $p$  systematically influences the location of the threshold, when measured in terms of  $\rho$  or  $\tau$ . It appears that the proportional increase in threshold value  $\tau_{\text{crit}}(p)/\tau_{\text{crit}}(1)$  is exactly matched by a proportional decrease in  $\rho_{\text{crit}}(p)/\rho_{\text{crit}}(1)$ .

In view of this observation, and recalling that  $\rho \cdot \tau = \sigma$ , we propose  $\sigma$  as the independent variable which best explains clustering. The greatest observed deviation of  $\sigma_{\text{crit}}(p)$  from  $\sigma_{\text{crit}}(1)$ , as  $p$  ranges from 0 to 1, is less than 1%; the critical threshold  $\sigma_{\text{crit}}(p)$  is independent of  $p$ . In contrast,  $\tau_{\text{crit}}(p)$  is a decreasing

function of  $p$ , and  $\tau_{\text{crit}}(0)$  differs from  $\tau_{\text{crit}}(1)$  by over 5%.

## 4 Discussion

We have seen that  $\sigma$ , the proportion of pairs of neighboring sites which are simultaneously occupied, does an excellent job of predicting the transition of the population from an essentially disconnected state to one which is essentially clustered. In Figure 5 we plot  $\sigma_{\text{crit}}(p_0)$ , the critical value of  $\sigma$  when  $p$  is fixed at some value  $p_0$ , and find that it is essentially independent of  $p_0$ .

This is in contrast to expectations of Iwasa (2000) and Kubo et al. (1996). There, it is argued that the parameter  $\tau$  – that is, the conditional probability that a site is occupied, *given* that a neighbor is occupied – controls the formation of clusters. (In fact, these authors discuss the distribution of cluster sizes, rather than the presence or absence of near-total aggregation. However, finite-size effects are more problematic for cluster size distributions than for detecting the onset of percolation (Stauffer and Aharony, 1991, Chapter 4), so we have focused on the latter problem.) It is not hard to construct a verbal argument supporting their expectation. Indeed, suppose that a fixed, focal site is occupied. Then  $\tau$  gives the probability that each neighboring site is occupied. Following this observation, it is superficially plausible that the “growth” of the cluster containing the focal site behaves like a model in which each site is occupied with probability  $\tau$ . The simulations of Iwasa (2000), run on a coarse ( $100 \times 100$ ) lattice for a sparse choice of parameters taken from a relatively narrow section of parameter space, initially seem compatible with this prediction.

If this heuristic were correct, then for any set of parameters  $(\beta, \mu, p)$ , the knowledge of the equilibrium  $\tau = \tau(\beta, \mu, p)$  would be sufficient to determine whether or not the population aggregates into a single, massive cluster. In Figures 4 and 5, we see that this prediction fails. It turns out that  $\tau_{\text{crit}}(0)$  is over 5% larger than  $\tau_{\text{crit}}(1)$ . The amount of global dispersal directly influences the location of the threshold as a function of  $\tau$ ;  $\tau$ , alone, does not determine the onset of aggregation. In fact, even though  $\tau$  accounts for pairwise interactions, it does no better than  $\rho$ , which is definitionally insensitive to pair correlations, at predicting clustering.

Since  $\sigma$ , the proportion of pairs of neighboring sites which are both occupied, encodes information both about mean density and about spatial aggregation, one might cautiously hope that clustering is tightly correlated with  $\sigma$ . We have seen that  $\sigma$  actually does an excellent job of predicting the transition from an essentially disconnected to essentially clustered state. On the square lattice, in which each site has exactly four neighbors, we numerically estimate this

threshold as approximately 0.352. (The computed value of  $\sigma_{\text{crit}}(1)$  is 0.3519, while the mean computed value of  $\sigma_{\text{crit}}(p)$  over all  $p$  is 0.3517.)

Because we simulate on an  $800 \times 800$  grid, rather than the  $100 \times 100$  grid of Iwasa (2000), we are able to test the competing hypotheses that  $\tau$  or  $\sigma$  explains aggregation. The data in Figure 5 provide clear support for the latter hypothesis.

We lack an analytic explanation for this threshold, and this seems to be an interesting problem in pure mathematics. Although a purely analytic expression for the threshold is presumably beyond reach, an optimist might hope to find a percolation problem whose critical value is exactly the square of that of site percolation on the square lattice. The persistent threshold  $\sigma_{\text{crit}}(p) \sim 0.352$  suggests that there exists a transformation from a configuration of our model to a configuration on a different graph. The resulting (hypothetical) configuration percolates when  $\sigma$  exceeds  $\sigma_{\text{crit}}$  on the original graph.

As an exemplar of such a relation, we recall that to a graph  $G$  one may associate its covering graph,  $G^c$  (Hughes, 1995, 7.4). There is a vertex in  $G^c$  for each edge in  $G$ , and two vertices in  $G^c$  are connected exactly if their corresponding edges in  $G$  share an endpoint. Since deleting an edge from  $G$  is equivalent to deleting a vertex from  $G^c$ , *bond* percolation on  $G$  is equivalent to *site* percolation on  $G^c$ , and the two processes share the same threshold. (Intriguingly, the critical value for site percolation on the covering graph of the square lattice is approximately 0.34.)

Returning to the interaction between aggregation and the shift in the critical value of  $\rho$ , we remark that such a phenomenon has been observed in correlated percolation problems. In correlated percolation (Weinrib, 1984) one assumes that occupation probabilities for distinct sites are related by a correlation function. As such, it may provide a suitable model for ecological processes; this promise has been borne out in predicting urban growth dynamics (Berling-Wolff and Wu, 2004; Makse et al., 1998). In the case where occupied sites are overdispersed – in the notation of Table 1,  $\sigma < \rho^2$  – the correlated percolation problem on the square lattice reduces to an uncorrelated percolation problem on a different lattice (Napiorkowski and Hemmer, 1980). For positively correlated percolation, we have the observed statistical dependence (Mendelson, 1999) of the percolation threshold on the strength of site correlation.

In the absence of a full analytic understanding of the percolation threshold, for now we content ourselves with observing that calculations based on patch occupancy are an important tool in assessing landscape connectivity (O’Neill et al., 1999) and vulnerability to disturbance (Guichard et al., 2003). The measurement of statistics such as  $\sigma$  is no more costly or error-prone than the simple assessment of patch occupancy. The simulation results shown here sug-

gest that calculating the proportion of *pairs* of patches composed of suitable, traversable habitat, rather than simply the proportion of such patches, may be a more reliable indicator of overall connectivity.

While in our model the variation between  $\tau_{\text{crit}}(0)$  and  $\tau_{\text{crit}}(1)$  is only on the order of 5%, in other systems this variation could be even larger. Examining Figure 2 in the light of Figure 5 we see that, roughly speaking, total aggregation only happens for large values  $\beta/\mu$ . At such high relative birth rates, the effect of  $p$  itself on the process, and thus on the resulting pattern, is rather minimal. Perhaps not surprisingly, in this region of parameter space  $\sigma$ ,  $\tau$  and  $\rho$  are tightly linked. The somewhat small variation of  $\tau_{\text{crit}}(p)$  reflects the coupling between  $\sigma$  and  $\tau$  for large  $\beta/\mu$ .

Just as the effect of changing  $p$  is large for small values of  $\beta/\mu$ ,  $\sigma$  and  $\tau$  are decoupled for fixed, small  $\beta/\mu$ . While we clearly see that  $\sigma$ , rather than  $\tau$ , drives clustering by examining high relative birth rates  $\beta/\mu$ , we expect that this distinction will have its largest impact for small  $\beta/\mu$ . More generally, we predict that in any process which magnifies the independence of  $\sigma$  and  $\tau$ , the explanatory power of pair statistics such as  $\sigma$ , as opposed to conditional probabilities such as  $\tau$ , will be greater.

We emphasize that the spatial birth-death process we study here gives rise to patterns in which local density shapes global clustering. In our system mortality is a purely mean-field effect, independent of spatial patterning, while (for  $p < 1$ ) the birth process is sensitive to spatial effects. Thus, as in the work of Kubo et al. (1996), we find that patterns of aggregation depend on local densities. We compare this with the mussel disturbance model of Guichard et al. (2003), in which local processes apparently counterbalance each other so that cluster statistics behave as if the population were uniformly distributed. Such a delicate balance of local antagonistic forces seems to dampen the effects of correlation on the percolation process. In contrast, in systems with asymmetric local processes, we expect that local densities govern aggregation.

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## References

- Achter, J., 2004. <http://lamar.colostate.edu/~jachter/biosim.html>, URL.
- Amritkar, R., Roy, M., February 1998. Percolation of finite-sized objects on a lattice. *Phys. Rev. E* 57 (2), 1269–1272.
- Berling-Wolff, S., Wu, J., Jan. 2004. Modeling urban landscape dynamics: A review. *Ecol. Res.* 19 (1), 119–129.
- Bolker, B., September 1999. Analytic models for the patchy spread of plant disease. *Bull. Math. Biol.* 61 (5), 849–874.
- Bolker, B., Pacala, S., 1999. Spatial moment equations for plant competition: Understanding spatial strategies and the advantages of short dispersal. *Am. Nat.* 153, 575–602.
- Boots, M., Sasaki, A., 2000. The evolutionary dynamics of local infection and global reproduction in host-parasite interactions. *Ecology Letters* 3 (3), 181–185.
- Cain, M., Milligan, B., Strand, A., September 2000. Long-distance seed dispersal in plant populations. *Am. J. Botany* 87 (9), 1217–1227.
- Carlson, D., Olson, R., 1993. Larval dispersal distance as an explanation for adult spatial pattern in 2 Caribbean reef corals. *J. Exp. Marine Biol. and Ecol.* 173 (2), 247–263.
- de Aguiar, M., Rauch, E., Bar-Yam, Y., March 2004. Invasion and extinction in the mean field approximation for a spatial host-pathogen model. *J. Stat. Phys.* 114 (5-6), 1417–1451.
- Deredec, A., Courchamp, F., 2003. Extinction thresholds in host-parasite dynamics. *Ann. Zool. Fennici* 40 (2), 115–130.
- Durrett, R., 1991. The contact process, 1974–1989. In: *Mathematics of random media* (Blacksburg, VA, 1989). Vol. 27 of *Lectures in Appl. Math.* Amer. Math. Soc., Providence, RI, pp. 1–18.
- Etter, R. J., Caswell, H., 1994. The advantages of dispersal in a patchy environment: effects of disturbance in a cellular automaton model. In: Young, C. M. (Ed.), *Reproduction, larval biology, and recruitment of the deep-sea benthos*. Columbia University Press, New York, pp. 284–305.
- Flather, C., Bevers, M., January 2002. Patchy reaction-diffusion and population abundance: The relative importance of habitat amount and arrangement. *Am. Nat.* 159 (1), 40–56.
- Grimmett, G., 1999. *Percolation*, 2nd Edition. Vol. 321 of *Grundlehren der Mathematischen Wissenschaften [Fundamental Principles of Mathematical Sciences]*. Springer-Verlag, Berlin.
- Guichard, F., Halpin, P., Allison, G., Lubchenco, J., Menge, B., 2003. Mussel disturbance dynamics; signatures of oceanographic forcing from local interactions. *Am. Nat.* 161 (4), 889–904.
- Harada, Y., Iwasa, Y., 1994. Lattice population dynamics for plants with dispersing seeds and vegetative propagation. *Res. Pop. Eco.* 36 (2), 237–249.

- Haraguchi, Y., Sasaki, A., 2000. The evolution of parasite virulence and transmission rate in a spatially structured population. *J. Theor. Biol.* 203 (2), 85–96.
- Harris, T. E., 1974. Contact interactions on a lattice. *Ann. Probability* 2, 969–988.
- Hiebeler, D., 2004. Spatially correlated disturbances in a locally dispersing population model. *J. Th. Biol.* In press.
- Hughes, B. D., 1995. *Random walks and random environments*. Vol. 1. Oxford Science Publications. The Clarendon Press Oxford University Press, New York, random walks.
- Hughes, B. D., 1996. *Random walks and random environments*. Vol. 2. Oxford Science Publications. The Clarendon Press Oxford University Press, New York, random environments.
- Iwasa, Y., 2000. Lattice models and pair approximation in ecology. In: Dieckmann, U., Law, R., Metz, J. (Eds.), *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge University Press, New York, NY, pp. 227–251.
- King, A., With, K., January 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecol. Model.* 147, 23–39.
- Kubo, T., Iwasa, Y., Furumoto, N., 1996. Forest spatial dynamics with gap expansion: total gap area and gap size distribution. *J. Theor. Biol.* 180, 229–246.
- Levin, S., 1992. The problem of pattern and scale in ecology. *Ecology* 73 (6), 1943–1967.
- Levin, S., Muller-Landau, H., May 2000. The evolution of dispersal and seed size in plant communities. *Evol. Ecol. Res.* 2 (4), 409–435.
- Liggett, T., 2004. Interacting particle systems – an introduction. In: Lawler, G. (Ed.), *School and Conference on Probability Theory*. Vol. 17 of ICTP Lecture Notes Series. pp. 1–29.
- Lloyd, M., 1967. Mean crowding. *J. Animal Ecol.* 36 (1), 1–30.
- Makse, H., Andrade, J., Batty, M., Havlin, S., Stanley, H., December 1998. Modeling urban growth patterns with correlated percolation. *Phys. Rev. E* 58 (6), 7054–7062.
- Matsuda, H., Ogita, N., Sasaki, A., Sato, K., 1992. Statistical mechanics of population – the lattice Lotka-Volterra model. *Prog. Theor. Phys.* 88, 1034–1049.
- Mendelson, K., December 1999. Percolation threshold of correlated two-dimensional lattices. *Phys. Rev. E* 60 (6), 6496–6498.
- Napiorkowski, M., Hemmer, P., 1980. Correlated percolation on a quadratic lattice. *Phys. Lett. A* 76 (5-6), 359–361.
- Nathan, R., Katul, G., Horn, H., Thomas, S., Oren, R., Avissar, R., Pacala, S., Levin, S., July 25 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418 (6896), 409–413.
- Newman, M., Ziff, R., November 2000. Efficient monte carlo algorithm and

- high-precision results for percolation. *Phys. Rev. Lett.* 85 (19), 4104–4107.
- O’Neill, R., Ritters, K., Wickham, J., Jones, K., 1999. Landscape pattern metrics and regional assessment. *Ecosystem Health* 5 (4), 225–233.
- Pacala, S., Deutschman, D., December 1995. Details that matter: The spatial distribution of individual trees maintains forest ecosystem function. *Oikos* 74 (3), 357–365.
- Pascual, M., Roy, M., Guichard, F., Flierl, G., 2002. Cluster size distributions: signatures of self-organization in spatial ecologies. *Phil. Trans. Royal Soc. London Ser. B* 357 (1421), 657–666.
- Peterson, G., June 2002. Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems* 5 (4), 329–338.
- Plotnick, R., Gardner, R., 1993. Lattices and landscapes. In: Gardner, R. (Ed.), *Predicting spatial effects in ecological systems*. Vol. 23 of *Lectures on Mathematics in the Life Sciences*. American Mathematical Society, Providence, RI, pp. 129–158.
- Reed, D., Raimondi, P., Carr, M.H. Goldwasser, L., July 2000. The role of dispersal and disturbance in determining spatial heterogeneity in sedentary organisms. *Ecology* 81 (7), 2011–2026.
- Sato, K., Matsuda, H., Sasaki, A., February 1994. Pathogen invasion and host extinction in lattice structured populations. *J. Math. Biol.* 32 (3), 251–268.
- Shanks, A., Grantham, B., Carr, M., February 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Applications* 13 (1), S159–S169.
- Socolar, J., Richards, S., Wilson, W., 2001. Evolution in a spatially structured population subject to rare epidemics. *Physical Review E* 6304 (4), 041908.
- Stauffer, D., Aharony, A., 1991. *Introduction to percolation theory*. Taylor & Francis Ltd., London.
- Tilman, D., January 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75 (1), 2–16.
- Tilman, D., Kareiva, P. (Eds.), 1997. *Predicting spatial effects in ecological systems*. Princeton University Monographs. Princeton University Press.
- van Groenendael, J., Klimeš, L., Klimešová, Hendriks, R., 1997. Comparative ecology of clonal plants. In: Silvertown, J., Franco, M., Harper, J. (Eds.), *Plant life histories*. Cambridge University Press, New York, NY, pp. 191–209.
- von Niessen, W., Blumen, A., June 1988. Dynamic simulation of forest fires. *Can. J. Forest Res.* 18 (6), 805–812.
- Weinrib, A., 1984. Long-range correlated percolation. *Phys. Rev. B* 29 (1), 387–395.
- Wiens, J., Schooley, R., Weeks, R., March 1997. Patchy landscapes and animal movements: Do beetles percolate? *Oikos* 78 (2), 257–264.
- With, K., Gardner, R., Turner, M., February 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78 (1), 151–169.

Figure 1. *Proportion of individuals in largest cluster as a function of density. Data from three runs are shown; pure local dispersal ( $p = 0$ ) ( $\diamond$ ); pure global dispersal ( $p = 1$ ) ( $\blacklozenge$ ); and a mixed strategy ( $p = 0.3$ ) ( $\times$ ). Note that for a given population density, a lower value of  $p$  means that a higher proportion of individuals is in the largest cluster.*

Figure 2. *Comparison of simulation with pair approximation. Steady-state population, both as predicted ( $\circ$ ) by equations (3) and (4) and as actually simulated ( $\times$ ), is shown as a function of the proportion of global dispersal ( $p$ ) and the relative birth rate ( $\beta/\mu$ ). The approximation does quite well over most of parameter space, except when dispersal is purely local ( $p = 0$ ) and relative birth rate is low.*

Figure 3. *Proportion of individuals in largest cluster as a function of  $\sigma$ , the proportion of neighboring sites which are simultaneously occupied. Independent of whether dispersal is local ( $p = 0$ ) ( $\diamond$ ), global ( $p = 1$ ) ( $\blacklozenge$ ) or mixed ( $p = 0.3$ ) ( $\times$ ), the value of  $\sigma$  controls the formation of the largest cluster.*

Figure 4. *Proportion of individuals in largest cluster as a function of  $\tau$ , the conditional probability that a site is occupied, given that a neighbor is occupied, shown for local ( $p = 0$ ) ( $\diamond$ ), global ( $p = 1$ ) ( $\blacklozenge$ ) and mixed ( $p = 0.3$ ) ( $\times$ ) dispersal.*

Figure 5. *The amount of global dispersal,  $p$ , systematically influences the threshold values of  $\rho$  ( $\diamond$ ) and  $\tau$  ( $\times$ ). In contrast, the threshold value of  $\sigma$  ( $\blacklozenge$ ) is insensitive to  $p$ . The horizontal line is  $y = 0.592746$ , the best available estimate for the critical value for site percolation on the square lattice.*

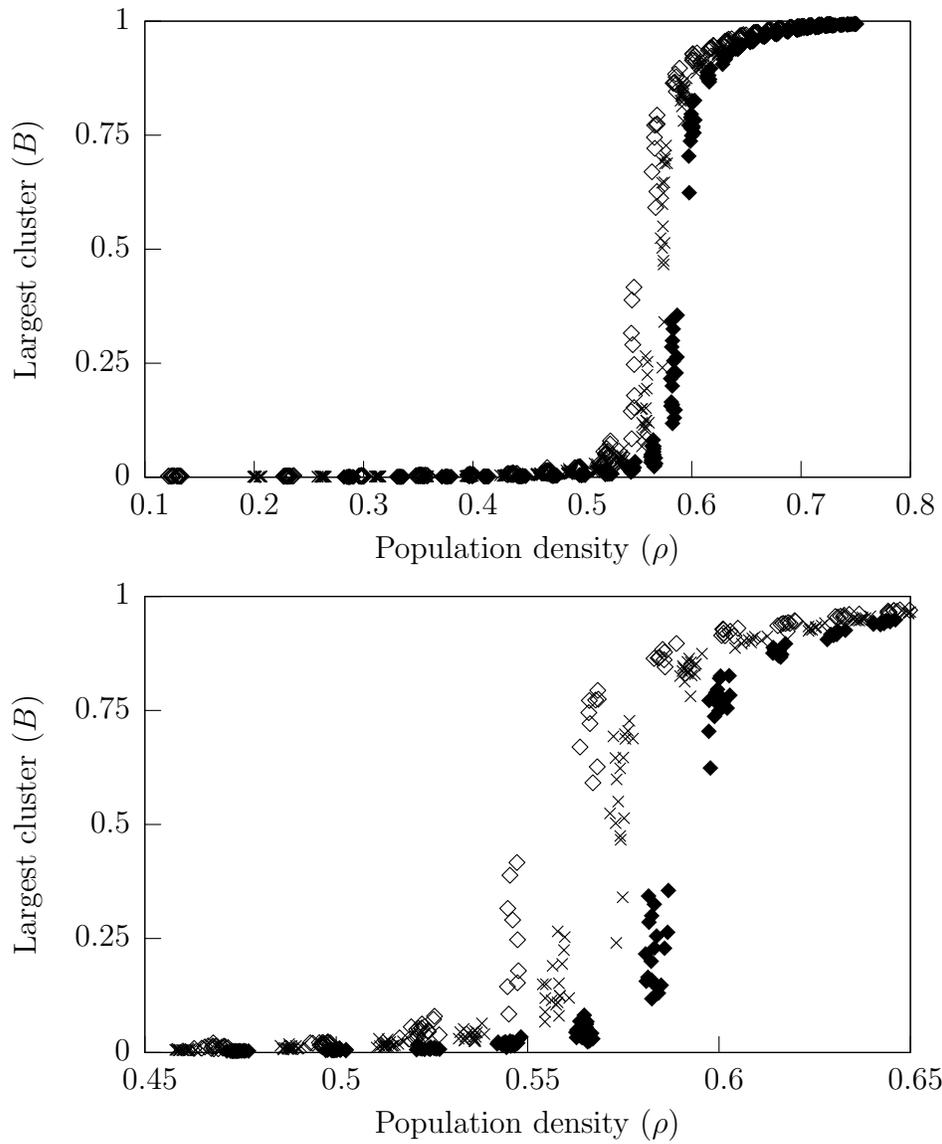


Fig. 1.

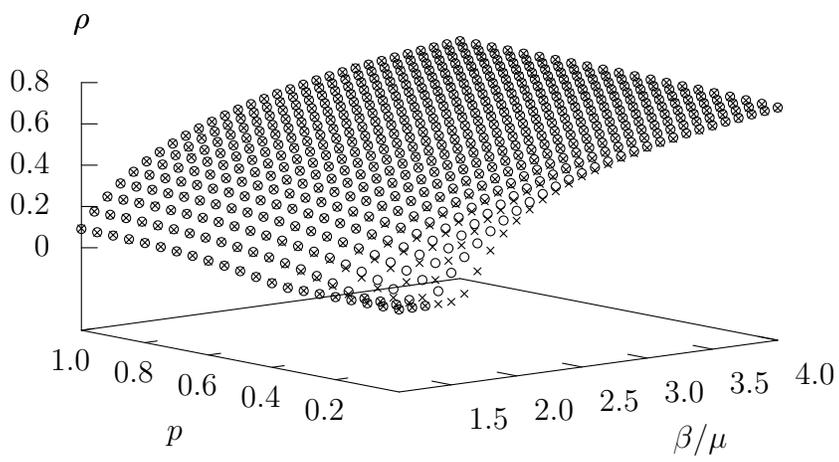


Fig. 2.

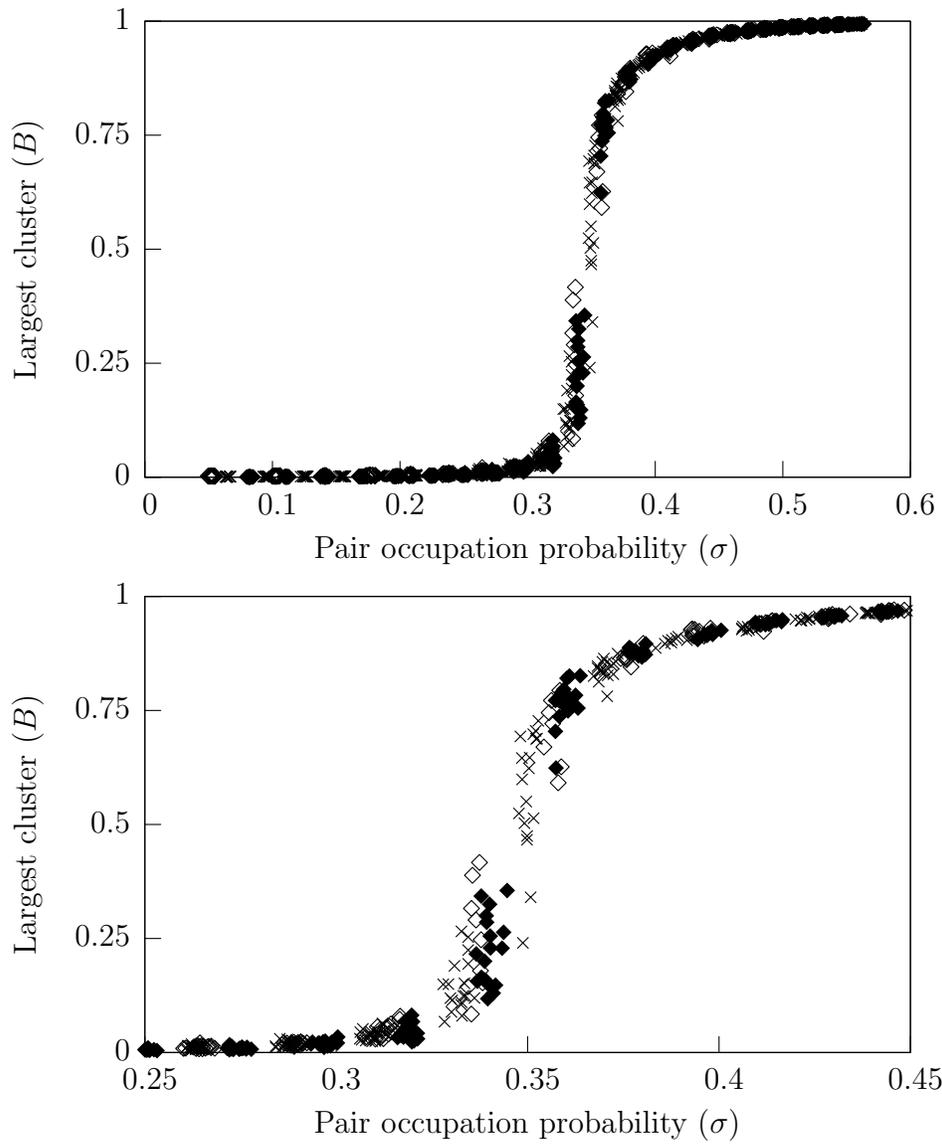


Fig. 3.

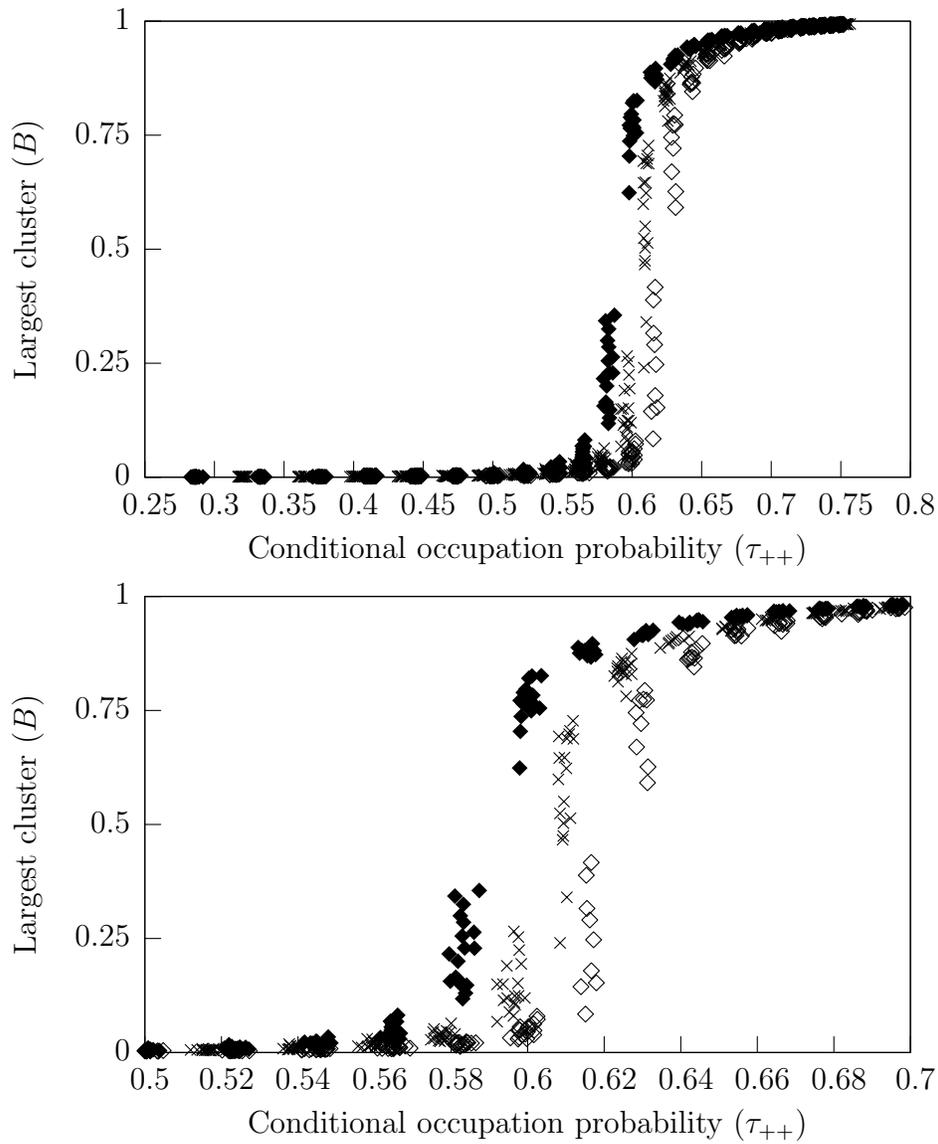


Fig. 4.

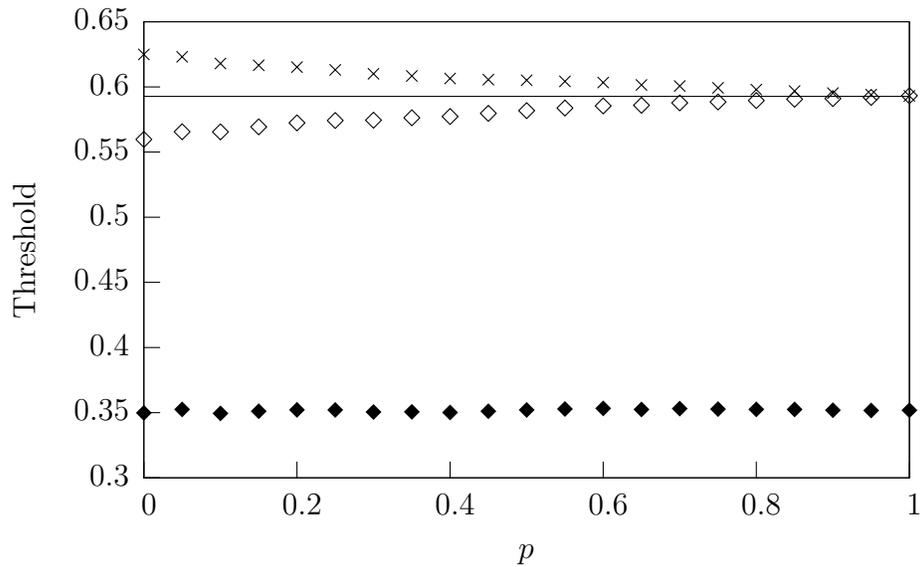


Fig. 5.

Table 1

*Model parameters and other symbols. The first group consists of model parameters; the second, of simulation attributes; and the third, of threshold functions.*

$\beta$	birth rate
$\mu$	death rate
$p$	probability of global birth
$\bar{p}$	probability of local birth
$N$	number of neighbors of a site
$\rho$	population density
$\sigma$	proportion of neighboring pairs which are both occupied
$\tau$ or $\tau_{+/+}$	probability a site is occupied, given that a neighbor is occupied
$\tau_{0/+}$	probability a site is empty, given that a neighbor is occupied
$\tau_{+/0}$	probability a site is occupied, given that a neighbor is empty
$B(\beta, \mu, p)$	proportion of occupied sites in the largest cluster
$\rho_{\text{crit}}(p_0)$	threshold of aggregation, as a function of $\rho$ , for fixed dispersal $p = p_0$
$\sigma_{\text{crit}}(p_0)$	threshold of aggregation, as a function of $\sigma$ , for fixed dispersal $p = p_0$
$\tau_{\text{crit}}(p_0)$	threshold of aggregation, as a function of $\tau$ , for fixed dispersal $p = p_0$