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"Theories of simplification and scaling in ecological systems"

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Theories of simplification and scaling in ecological systems

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INTRODUCTION: THE CHALLENGE OF SCALING

The problem of scaling is at the heart of ecological theory, the essence of understanding and of the development of a predictive capability (Levin 1992). The description of any system depends on the spatial, temporal and organizational perspective chosen; hence it is essential not only to understand how patterns and dynamics vary with scale, but also how patterns at one scale are manifestations of processes operating at other scales (Haury et al. 1978, Levin 1992). Evolution has shaped the characteristics of species in ways that result in scale displacement: Each species experiences the environment at its own unique set of spatial and temporal scales, and interfaces the biota through unique assemblages of phenotypes. In this way, coexistence becomes possible, and biodiversity is enhanced. By averaging over space, time and biological interactions, a genotype filters variation at fine scales and selects the arena in which it will face the vicissitudes of Nature. Variation at finer scales is then noise, of minor importance to the survival and dynamics of the species, and consequently of minor importance in any attempt at description.

Similarly, humans select scales in any attempt to comprehend the patterns of Nature. Order out of chaos is a recurrent theme in scientific investigation, across the broad sweep of natural and social sciences. The notion that what we see is a complex and confusing manifestation of an underlying order can be seen as fundamental to religious philosophy; to Plato's teachings; to the search for grand unifying theories in physics; and even to the practice of psychiatry. Jung wrote "In all chaos there is a cosmos, in all disorder a secret order." In describing natural and unnatural systems alike, we must find ways to suppress the irrelevant detail that cloaks the basic truths, and allow those truths to emerge. This paper is a modest attempt to review some techniques for doing that for a limited class of models of ecological processes.

PATTERN FORMATION

The search for scaling laws is ineluctably intertwined with pattern and process: the detection and description of pattern, and its relation to process. Statistical methodologies are invaluable tools for discovering relationships and suggesting mechanisms, but will not be discussed further in this limited review. The problem of pattern formation and maintenance, however, is central to our theme, and will reassert itself repeatedly throughout this paper. There is no pattern without variation, and the theory of pattern is a theory of how diversity arises in potentially uniform systems, of what limits diversity, and of the apportionment of the causes of diversity among exogenous and endogenous causes. Hence theories of biological diversity echo themes from the literature on pattern (Levin 1978a, 1981, 1988). Again, as in so many aspects of religion, philosophy and science, order arises from an opposition of forces, stimulatory and repressive: *Short-range activation* enhances deviations from uniformity, breaking symmetry and instigating pattern; *long-range inhibition* constrains the spread of novelty. The forces eventually may achieve a sort of balance, such that patterning is sustained. This theme is evident in a number of papers in this book (e.g. Tilman and Lehman [Chapter X], Hubbell [Chapter Y].

The simplest ecological example of pattern forming in this way comes from considering predator-prey systems in which prey move on more limited spatial scales than predators. Prey are activators: A small increase in prey density will stimulate growth of the predator population, and also the prey if an Allee effect exists. But those stimulatory influences will be short-range, limited to the scale on which prey move. On the broader scale of predator movement, the inhibitory influence of predators tends to stabilize pattern, leading to alternating regions of high and low density (Segel and Jackson 1972, Levin 1974).

Similar effects can be seen in the sinusoidal front patterns sometimes seen in wildebeest herds (Gueron and Levin 1993), although the mechanisms are different. Animals have "personal zones" about them, and tend to move away from others that intrude into that space (Hediger 1950). In the model of Gueron and Levin (1993), the consequence is that animals in the lead speed up, and trailing animals slow down, if they are in each other's personal space. This local effect can serve to destabilize an otherwise uniform front, causing inhomogeneities to begin to develop. However, as distances between individuals increase, repulsion is replaced by attraction, as individuals seek to remain with the herd. The result is the maintenance of stable wave-like patterns, again from the balance between short-range activation and long-range inhibition.

The story is, as in these two examples, most easily told in space (Gierer and Meinhardt 1972), which therefore will be the focus of the rest of this paper; but the issue is the same in other dimensions (Levin and Segel 1985, Holling 1992). In Levin and Segel (1982), assortative mating and apostatic selection by predators provide the activation and inhibition that lead to diversity in aspect variables such as wing coloration or pattern; a more general review of such phenomena is given in Levin and Segel (1985). Holling (1992) observes similarly the emergence of non-uniform distributions in various population and ecosystem variables. In particular, through such mechanisms, the dynamics of independent components become entrained and systems self-organize into units that interact strongly within, and weakly (and on longer time scales) with other units (Simon and Ando 1961, Paine 1980). Recognition of the structures that develop becomes key to understanding the dynamical organization of these self-organized networks (Iwasa et al. 1987, 1989, Holling 1992, Kauffman 1993).

In standard usage (see Barenblatt 1994), scaling laws are power laws relating variables, and reflect self-similarity: recapitulation of patterns across scales of space and time. Such self-similar patterns have been observed often in ecological systems and the output of models (Levin and Buttel 1987, Levin 1992, Moloney et al. 1992), and motivate a search for explanation. Scaling laws may be derived phenomenologically based on observations, or through dimensional or other analyses of constitutive laws (e.g. Taylor 1950). To develop understanding, it is best to be able to proceed from mechanistic laws that capture basic interactions, through analysis of how properties change with scale. In physics, e.g. fluid mechanics, those laws may be conservation laws or other relations derived from first principles, and involving properties such as densities. In ecology, first principles are typically expressed at small scales or the level of individuals, and the first step in deriving scaling laws is to simplify the morass of information to derive macroscopic relationships. The next several sections describe ways to do this, in the hope of guiding the search for scaling laws through simplification.

FROM MEAN FIELDS TO INDIVIDUALS

The classical approach to modeling ecological systems (Volterra 1926) ignores space completely, and in essence assumes that every individual is equally accessible to every other individual; the result is a system of differential or difference equations for the mean abundances of the various types. Because every individual is assumed to see the average or mean field, such equations comprise the mean field description of the system.

The mean field approach is a sensible place to begin, but ignores much of what is important about the dynamics of ecological communities. In reality, interactions typically are restricted to a subset of the individuals in the population; more generally, there is a likelihood or preference structure for the probability of interactions between two individuals as a function of the distance between them, either in real space or in some abstract character space. The localization of interactions is known to have a fundamental influence on dynamics; in epidemiology, for example, the potential for spread is fundamentally altered by the presence of highly mixing core groups (Castillo-Chavez et al. 1989, Anderson and May 1991). Furthermore and more generally, the increased potential for persistence and coexistence due to isolation and founder effects (See Levin 1974) has led to selection for a wide variety of traits that allow exploitation of that fact, and that would not be selected in a well-mixed environment. Examples include the familiar life history traits associated with r-selected species- high dispersal capability, dormancy, and the capability for rapid growth in high light environments- but also include competitive strategies such as allelopathy (Chao and Levin 1981, Durrett and Levin 1996) and altruistic strategies such as reduced resource exploitation (Kinzig and Harte 1996, Klopfer *manuscript*). Obviously, spatially structured models are essential to explore such features.

Recognition of the inadequacy of mean field models is not a recent phenomenon. In epidemiology and population genetics, it was acknowledged in the first part of this century (Brownlee 1911, Fisher 1937, Haldane 1948), and the literature is extensive on the use of diffusion models for the spread of advantageous alleles (Fisher 1937, Kolmogorov et al. 1937) and other dynamic aspects of population genetics (Dobzhansky and Wright 1947). In ecology, it was Skellam's seminal paper that stimulated the application of diffusion approximations to the spread of species, and a variety of important ecological issues were addressed through this framework (Skellam 1951, Kierstead and Slobodkin 1953, Okubo 1980, see review in Levin 1976). But such diffusion models, and the diffusion- reaction systems that were introduced by simply adding diffusion terms (plus possibly advection) to the equations for interacting species, are limited in their range of application. In particular, because diffusion models imply infinite speeds of propagation, they prevent the transient isolation that often is essential to persistence of competitively inferior types. Furthermore, the deterministic approach of the diffusion-reaction systems precludes explicit consideration of stochastic terms, such as localized disturbances. As will be discussed later, diffusion limits often can be derived to reflect the mean behavior of stochastic systems; but it is in the limiting process that leads to these approximations, which will differ from the simplistic ones obtained by simply appending diffusion terms to reaction equations, that the rules of scaling become apparent.

Recognition of these limitations has led to a variety of other formulations, including those where space is discrete (patchy) (Levin 1974); among these are the metapopulation models that have attracted considerable interest in recent years in a wide variety of applications (Levin and Paine 1974, Paine and Levin 1981, Pickett and White 1985, Chesson 1986, Gilpin and Hanski 1991). In the last few years, encouraged by rapidly increasing computational capabilities, attention has shifted to individual-based models (DeAngelis and Gross 1992) and spatial stochastic models such as interacting particle models (Durrett and Levin 1994a), in which detailed information concerning spatial distributions is retained. But such models by themselves generate cartoons, and much more detail than we have a right to know. In Book VI of Plato's Republic, Socrates says "The many, as we say, are seen but not known, and the ideas are known but not seen." It is those unseen ideas that must be extracted in order to determine the essence of what is responsible for fundamental patterns; all else is commentary. The extraction process involves the derivation of the scaling laws themselves.

The differences among the various modeling approaches expose the consequences of different modeling assumptions. Durrett and Levin (1994a) compare mean field, reaction-diffusion, metapopulation and interacting particle models of a variety of types of interactions; no two are identical in their predictions. In particular, for systems in which a successional hierarchy is assumed, coexistence is found under certain conditions in the interacting particle and metapopulation models when it would not be possible in the mean field or reaction diffusion descriptions. The reason is apparent: The first two models allow the early colonist to remain isolated sufficiently long that it can build up its local population to a critical size; the infinite speed of propagation in the diffusion models makes this impossible in those representations. It is obvious that the nature of movement and the scale of interactions play fundamental roles in the persistence of species and the maintenance of biodiversity.

RANDOM WALKS AND DIFFUSION

The simplest model of movement is the random walk, which also provides an instructive case study for deriving scaling laws. In particular, we introduce here three familiar approaches to deriving a diffusion limit of a random walk, since these will motivate the three main approaches we exploit for more complicated problems. The simple random walk assumes that individuals do not interact, so the resulting equations are linear in form and fairly simply derived; the fundamental issues are retained, however, when nonlinearities enter.

(i) *Hydrodynamic limits of interacting particle models.* Imagine that individuals are confined to move from point to point on a line, with points being equally spaced at distances δx apart. Assume further that the net flux from site x to site $x + \delta x$ in a small time δt, beginning at time t, is proportional to the difference $N(x,t) - N(x + \delta x, t)$, where $N(x,t)$ is the (expected) number of individuals at x at time t. If the constant of proportionality $D\delta t$ is the same for all pairs of sites, then it follows that N changes according to the rule

$$N(x, t + dt) = N(x,t) + D\delta t[N(x + \delta x, t) + N(x - \delta x, t) - 2N(x,t)] \tag{1}$$

This defines the random walk for a given grid size and given time step. If one allows the time step and lattice size to shrink to zero in a compatible way (that is, so that the series of models with finer and finer steps represent approximations to the same basic process), then (1) gives way in the limit to the familiar diffusion equation

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} \tag{2}$$

(See, for example, Murray 1990 or Okubo 1980). This process works equally well in any number of dimensions, and can be extended to cover situations in which movement is biased or spatially variable.

(ii) *Lagrange to Euler* The approach above focuses attention on a particular location, and simply counts the number of individuals at that site and quantifies the fluxes among sites. An alternative, and equivalent, method is to follow each individual as it makes its way though space. In fluid dynamics, this approach bears the name of Lagrange. Again, one may assume that movement is among points on the line separated by distances δx, and occurring in time steps δt. $N(x,t)$ now reflects the probability that an individual will be found at x at time t; for example, for a point release of individuals, the probability distribution will take a binomial form. In the limit, as δx and δt tend to zero in harmony with one another, the binomial distribution becomes the normal, with variance $2Dt$, and the distribution is again seen to be governed by the equation (2) for any initial distribution. Here D enters through the limit of the ratio of $(\delta x)^2/\delta t$ as both δx and δt go to zero. The end result is the same as in the earlier section, but the process is fundamentally different. Again, extensions to higher dimensions and biased diffusion are straightforward. The limiting equation (2), in the jargon of fluid dynamics, is known as the Eulerian formulation of the problem, after Euler.

(iii) *Moment expansions* The previous two approaches are familiar to anyone who has dealt with the diffusion equation. A third approach, less familiar, uses very different methods, and at the same time makes explicit exactly what is being ignored in the diffusion approximation. In this approach, one assumes that the probability that an individual will be at x at time $t + \delta t$ is given by the integral representation

$$N(x,t+\delta t) = N(x,t)(1-k\delta t) + k\delta t \int N(x-y,t)P(y)dy \tag{3}$$

where the integral is taken over all space.

This reflects the assumption that an individual moves in time δt with a certain probability, and that the distance of movement is not limited to nearest neighbors; rather, it is governed by a probability distribution $P(x)$ for moving a distance x. In the simplest case, $P(x)$ will be a symmetric function decreasing from its (maximum) value at 0; but biased diffusion may be reflected in a non-symmetric P, and movement by "great leaps" may mean that $P(x)$ does not have its peak at 0 (Okubo and Levin 1989), or that long tails or even secondary peaks are possible (Mollison 1977). This approach may be thought of either as providing an Eulerian description of the expected number of particles at x, or as a Lagrangian description of the probability that an individual particle will be at x, at time t.

In this case, the limiting process bears some unique features that distinguish it from the previous two examples. $N(x-y,t)$ must be expanded in a Taylor series about x before δt is allowed to shrink to zero. In the absence of bias, a diffusion term emerges as the lowest order term in the expansion (with coefficient proportional to the variance of P), but the next non-zero term (that of fourth order) modifies that based on the kurtosis of $P(x)$; higher order terms also appear. The resulting equation, if left undisturbed, has infinite order, so the usual assumption is that all terms beyond the leading term are negligible, resulting in the standard diffusion equation. More generally, however, one might retain the fourth-order term as a correction (Cohen and Murray 1981, Levin and Segel 1985), or seek to represent it in terms of the variance so that a modified diffusion equation results. If the fourth-order term is not discarded, one can obtain phenomena (such as Mollison's "great leaps forward" or stabilization of the front of advance) that are not possible in the second-order (diffusion) approximation.

Equation (2) provides detailed spatial information regarding the dynamics of a homogenous spatial stochastic process. If one integrates with respect to space, one finds reassuringly that

$$< dN/dt >= 0, \tag{4}$$

where $<>$ denotes the expectation at any point in space; this confirms the fact that movement is a conservative process. Adding the possibility of birth (or death) anywhere at net per capita rate r yields the equation

$$\frac{d}{dt} < N >=< \frac{dN}{dt} >= r < N >, \tag{5}$$

implying exponential growth of the mean.

Nonlinearities introduce another level of complexity, however. If, for example, deaths depend on the density in some neighborhood, the averaging process involves variance and spatial correlations; the dynamics of $d < N > /dt$ are not closed. In this case, one must either "close" the system by representing the higher moments in terms of the mean, or complement the basic equation with equations for the moments, ultimately closing the system at a later point. We return to this "moment closure" problem in §VII.

RENORMALIZATION AND SCALING

The scale of a process is the range over which it varies according to some criterion, or simply the range over which measurements are averaged. Scaling laws, in their simplest form, are power-law relationships among measurements made at different scales, as seen in subjects from autecology (Peters 1983, Harvey and Pagel 1991) to physics (as in Kepler's laws) to clouds and coastlines (Mandelbrot 1977). Kadanoff (1966) suggests that they occur when a system, over some range, "looks the same on all length scales." Goldenfeld (1992) argues that this is not quite correct, but a good starting point for discussion. The formal approach is through renormalization groups (Wilson 1983, Goldenfeld 1992), which makes rigorous the scaling process through the derivation of equations for blocks of cells in terms of the units that make them up, then iterates the process. Thus, the methods discussed in the preceding section may be seen as steps towards a theory of renormalization for spatial stochastic systems in ecology.

The theory of renormalization groups arose to deal with the phenomenon of critical phenomena and phase transitions in physics (Ma 1976); similar phase transitions occur in many spatial problems in ecology, and suggest parallel approaches, see e.g., Solé et al. 1995-96. Consider, for example, the introduction of a species into an environment where a competitor is already established. Our starting point (Durrett and Levin 1994b) is the interaction between two species whose dynamics are specified by the interaction matrix

$$M = \begin{bmatrix} a & b \\ c & d \end{bmatrix} \tag{6}$$

The terms of the matrix M are assumed to specify the net payoffs to each type when interacting with individuals of a particular type. Thus, a is the payoff for type 1 when dealing with type 1, b is the payoff for type 1 versus type 2, etc. In the mean field version, this leads to the equations

$$\begin{aligned} \frac{dH}{dt} &= H(a\frac{H}{H+D} + b\frac{D}{H+D} - k(H+D)) \\ \frac{dD}{dt} &= D(c\frac{H}{H+D} + d\frac{D}{H+D} - k(H+D)) \end{aligned} \tag{7}$$

in which a, for example, now should be interpreted as the mean per capita growth rate for type 1 in a region in which type 2 is rare, etc. Here, k indicates a density-dependent death rate (A density -independent component of mortality is included in the "game" matrix M). For definiteness, we assume first

$$M = \begin{bmatrix} .7 & .4 \\ .4 & .7 \end{bmatrix}, \tag{8}$$

which reflects the fact that individuals do better in the company of their own type. For this system, then, initial conditions will have an important influence on which type prevails.

Gandhi et al. (1996), considering a variant on this system in which space is a continuum and every randomly-walking individual carries an interaction neighborhood with it, show that, at low initial densities of the invader, the system specified by (8) is well-described by the mean-field approximation; at higher initial densities, however, the situation is more complicated, and a phase transition (shifting dominance to the invader) occurs when the initial density exceeds the density of the resident. Close to the critical point, power-law behavior prevails; that is, the time to extinction of the losing type increases as a power of the initial density.

Simulations show that, away from the critical point, the density of the introduced type is everywhere low. Every invader individual is surrounded by individuals of the opposite type, and the invasion is quelled before it can get started. No beachheads are established, and the system remains essentially spatially homogeneous; hence, mean field theory is applicable. Beyond a threshold introduction density, however, the rare type forms monospecific clusters within a sea of the common type on a rapid time scale (Fig. 1). On a much longer time scale, those clusters shrink in proportion to their surface curvature and diffusion (Gandhi et al. 1996), leading to a relationship of the form

$$\frac{dR}{dt} \sim -\frac{\mu}{R} \tag{9}$$

in which R is the radius of a cluster and μ is the diffusion constant associated with individual movement.

Integration shows that the extinction time of a cluster is thus proportional to R_0^2/μ, where R_0 is the initial size of a cluster. From this, it follows that the extinction time satisfies a power law scaling in relation to initial density. The agreement of theory and simulation can be seen in Fig. 2 where, for large grid size, the time to extinction is shown as a function of initial density. Note the agreement between mean field theory and the simulations for low initial density, and the scaling near the threshold x_c, where a phase transition takes place.

One can approximate the spatial dynamics of this model in the traditional manner, by appending diffusion terms to the mean field equation (7) to yield the classical reaction diffusion system

$$\begin{aligned}
\frac{\partial H}{\partial t} &= \Delta u + \{H(a\frac{H}{H+D} + b\frac{D}{H+D} - k(H+D))\} \\
\frac{\partial D}{\partial t} &= \Delta v + \{D(c\frac{H}{H+D} + d\frac{D}{H+D} - k(H+D))\}
\end{aligned} \tag{10}$$

Here space has been normalized so that the diffusion coefficients (assumed to be identical) equal unity. Simulations of these equations produce patterns (Fig. 3) that capture the mean features of the spatial dynamics (see Gandhi et al. 1996, Durrett and Levin 1994b), and assure eventual extinction of one type (depending on initial conditions). However, this phenomenological approach to deriving a diffusion approximation for the spatial stochastic process does not work in general (Durrett and Levin 1994b). The more appropriate way to this end is to derive a hydrodynamic limit, starting from an individual based formulation and proceeding formally. An example is given in the next section.

HYDRODYNAMIC LIMITS OF PARTICLE SYSTEMS

The process of taking hydrodynamic limits is a standard one, but often difficult when interactions are nonlinear. To illustrate this point, we modify the matrix (6) from the form (8), replacing it by

$$M = \begin{bmatrix} -.6 & .9 \\ -.9 & .7 \end{bmatrix} \tag{11}$$

This is usually termed *prisoners' dilemma*, but we more generally use the nomenclature *hawks* and *doves* for the two species.

As will be described below, we also will for simplicity modify the scheme describe in the previous section to assume a fixed spatial grid divided into cells. For this example, type 1 (termed hawks) outcompetes type 2 (termed doves) under any conditions, but hawks drive themselves to extinction when isolated. Doves, in contrast, always lose out in competition, but are self-sustaining in the absence of hawks (see Durrett and Levin 1994b).

In the mean field version of the dynamics, the outcome is straightforward and unequivocal: Hawks eliminate doves, then drive themselves to extinction. Spatial localization can be achieved naively by again adding diffusion terms to the equations (7), but the result is the same. Under random initial spatial conditions, some areas initially are taken over by doves, others by hawks; on a longer time scale, however, the clusters of hawks form advancing fronts or blobs that take over the system, followed by waves of death as the hawks drive themselves to extinction.

A more biologically realistic way to introduce space is to treat individuals as individuals, which is both politically and mathematically correct. Space (two dimensions) is divided up into cells centered at the nodes of the integer lattice $S = Z^2$, where Z is the set of all integers. Let $\eta(t,x)$, $\zeta(t,x)$ represent the numbers of hawks and doves respectively in the unit square centered at the lattice point x; η and ζ are both integers. The dynamics are reflected by three processes, each with its own characteristic range:

Migration: Each individual, at rate μ, changes its location to a randomly chosen site within a neighborhood N_1. The notion of rate means that time is treated as continuous, and that $\mu h + o(h)$ is the probability that the event (movement) will occur in a small time step h. The notation $o(h)$ indicates a term of an order negligible relative to h for h small.

Mortality: Death may occur either due to the density independent term buried in M, or due to density dependence at rate $k\{\eta(t,x) + \zeta(t,x)\}$, where here the squiggly brackets indicate that η and ζ are averaged over a neighborhood N_2.

Game step: The interactions specified by M are also localized, with their own characteristic neighborhood N_3. Dynamics are as in the mean field version, except that the relevant densities used in determining growth rates are the averages of η and ζ taken over N_3; the average can be chosen to be a weighted one, with for example nearer neighbors bearing greater influence. We ignore that complication here.

The interacting particle system specified above has very different dynamics than the mean field or reaction diffusion systems. Locally, the dynamics are exactly as for the mean field system: Hawks eliminate doves, then themselves. But if N_3 is sufficiently small, that dynamic simply create gaps – targets of opportunities for doves to reestablish themselves. The system has the potential to persist indefinitely (the expected persistence time, of course, depends on grid size in any simulations). Although phrased in terms of hawks and doves (or more strictly, players in "prisoner's dilemma," the model works equally well for epidemiological systems (susceptibles and infectives), or for obligate successional series.

As already mentioned, adding diffusion terms to the mean field equations does not lead to fundamentally different dynamics, and hence does not provide a good approximation to the interacting particle system (ips). There is a way, however, to derive a "hydrodynamic" diffusion limit that does capture the essential feature of the particle system: persistence. Recall that, in the ips, individuals are units. Imagine, as in the previous section, that each such individual is performing an independent random walk on the grid; it may be established then that the joint distribution of the number of individuals in any finite subset of the grid will converge to one specified by independent Poisson variables. This is the critical step in the limiting process, and the same assumption will reappear in the next sections. If migration occurs on a much faster time scale than births and deaths, sites near x at time t may be treated as independent, so that the numbers of hawks and doves are Poisson with means $u(x,t)$ and $v(x,t)$ respectively. If the spatial step is now shrunk to zero, as before (specifically, individuals on a lattice with spacing ϵ perform random walks at a rate that scales with $1/\epsilon^2$), u and v may be shown in the limit (see Durrett and Levin 1994b) to satisfy a set of reaction diffusion equations

$$\begin{aligned}\frac{\partial u}{\partial t} &= \Delta u + u\{r + g(a\frac{u}{u+v} + b\frac{v}{u+v}) - k(u+v)\},\\ \frac{\partial v}{\partial t} &= \Delta v + v\{s + g(c\frac{u}{u+v} + d\frac{v}{u+v}) - k(u+v)\}\end{aligned} \qquad (12)$$

where Δ is the two dimensional Laplacian (sum of second partial derivatives); r and s are the net birth rates of isolated hawks and doves; and

$$g = g(u,v) = 1 - \exp(-|N|(u+v)), \tag{13}$$

where $[N]$ is the number of points in the neighborhood N_3. Note that the effect of the "proper" limiting process is a set of equations that introduces the standard diffusion term, but modifies the dynamic equations to minimize the importance of the hawk- dove interaction at low densities (g vanishes as $u, v \to 0$). The significance of this is that small isolated dove populations are protected from invasion by "nanohawks" (Mollison 1977) moving at faster than the speed of light, and are able to build up local densities. The modified dynamical system, with diffusion suppressed, now has a globally attracting equilibrium, and so will persist .

FROM LAGRANGE TO EULER

The second method introduced for deriving macroscopic laws for nonlinear systems begins by following an individual as it moves through space, leading to a Lagrangian description of the dynamics. In this approach, typically, one deals either with effects on the acceleration of an individual (e.g. Sakai 1973, Okubo 1986, Grünbaum 1992), or on the velocity (Aoki 1982, Huth and Wissel 1990, Gueron and Levin 1993). For the purposes of this discussion, we will use the Newtonian momentum focus on accelerations, leading to an equation for the acceleration of an individual in terms of the forces acting upon it. These forces will include density-dependent ones for example inherited from the fluid dynamics, or representing taxis with regard say to thermal or chemical signals that are not generated by other individuals; they will also include the nonlinear responses of individual to the location, densities or velocities of other individuals. Models of this sort have been used widely to simulate animal grouping (see for example Heppner and Grenander 1990, Grünbaum 1992, 1994).

To proceed to the Eulerian description of this system (in one dimension), the nonlinear equivalent of (2), one must determine the flux $J(x,t)$ and average velocity $U(x,t)$ of individuals, with the objective of deriving an equation for the density distribution $p(x,t)$. Typically, one seeks a conservation equation

$$\frac{\partial p}{\partial t} = -\frac{\partial J}{\partial x} \tag{14}$$

where $J = pU$ (Grünbaum 1992); the challenge is to relate U to individual behaviors. As in the preceding section, one way to do that is to assume that the distribution of neighbors is Poisson, with mean given by the density distribution. Making this assumption allows one to proceed (non-trivially) to an Eulerian description, typically including integral terms (reflecting the fact that individuals are responding to the dynamics of other individuals in a non-vanishing neighborhood of their location Grünbaum 1992, 1994). A similar partial-differential integral formulation will appear in the next section, in a quite different context, but for similar reasons.

MOMENT EXPANSIONS AND MOMENT CLOSURE

The application of moment methods to spatial stochastic processes is well illustrated with a simple model, the contact process, which then can be generalized to a widely-used forest growth simulator. In the basic contact process (Durrett and Levin 1994a), cells are either occupied or empty. Occupied cells may become extinct at rate δ, or colonize empty neighbors at rate λ, so that the dynamics of the mean probability of occupancy is (Durrett and Levin 1996).

$$\frac{du(1)}{dt} = -\delta u(1) + n\lambda u(01), \tag{15}$$

where n is the number of neighboring cells considered, $u(1)$ is the probability a cell is occupied, and $u(01)$ is the probability that an ordered pair of cells will be in the configuration unoccupied-occupied. (12) specifies the dynamics of the mean, but does not provide a closed description. To close it, one either must make some assumption about how $u(01)$ relates to $u(1)$ (in the mean-field approximation, for example, $u(01) = u(1)[1 - u(1)]$, or write an equation for the dynamics of $u(01)$. The trouble with this is that the latter equations will include terms like $u(001)$ and other triples. The system of equations for the moments, essentially for the moment-generating function, is infinite, unless truncated by a closure rule at some point. The hope is that higher order approximations (truncation at a later stage) will lead to greater accuracy, but that depends upon the particular dynamics. For (15), the second order approximation, say with $n = 4$, appends a second equation

$$\dot{v} = -(\lambda + \delta)v + \delta(u - v) - 3\lambda v \frac{(2v + u - 1)}{(1 - u)} \tag{16}$$

to (15), where $u = u(1), v = u(01)$.

This decoupling approximation, called pair-approximation (Matusda et al. 1992), has been carried out for many models of population dynamics of plants (Harada and Iwasa 1994, Harada et al. 1995), and sometimes predicts qualitative results accurately when mean-field dynamics fail (e.g. Sato et al. 1994). Although the pair-approximation is not accurate in the basic contact process near critical values, it is surprisingly accurate if the system includes a small random long range dispersal that makes the spatial pattern closer to random (Harada and Iwasa 1994). The same tendency has been seen for point processes, such as the forest model SORTIE (Bolker and Pacala 1996).

The second-order approximation not only gives improved estimation of the actual dynamics (Fig. 4), but also provides information on biologically important clustering (Fig. 5). The contact process is a prototypical model for forest growth, species invasion, epidemic spread and forest fire (see e.g. Durrett 1988). Its wide-reading applicability is reflected in its appearance (in modified form) throughout this book (see, for example, Chapters X,Y and Z). Furthermore, extending ideas of Hubbell (1992, 1995 and Chapter Z, this volume), Durrett and Levin (1996) use generalizations of this model to derive species-area relationships, prototypical scaling laws.

Moment closure methods can be applied whenever there is variation in some characteristic, be it with regards to space, functional properties, or the uncertainty associated with a particular realization of a stochastic process. For example, consider the problem of competition between two species, distributed across two patches. It is easy to show (Levin 1978b), that under local Lotka-Volterra dynamics, and conservative coupling, the equations for the spatial means of the two species are

$$\begin{aligned}\frac{d\bar{u}}{dt} &= r\bar{u}(k - a\bar{u} - b\bar{v}) - ra\sigma_u^2 - rb\ cov(u,v)\\ \frac{d\bar{v}}{dt} &= s\bar{v}(L - c\bar{u} - d\bar{v}) - sc\ cov(u,v) - sd\sigma_v^2\end{aligned} \tag{17}$$

in which σ_u^2 and σ_v^2 are the spatial variances of u and v. If the densities in the two patches are identical, mean field theory works perfectly and the variance, covariance terms vanish. More generally, however, the system (17) is not closed, and must be extended to include closure rules, or equations for the variances and covariances (which in turn must be closed or extended). When more patches are involved and movement is not purely local, the entire spatial correlation function may be implicated, as we discuss in the next example.

For a spatial stochastic process, one may consider either spatial or ensemble moments, where "ensemble" refers to the set of all possible realizations of the stochastic process. Under appropriate assumptions, including those discussed here, the process is ergodic, and there is an equivalence between spatial and ensemble moments; other examples discussed in this paper would not, however, simplify in this way.

The same approach can be applied to more sophisticated "contact" processes, in continuous space, such as neighborhood models with finite dispersal or the forest growth simulater SORTIE. For example, in a single species version of this model (see Bolker and Pacala 1996), discussed in more detail in Pacala and Levin (this volume), births to an individual at a site in continuous space are determined by a weighted function of densitites of individuals in a neighborhood of the focal individual, with a weighting that decreases with distance. Again, all processes are stochastic, and one takes expectations over the infinite ensemble of possible realizations, obtaining a description of the form

$$\frac{dn}{dt} = H(n) - \alpha \int_{-\infty}^{\infty} U(r)c(r)dr, \tag{18}$$

where n is mean occupancy.

Here $H(n)$ is a term that depends on n alone (the "mean field" term), $U(r)$ is the *competition kernel*, and $c(r)$ is the covariance at lag r. Once again, (18) gives the dynamics of n in terms of variables other than n, so the system is not closed. The approach then is to complement (18) with a second equation, a partial differential integral equation, for the dynamics of $c(r)$, and then to close the series by making appropriate assumptions about the higher moments. This powerful approach is developed further in Pacala and Levin (this volume).

SUMMARY

In this paper, we have introduced a number of approaches to describing simplification and scaling laws for spatial stochastic ecological models. Scaling laws are power law relationships that relate measurements on one scale to another; but the techniques of simplification provide more general ways to develop quantitative relationships among phenomena on different scales. Through a series of examples, we introduce the classical notions of hydrodynamic limits of particle systems, and Eulerian descriptions of individual-based (Lagrangian) models. Though different in detail, there are remarkable similarities in how the limiting processes are carried out.

In the last quarter-century, especially since the work of Kadanoff and Wilson, renormalization methods have provided a powerful approach to developing scaling laws. The use of moment closure techniques bears relation to renormalization, and is discussed in considerable detail. In general, approaches to simplification and scaling hold the potential to revolutionize the modeling of spatial dynamics in ecology. Further examples are given in Pacala and Levin (this volume); the ultimate goal is to show, through scaling, what detail, either in real systems or individual-based simulations, is essential to understanding pattern and process on higher scale. Without such rules, the modeling process lacks robustness; with it, we may achieve genuine understanding of spatial dynamics.

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FIGURE CAPTIONS

Fig. 1 Snapshots from simulation at $t = 0, 15, 30, 45, 60, 75$ (see text). S_1 particles are light grey and S_2 particles are black. The run required a million particles on an 128×128 grid (from Gandhi et al. 1996).

Fig. 2 Time to extinction as a function of initial density; x_c is density of resident type. Solid line is mean-field approximation; dotted line is approximation from surface-effect theory. Linear dimension of grid is 256 ◇, 128 +, 64 □, 32 × (modified from Gandhi et al. 1996).

Fig. 3 Snapshots from a simulation of the reaction-diffusion system at $t = 50, 100, 200, 650$. Initial conditions correspond to setting initial density of invader at $.99x_c$, grid size at 256×256. Black corresponds to areas occupied by S_2 and white corresponds to areas occupied by S_1. Notice that the PDE captures the formation of clusters and their evolution through surface effects (from Gandhi et al. 1996).

Fig. 4 Occupancy fraction as function of recovery rate δ, for contact process. ◇ is simulation, ○ is mean-field approximation, + is pair approximation (from Levin and Durrett 1996).

Fig. 5 Correlation structure, expressed as proportion of pairs in unoccupied/occupied configuration, versus recovery rate for contact process. ◇ is simulation, ○ is mean-field approximation, + is pair approximation (from Levin and Durrett 1996).

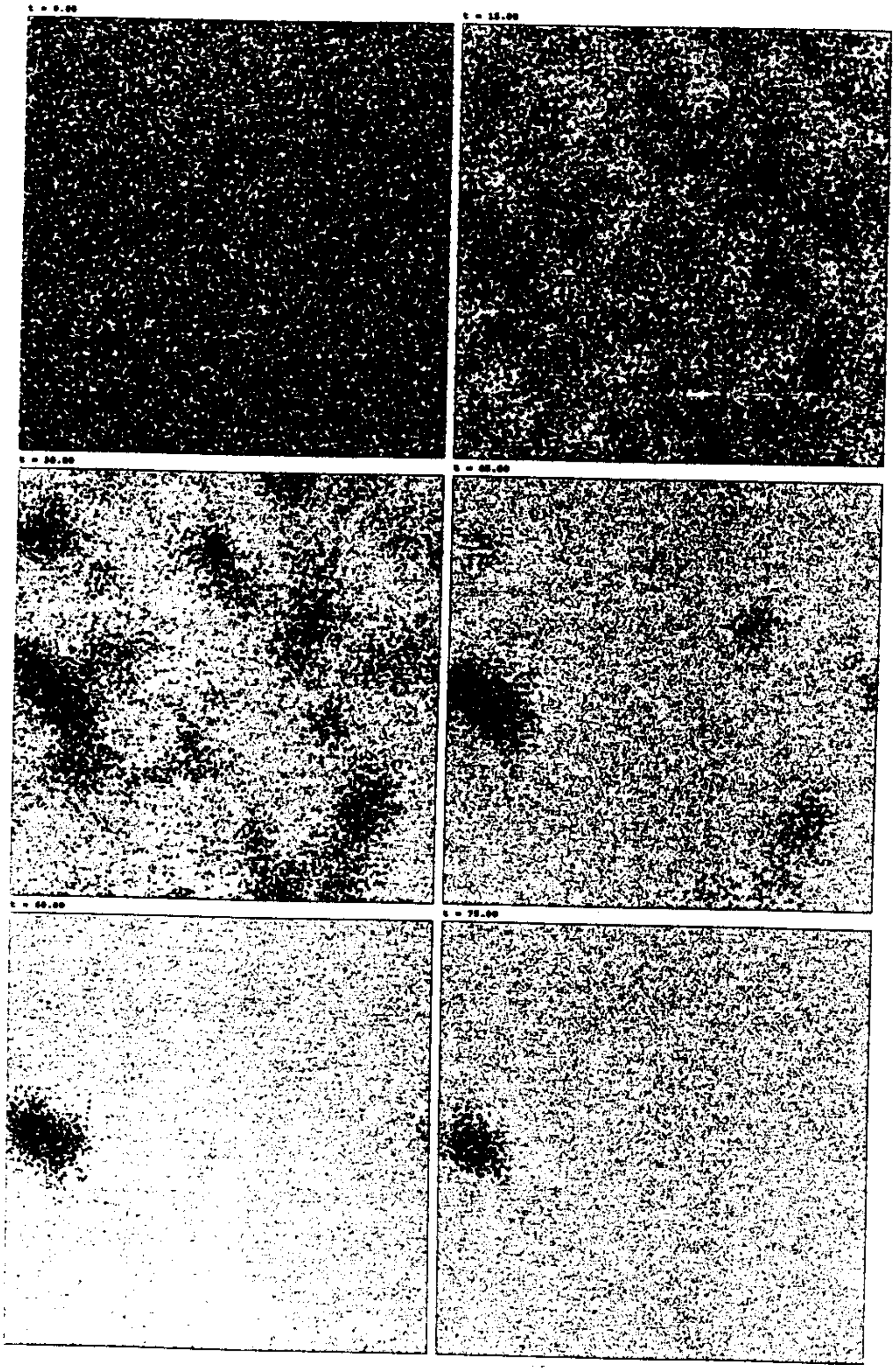

Figure 1

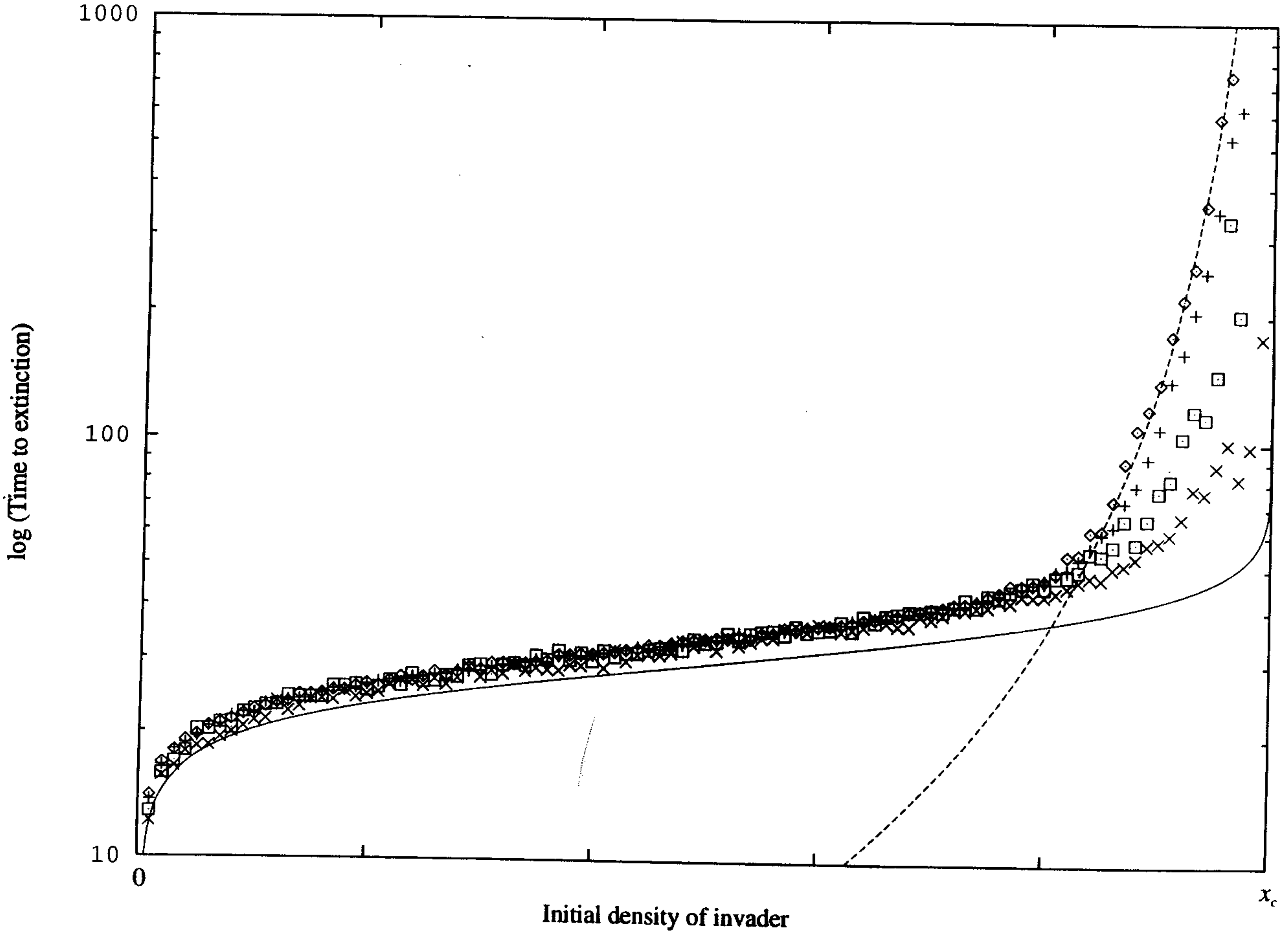
1000
100
10
0
x_c
log (Time to extinction)
Initial density of invader

Figure 2

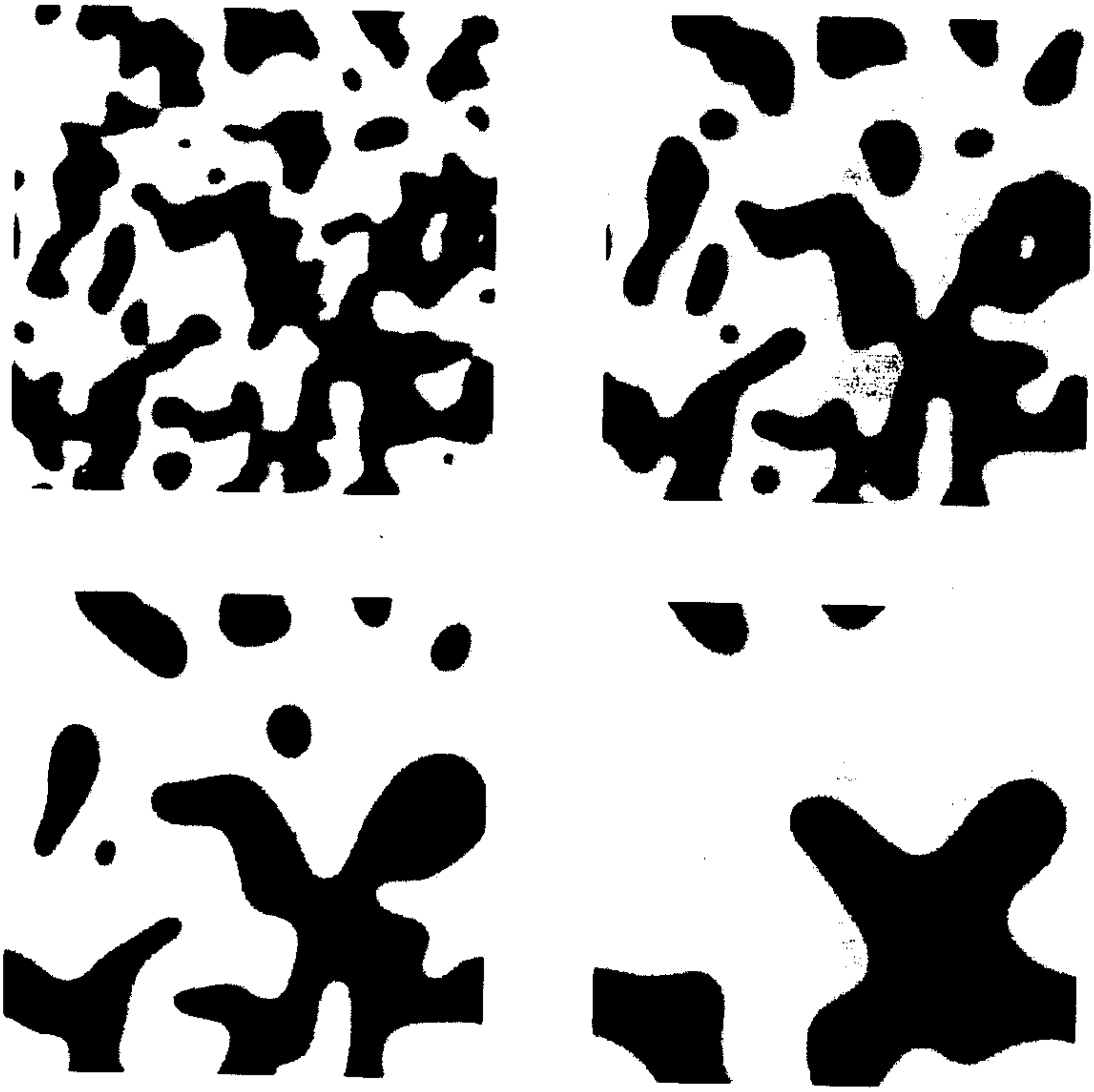

Figure 3

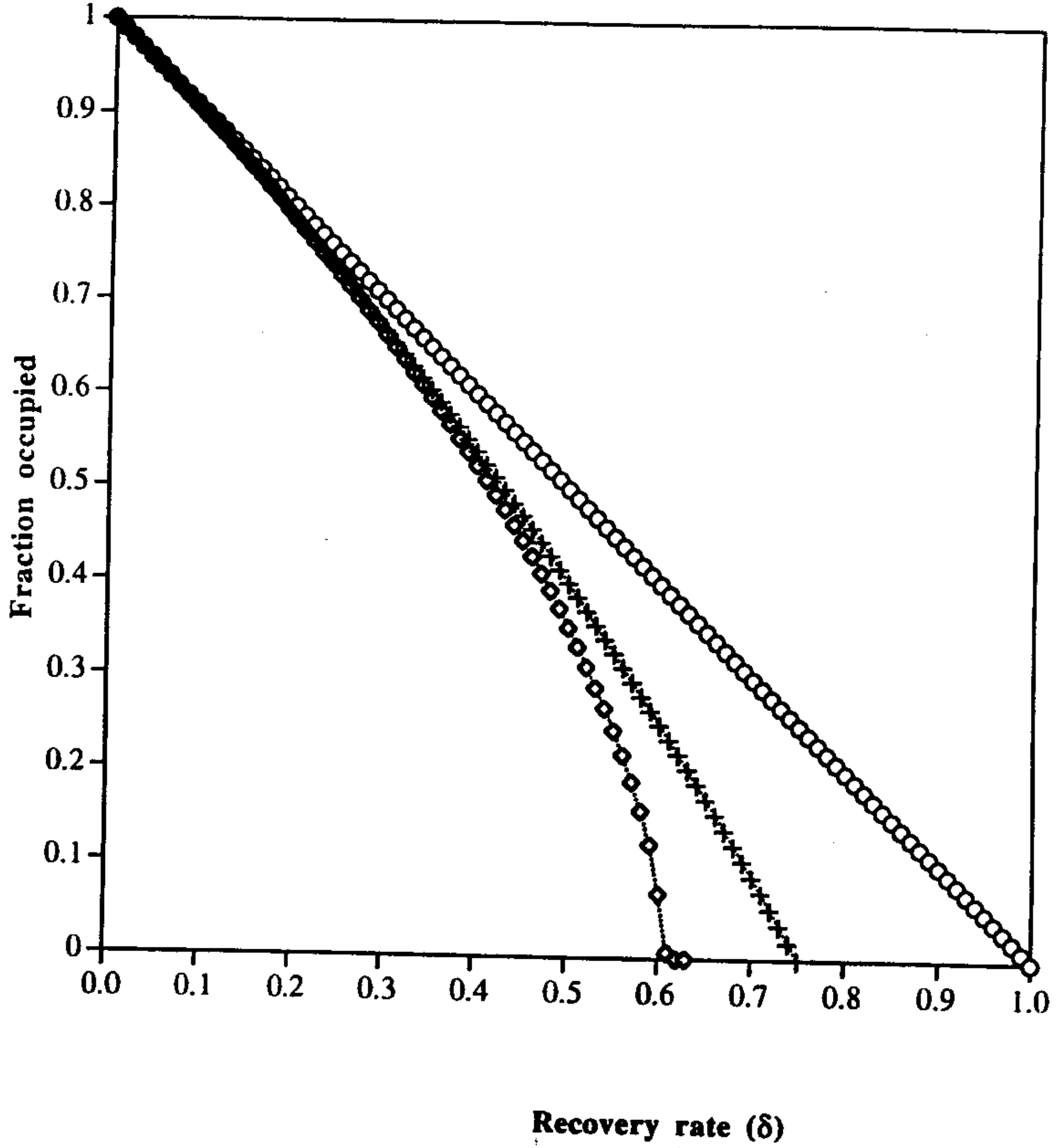
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Fraction occupied
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Recovery rate (δ)

Figure 4

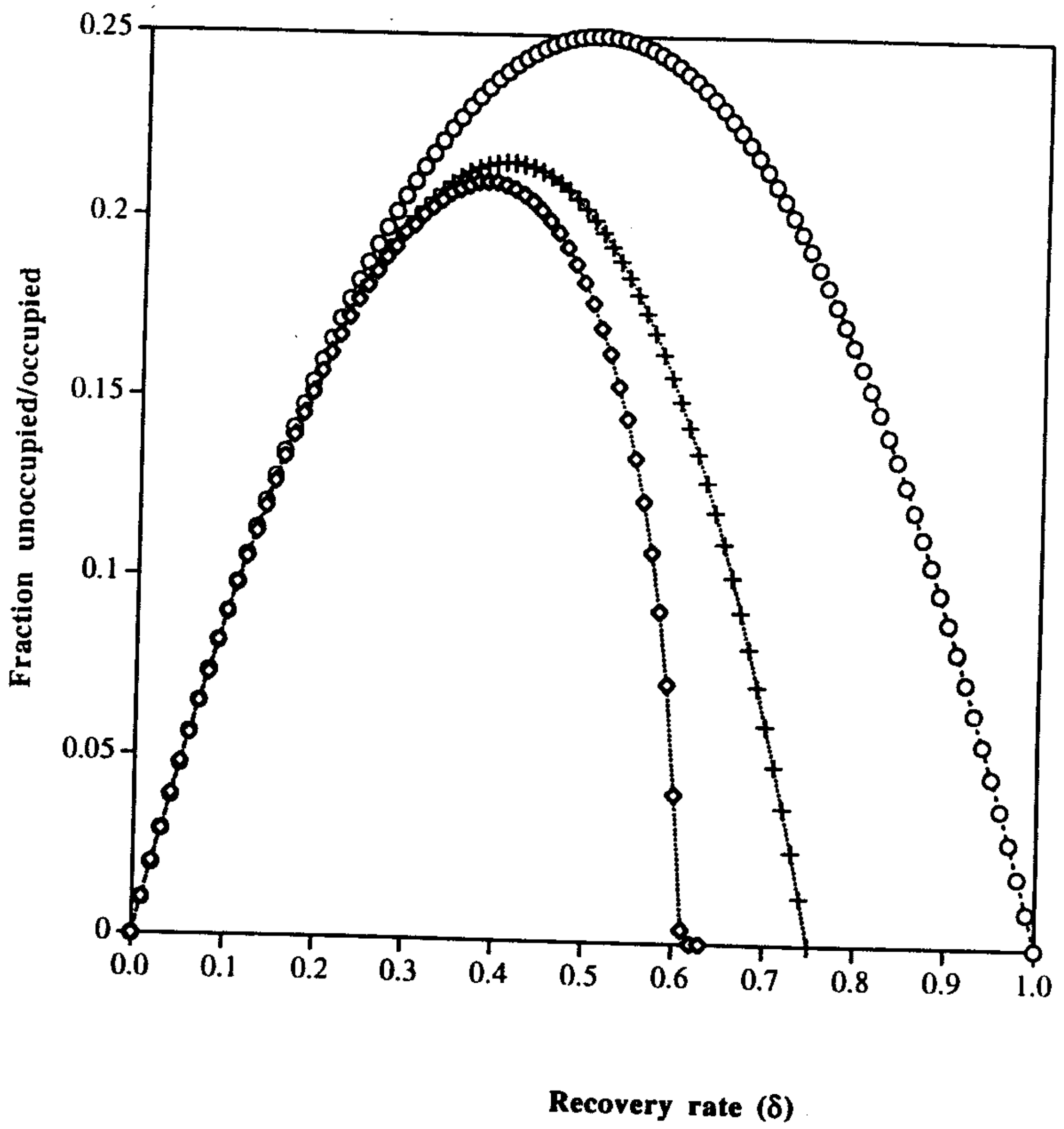
0.25
0.2
0.15
0.1
0.05
0
Fraction unoccupied/occupied
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Recovery rate (δ)

Figure 5

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