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**THEORIES OF SIMPLIFICATION  
AND SCALING OF SPATIALLY DISTRIBUTED  
PROCESSES**

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## CHAPTER TWELVE

# Theories of Simplification and Scaling of Spatially Distributed Processes

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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 to understand not only how patterns and dynamics vary with scale, but also how patterns at one scale are manifestations of processes operating at other scales (Haury, McGowan, and Wiebe 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.

In attempting to model ecological interactions in space, contributors throughout this book have struggled with a trade-off between simplification and "realistic" complexity and detail. Although the challenge of simplification is widely recognized in ecology, less appreciated is the intertwining of

scaling questions and scaling laws with the process of simplification. In the context of this chapter, simplification will in general mean the use of spatial or ensemble means and low-order moments to capture more detailed interactions by integrating over given areas. In this way, one can derive descriptions of the behavior of the system at different spatial scales, which provides the essentials for the extraction of scaling laws by examination of how system properties vary with scale.

#### 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 they 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 chapter. 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* constraints 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 chapters in this book (e.g., Lehman and Tilman, Chapter 8).

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 do 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 wavelike 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 chapter, but the issue is the same in other dimensions (Levin and Segel 1985; Holling 1992). 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 timescales), 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, Levin, and Andreasen 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, for example 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) simplifies by ignoring 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 it 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.

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, Petrovsky, and Piskunov 1937) and other dynamic aspects of population genet-

ics (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 reaction-diffusion 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 reaction-diffusion 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 1994b), 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 and of the different scales of biological interactions they represent. Durrett and Levin (1994b) 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.

#### 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 next section

may be seen as steps toward 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, for example, Solé et al. (1996). Consider, for example, the introduction of a species into an environment where a competitor is already established. Our starting point (Durrett and Levin 1994a) is the interaction between two species whose dynamics are specified by the interaction matrix

$$M = \begin{bmatrix} a & b \\ c & d \end{bmatrix}. \quad (12.1)$$

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

$$\begin{aligned} \frac{dH}{dt} &= H \left[ a \frac{H}{H+D} + b \frac{D}{H+D} - k(H+D) \right] \\ \frac{dD}{dt} &= D \left[ c \frac{H}{H+D} + d \frac{D}{H+D} - k(H+D) \right] \end{aligned} \quad (12.2)$$

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

$$M = \begin{bmatrix} 0.7 & 0.4 \\ 0.4 & 0.7 \end{bmatrix}, \quad (12.3)$$

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, Levin, and Orszag (1998), 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 matrix 12.3 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 low everywhere. 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 timescale (Figure 12.1). On a much longer time scale, those clusters shrink in proportion to their surface curvature and diffusion (Gandhi et al. 1998), leading to a relationship of the form

$$\frac{dR}{dt} \sim -\frac{\mu}{R} \quad (12.4)$$

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

Integration shows that the extinction time of a cluster is thus proportional to  $R_0^2/\mu$ , 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 Figure 12.2 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.

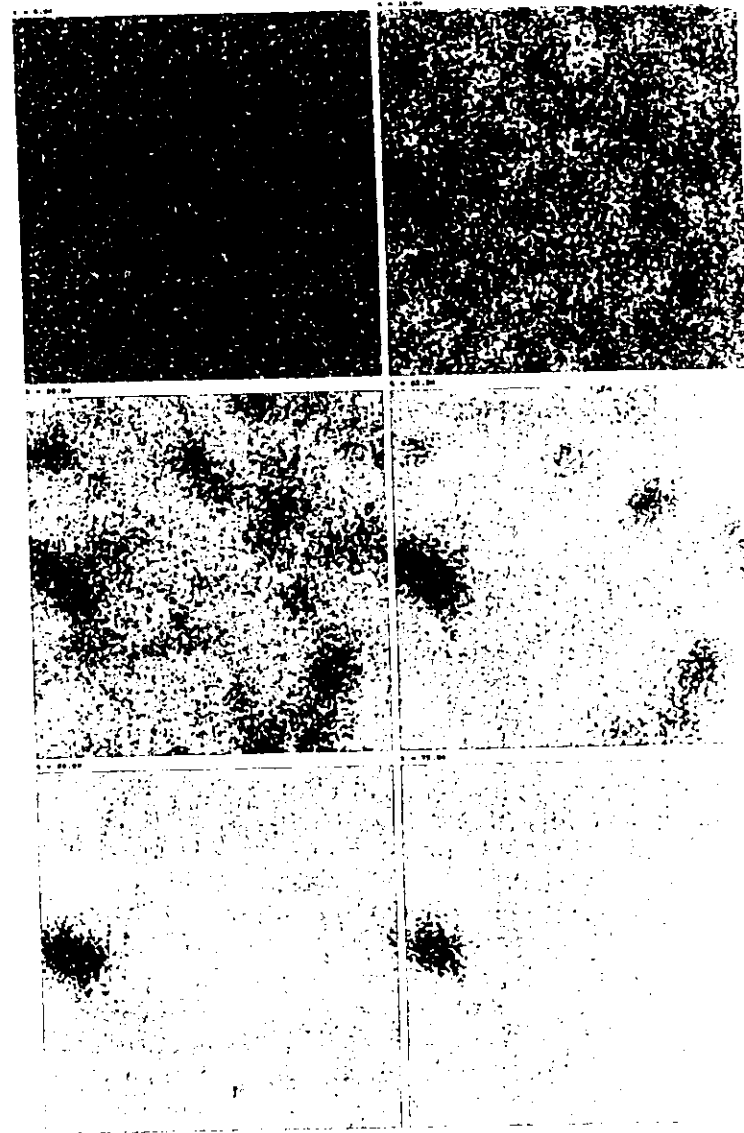


FIGURE 12.1. Snapshots from simulation at  $t = 0, 15, 30, 45, 60, 75$  (see text).  $S_1$  particles are light gray, and  $S_2$  particles are black. The run required a million particles on an  $128 \times 128$  grid (from Gandhi et al. 1998).

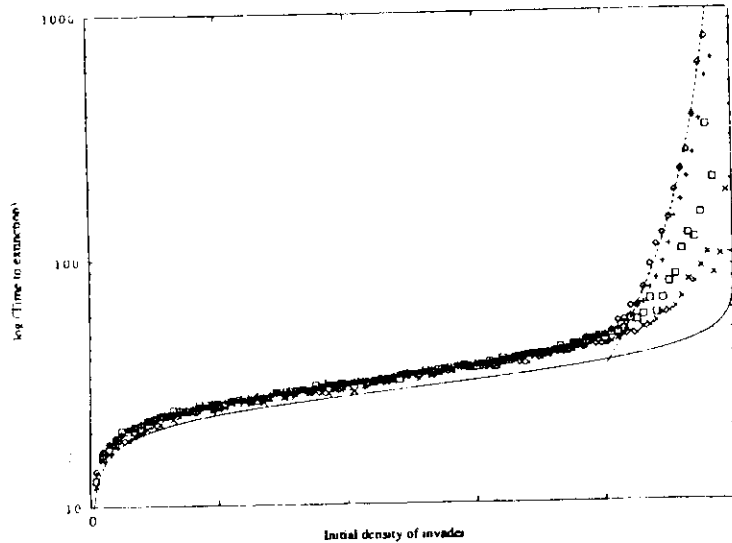


FIGURE 12.2. Time to extinction as a function of initial density;  $x_i$  is density of resident type. Solid line is mean-field approximation; dotted line is approximation from surface-effect theory. Linear dimension of grid is 256 ( $\diamond$ ), 128 (+), 64 ( $\square$ ), 32 ( $\times$ ) (modified from Gandhi et al. 1998).

One can approximate the spatial dynamics of this model in the traditional manner, by appending diffusion terms to the mean-field Equation 12.2 to yield the classical reaction-diffusion system

$$\begin{aligned} \frac{\partial H}{\partial t} &= \Delta u + \left[ H \left( a \frac{H}{H+D} + b \frac{D}{H+D} - k(H+D) \right) \right] \\ \frac{\partial D}{\partial t} &= \Delta v + \left[ D \left( c \frac{H}{H+D} + d \frac{D}{H+D} - k(H+D) \right) \right]. \end{aligned} \tag{12.5}$$

Here space has been normalized so that the diffusion coefficients (assumed to be identical) equal unity. Simulations of these equations produce patterns (Figure 12.3) that capture the

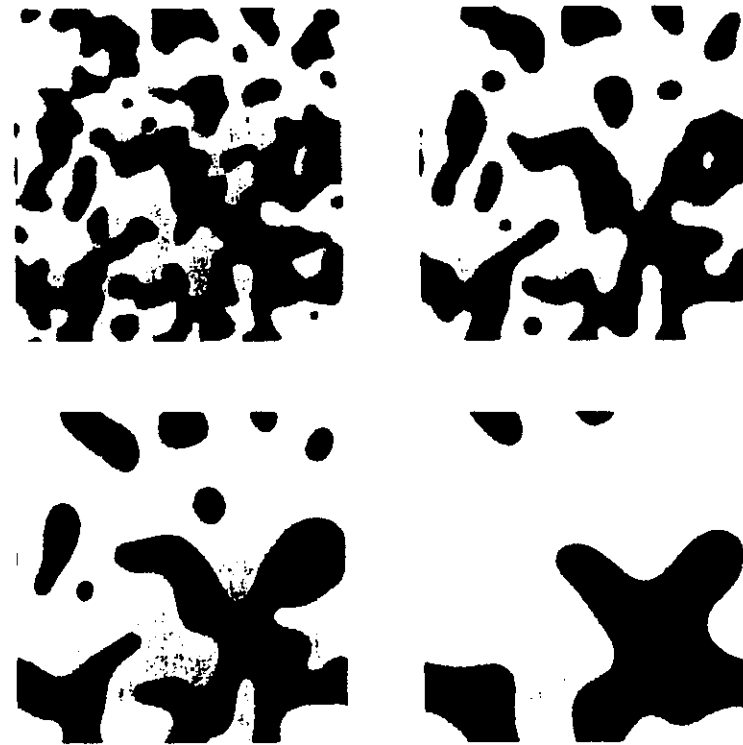


FIGURE 12.3. Snapshots from a simulation of the reaction-diffusion system at  $t = 50, 100, 200, 650$ . Initial conditions correspond to setting initial density of invader at  $0.99x_i$ , grid size at  $256 \times 256$ . Black corresponds to areas occupied by  $S_2$ , and white corresponds to areas occupied by  $S_1$ . Notice that the PDE captures the formation of clusters and their evolution through surface effects (from Gandhi et al. 1998).

mean features of the spatial dynamics (see Gandhi et al. in preparation; Durrett and Levin 1994a) 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 1994a), and we do not have clear rules for when it will. 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 a later section.

#### APPROACHES TO SIMPLIFICATION AS ILLUSTRATED BY THEORIES OF RANDOM WALKS AND DIFFUSION

The variety of ways discussed earlier to capture the role of space provide alternative descriptions for the same systems. That systems are composed of individuals, for example, does not mean that there are not emergent system behaviors that can be described in terms of global means and variances, or that useful information cannot be obtained by subdividing space into cells that are treated as homogeneous within. Systems have characteristic dynamics on a range of scales, and, either for convenience or biological importance, a variety of these may deserve attention.

Individual-based models have the advantage that they are closest in detail to real systems; that advantage is also a disadvantage in that they retain all of the detail that may hide what is really important at broader scales. The challenge then is to understand how those collective dynamics arise from the detailed interactions, that is, to build a statistical theory of collective dynamics. This is a problem that is at the core of inquiry throughout science. How is information transferred across scales? In this section we illustrate a variety of approaches to this question for a single example, the movement of individuals under density independence. Pedagogically this is valuable because random walks are easily visualized; more importantly, the structures of the underlying models embody the essential features of a wide range of stochastic processes and provide the foundation for their approximation through "diffusion limits." The approach in this section, to simplify by deriving equations for aggregate dynamics that integrate over a given region, obviously provides a mechanism for scaling among regions of different sizes.

The simplest model of movement is the random walk. 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.

1. *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  $\delta x$  apart. Assume further that the net flux from site  $x$  to site  $x + \delta x$  in a small time  $\delta t$ , 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

$$N(x, t + dt) = N(x, t) + D \delta t [N(x + \delta x, t) + N(x - \delta x, t) - 2N(x, t)]. \quad (12.6)$$

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 Equation 12.6 gives way in the limit to the familiar diffusion equation

$$\frac{\partial N}{\partial t} = D \frac{\partial^2 N}{\partial x^2} \quad (12.7)$$

(see, e.g., 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, either of which may lead to inclusion of a first derivative in  $x$ , an "advection" term. Equation 12.7 is a special case of what is known as a Fokker-Planck, or forward Kolmogorov, diffusion equation for the density function of a stochastic process.

2. *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 through 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  $\delta x$ , and occurring in time steps  $\delta t$ .  $N(x, t)$  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  $\delta x$  and  $\delta t$  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 12.7 for any initial distribution. Here  $D$  enters through the limit of the ratio of  $(\delta x)^2/\delta t$  as both  $\delta x$  and  $\delta t$  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 12.7, in the jargon of fluid dynamics, is known as the Eulerian formulation of the problem, after Euler.

3. *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

$$N(x, t + \delta t) = N(x, t)(1 - k \delta t) + k \delta t \int N(x - y, t)P(y) dy, \tag{12.8}$$

where the integral is taken over all space.

This reflects the assumption that an individual moves in time  $\delta t$  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 zero; but biased diffusion may be

reflected in a nonsymmetric  $P$ , and movement by "great leaps" may mean that  $P(x)$  does not have its peak at zero (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  $\delta t$  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 nonzero 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 12.7 provides detailed spatial information regarding the dynamics of a homogeneous spatial stochastic process. If one integrates with respect to space, one finds reassuringly that

$$\left\langle \frac{dN}{dt} \right\rangle = 0, \tag{12.9}$$

where  $\langle \rangle$  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

$$\frac{d}{dt} \langle N \rangle = \left\langle \frac{dN}{dt} \right\rangle = r \langle N \rangle, \quad (12.10)$$

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  $d\langle N \rangle/dt$  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 a later 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 12.1 from the form 12.3, replacing it by

$$M = \begin{bmatrix} -0.6 & 0.9 \\ -0.9 & 0.7 \end{bmatrix}. \quad (12.11)$$

This is usually termed "Prisoner's Dilemma," but we more generally use the nomenclature "hawks" and "doves" for the two species.

As will be described below, for simplicity we will also modify the scheme described 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 1994a).

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 Equation 12.7, 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 timescale, 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  $x$ ;  $\eta$  and  $\zeta$  are both integers. The dynamics are reflected by three processes, each with its own characteristic range:

*Migration:* Each individual, at rate  $\mu$ , 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 braces indicate that  $\eta$  and  $\zeta$  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  $\eta$  and  $\zeta$  taken over  $N_3$ ; the average can be chosen to be a weighted one, for example, with 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 creates 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 timescale 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  $\epsilon$  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 1994a) to satisfy a set of reaction-diffusion equations

$$\begin{aligned} \frac{\partial u}{\partial t} &= \Delta u + u \left[ r + g \left( a \frac{u}{u+v} + b \frac{v}{u+v} \right) - k(u+v) \right] \\ \frac{\partial v}{\partial t} &= \Delta v + v \left[ s + g \left( c \frac{u}{u+v} + d \frac{v}{u+v} \right) - k(u+v) \right], \end{aligned} \tag{12.12}$$

where  $\Delta$  is the two-dimensional Laplacian (sum of second partial derivatives),  $r$  and  $s$  are the net birth rates of isolated hawks and doves, and

$$g = g(u, v) = 1 - \exp[-\{N\}(u + v)] \tag{12.13}$$

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  $u, v \rightarrow 0$ ). 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 with effects either on the acceleration of an individual (e.g., Sakai 1973; Okubo 1986; Grünbaum 1992) or the velocity (Aoki 1982; Huth and Wissel 1992; 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 an individual to the location, densities, or velocities of other individuals. Models of this sort have been used widely to simulate animal grouping (see, e.g., Heppner and Grenander 1990; Grünbaum 1992, 1994).

To proceed to the Eulerian description of this system (in one dimension), the nonlinear equivalent of Equation 12.2, 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

$$\frac{\partial p}{\partial t} = -\frac{\partial J}{\partial x}, \quad (12.14)$$

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 the mean given by the density distribution. Making this assumption allows one to proceed (nontrivially) to an Eulerian description, typically including integral terms, reflecting the fact that individuals are responding to the dynamics of other individuals in a nonvanishing 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 1994b), cells are either occupied or empty. Occupied cells may become extinct at rate  $\delta$ , or colonize empty neighbors at rate  $\lambda$ , so that the dynamics of the mean probability of occupancy is (Levin and Durrett 1996)

$$\frac{du(1)}{dt} = -\delta u(1) + n\lambda u(01), \quad (12.15)$$

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. Equation 12.12 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. Equation 12.15, the second-order approximation, say, with  $n = 4$ , appends a second equation

$$\dot{v} = -(\lambda + \delta)v + \delta(u - v) - 3\lambda v \frac{(2v + u - 1)}{(1 - u)} \quad (12.16)$$

to Equation 12.15, where  $u = u(1)$ ,  $v = u(01)$ .

This decoupling approximation, called pair approximation (Matsuda 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, Matsuda, and Sasaki 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 1997).

The second-order approximation not only gives improved estimation of the actual dynamics (Figure 12.4) but also provides information on biologically important clustering (Figure 12.5). The contact process is a prototypical model for forest growth, species invasion, epidemic spread, and forest fire (see, e.g., Durrett 1988). Its wide-ranging applicability is reflected in its appearance (in modified form) throughout this book (see,

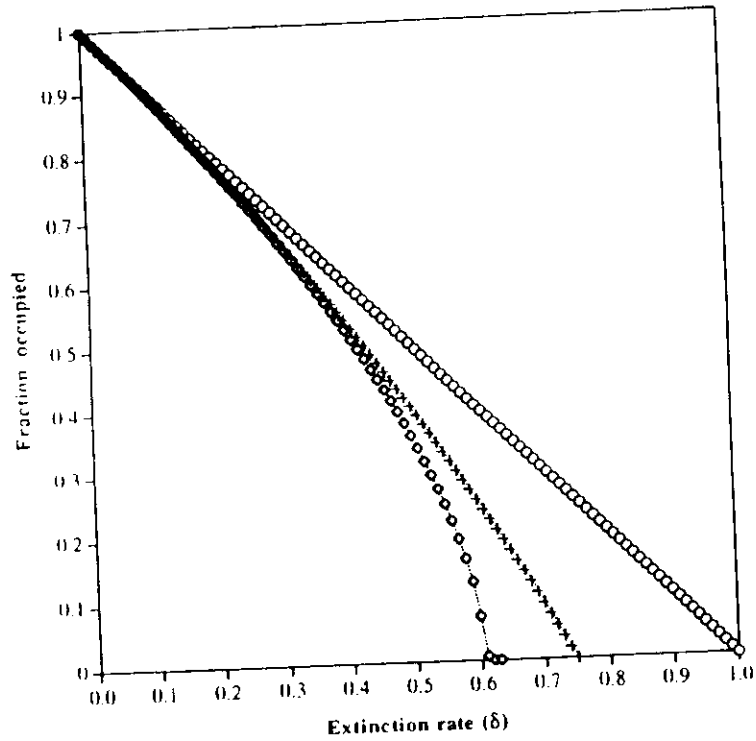


FIGURE 12.4. Occupancy fraction as a function of extinction rate  $\delta$ , for contact process.  $\diamond$  is simulation,  $\circ$  is mean-field approximation,  $+$  is pair approximation (from Levin and Durrett 1996).

e.g., Chapters 5, 8, and 9). Furthermore, extending ideas of Hubbell (1995, 1997), 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 1978a), that under local Lotka-Volterra dynamics, and conservative coupling, the equations for the spatial means of the two

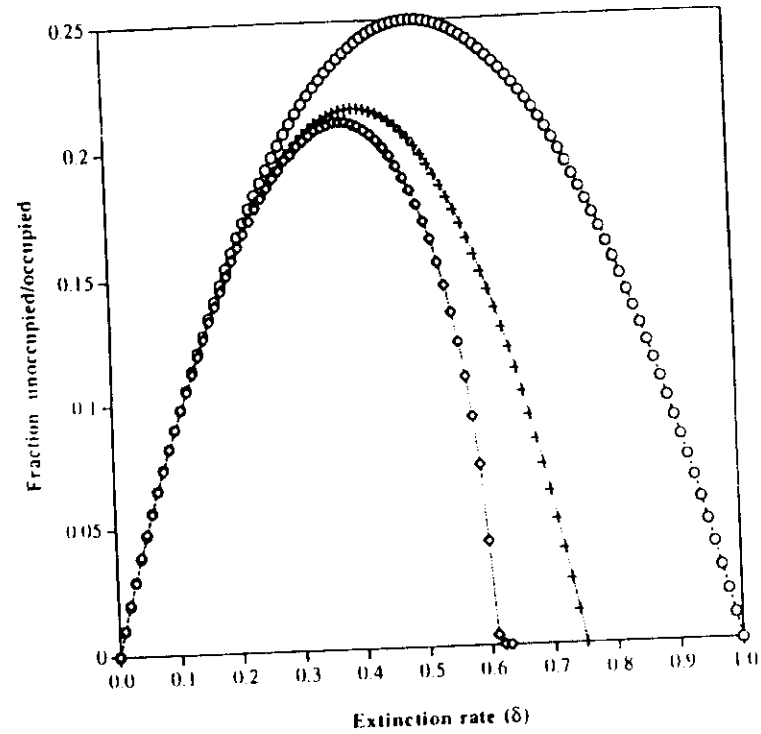


FIGURE 12.5. Correlation structure, expressed as proportion of pairs in unoccupied/occupied configuration, versus extinction rate for contact process.  $\diamond$  is simulation,  $\circ$  is mean-field approximation,  $+$  is pair approximation (from Levin and Durrett 1996).

species are

$$\frac{d\bar{u}}{dt} = r\bar{u}(k - a\bar{u} - b\bar{v}) - ra\sigma_u^2 - rb \text{cov}(u, v)$$

$$\frac{d\bar{v}}{dt} = s\bar{v}(L - c\bar{u} - d\bar{v}) - sc \text{cov}(u, v) - sd\sigma_v^2 \quad (12.17)$$

in which  $\sigma_u^2$  and  $\sigma_v^2$  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 12.17 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 chapter 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 simulator SORTIE. For example, in a single-species version of this model (see Bolker and Pacala 1997), discussed in more detail in Pacala and Levin (Chapter 9), births to an individual at a site in continuous space are determined by a weighted function of densities 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

$$\frac{dn}{dt} = H(n) - \alpha \int_{-\infty}^{\infty} U(r)c(r) dr, \quad (12.18)$$

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, Equation 12.18 gives the dynamics of  $n$  in terms of variables other than  $n$ , so the system is not closed. The approach then is to complement Equation 12.18 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 (Chapter 9).

## SUMMARY

In this chapter 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. Although 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 (Chapter 9); 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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## REFERENCES

- Aoki, I. 1982. A simulation on the schooling mechanism in fish. *Bull. Jap. Soc. Sci. Fish.* **48**:1081-1088.
- Barenblatt, G. I. 1994. *Scaling phenomena in fluid mechanics*. Cambridge University Press, Cambridge, England.
- Brownlee, J. 1911. The mathematical theory of random migration and epidemic distribution. *Proceedings of the Royal Society Edinburgh* **31**:262-289.
- Bolker, B. M., and S. W. Pacala. 1996. Understanding stochastically driven spatial pattern formation in ecological systems using moment equations. *Theoretical Population Biology*. *Submitted*.
- Chesson P. 1986. Environmental variation and the coexistence of species. Pages 240-254 *in* J. Diamond, and T. J. Case, editors. *Community ecology*. Harper and Row, New York, New York, USA.
- Cohen, D. S., and J. D. Murray. 1981. A generalized diffusion model for growth and dispersal in a population. *Journal of Mathematical Biology* **12**:237-249.
- DeAngelis, D. L. and L. J. Gross. 1992. Individual-based models and approaches in ecology: populations, communities and ecosystems. Chapman & Hall, New York, New York, USA
- Dobzhansky, T., and S. Wright. 1947. Genetics of natural populations. XV. Rate of diffusion of a mutant gene through a population of *Drosophila pseudoobscura*. *Genetics* **32**:303-324.
- Durrett, R. 1988. Crabgrass, measles and gypsy moths: An introduction to modern probability. *Bulletin of the AMS* **18**:117-143.
- Durrett, R., and S. A. Levin. 1994a. Stochastic spatial models: a user's guide to ecological applications. *Philosophical Transactions of the Royal Society of London, Series B* **343**:329-350.
- Durrett, R., and S. A. Levin. 1994b. The importance of being discrete (and spatial). *Theoretical Population Biology* **46**:363-394.



- Durrett, R., and S. A. Levin. 1996. Spatial models for species area curves. *Journal Theoretical Biology* 179:119–127.
- Fisher, R. A. 1937. The wave of advance of advantageous genes. *Annals of Eugenics* 7:355–369.
- Gandhi, A., S. A. Levin, and S. Orszag. 1996. "Critical slowing down" in time-to-extinction: An example of critical phenomena in ecology. Submitted.
- Gierer, A., and H. Meinhardt. 1972. A theory of biological pattern formation. *Kybernetik* 12:30–39.
- Gilpin, M. E., and I. Hanski, editors. 1991. *Metapopulation dynamics*. Academic Press, London, England.
- Goldenfeld, N. 1992. Lectures on phase transitions and the renormalization group. *Frontiers in physics*. Addison Wesley, Reading, Massachusetts, USA.
- Grünbaum, D. 1992. Local processes and global patterns: Biomathematical models of bryozoan feeding currents and density dependent aggregations in Antarctic krill. Dissertation. Cornell University, Ithaca, New York, USA.
- Grünbaum, D. 1994. Translating stochastic density-dependent individual behavior with sensory constraints to a Eulerian model of animal swarming. *Journal of Mathematical Biology* 33:139–161.
- Gueron S., and S. A. Levin. 1993. Self-organization of front patterns in large wildebeest herds. *Journal of Theoretical Biology* 165:541–552.
- Haldane, J. B. S. 1948. The theory of cline. *Journal of Genetics* 48:277–284.
- Harada, Y., H. Ezoe, Y. Iwasa, H. Matsuda and K. Sato. 1995. Population persistence and spatially limited social interaction. *Theoretical Population Biology* 48:65–91.
- Harada, Y. and Y. Iwasa. 1994. Lattice population dynamics for plants with dispersing seeds and vegetative propagation. *Res. Pop. Ecol.* 36:237–249.
- Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford, England.
- Haurv, L. R., J. A. McGowan, and P. H. Wiebe. 1978. Patterns and processes in the time-space scales of plankton distributions. Pages 277–327 *in* J. H. Steele, editor. *Spatial*

- pattern in plankton communities. Plenum, New York, New York, USA.
- Hediger, H. 1950. *Wild Animals in Captivity*. Butterworth, London, England.
- Heppner, F., and U. Grenander. 1990. A stochastic nonlinear model for coordinated bird flocks. Pages 233–238 *in* S. Krusna, editor. *The ubiquity of chaos*. AAAS Publications, Washington, D.C., USA.
- Holling, C. S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. *Ecological Monographs* **62**:447–502.
- Hubbell, S. P. 1995. Towards a theory of biodiversity and biogeography on continuous landscapes. Pages 173–201 *in* G. R. Carmichael, G. E. Folk, and J. L. Schnoor editors. *Preparation for global change: a midwestern perspective*. SPB Academic Publishing, Amsterdam, The Netherlands.
- Hubbell, S. P. 1997. *A Theory of Biogeography and Relative Species Abundance*. Princeton University Press, Princeton, New Jersey, USA. To appear.
- Huth, A., and C. Wissel. 1992. The simulation of the movement of fish schools. *Journal of Theoretical Biology* **156**:365–385.
- Iwasa, Y., S. A. Levin, and V. Andriksen. 1987. Aggregation in model ecosystems. I. Perfect aggregations. *Ecological Modelling* **37**:287–302.
- Iwasa, Y., S. A. Levin, and V. Andriksen. 1989. Aggregation of model ecosystems. II. Approximate aggregations. *IMA Journal of Mathematics Applied in Medicine & Biology* **6**:1–23.
- Kadanoff, L. P. 1966. Scaling laws for Ising model near  $T_c$ . *Physics* **2**:263–272.
- Kauffman, S. 1993. *The origins of order*. Oxford University Press, New York, New York, USA.
- Kierstead, H., and L. B. Slobodkin. 1953. The size of water masses containing plankton blooms. *Journal of Marine Research* **12**:141–147.
- Kolmogorov, A. I. Petrovsky, and H. Piscunov. 1937. Étude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique. *Moscow University Bulletin Series International Section A*. 1:1–25.

- Lehman, C. L., and D. Tilman. 1996. Competition in spatial habitats. This volume.
- Levin, S. A. 1974. Dispersion and population interactions. *American Naturalist* 108:207-228.
- Levin, S. A. 1976. Population dynamic models in heterogeneous environments. *Annual Review of Ecology and Systematics* 7:287-311.
- Levin, S. A. 1978a. Population models and community structure in heterogeneous environments. Pages 439-475. in S. A. Levin, editor. *Mathematical Association of America study in mathematical biology II: Populations and communities*. *Studies in Mathematics* 16. *Mathematical Association of America*, Washington, D.C., USA.
- Levin, S. A. 1978b. Pattern formation in ecological communities. Pages 433-465 in J. H. Steele, editor. *Spatial pattern in plankton communities*. *Proceedings of the NATO Conference on Marine Biology*, Erice, Sicily, November 1977. *Plenum Press*, New York, New York, USA.
- Levin, S. A. 1981. Mechanisms for the generation and maintenance of diversity. Pages 173-194 in R. W. Hiorns, and D. Cooke, editors. *The mathematical theory of the dynamics of biological populations*. *Academic Press*, London, England.
- Levin, S. A. 1988. Pattern, scale, and variability: an ecological perspective. Pages 1-12 in A. Hastings, editor. *Community ecology*. *Lecture notes in biomathematics* 7. *Springer-Verlag*, Heidelberg, Germany.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1967. Reprinted 1995. Pages 277-326 in J. H. Steele and T. Powell, editors. *Ecological time series*. *Chapman & Hall*, New York, New York, USA.
- Levin, S. A., and L. Buttel. 1987. Measures of patchiness in ecological systems. *Ecosystems Research Center Report No. ERC-130*, *Cornell University*, Ithaca, New York, USA.
- Levin, S. A., and R. Durrett. 1996. From individuals to epidemics. *Philosophical Transactions of the Royal Society of London*, Series B. To appear.
- Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences, U.S.A.* 71:2744-2747.

- Levin, S. A., and L. A. Segel. 1985. Pattern generation in space and aspect. *SIAM Review* 27:45–67.
- Ma, S. K. 1976. Modern theory of critical phenomena. Benjamin, New York, New York, USA.
- Mandelbrot, B. B. 1977. Fractals: form, chance, and dimension. Freeman, San Francisco, California, USA.
- Matsuda, H., N. Ogita, A. Sasaki and K. Sato. 1992. Statistical mechanics of population: the lattice Lotka-Volterra model. *Progress in Theoretical Physics* 88:1035–1049.
- Mollison, D. 1977. Spatial contact models of ecological and epidemic spread. *Journal of the Royal Statistical Society B* 39:283–326.
- Moloney, K. A., S. A. Levin, N. R. Chiariello, and L. Buttel. 1992. Pattern and scale in a serpentine grassland. *Theoretical Population Biology* 39:63–99.
- Murray, J. D. 1990. Mathematical biology. *Biomathematics* 19. Springer-Verlag, Heidelberg, Germany.
- Okubo, A. 1980. Diffusion and ecological problems: mathematical models. Lecture notes in biomathematics 10. Springer-Verlag, Heidelberg, Germany.
- Okubo, A. 1986. Dynamical aspects of animal grouping; swarms, schools, flocks and herds. *Adv. Biophys.* 22:1–94.
- Okubo, A., and S. A. Levin. 1989. A theoretical framework for the analysis of data on the wind dispersal of seeds and pollen. *Ecology* 70:329–338.
- Pacala, S. W., and S. A. Levin. 1996. Biologically generated spatial pattern and the coexistence of competing species. This volume.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. The Third Tansley Lecture. *Journal of Animal Ecology* 49:667–685.
- Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* 51:145–178.
- Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, England.

- Pickett, S. T. A., and P. S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.
- Sakai, S. 1973. A model for group structure and its behavior. *Biophysics (Japan)* **13**:82–93.
- Sato, K., H. Matsuda and A. Sasaki. 1994. Pathogen invasion and host extinction in a lattice structured population. *Journal of Mathematical Biology* **32**:251–268.
- Segel, L. A. and J. Jackson. 1972. Dissipative structure: An explanation and an ecological example. *Journal of Theoretical Biology* **37**:545–559.
- Simon, H. A., and A. Ando. 1961. Aggregation of variables in dynamic systems. *Econometrica* **29**:111–138.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**:196–218.
- Solé, R. V., S. C. Manrubia, B. Luque, J. Delgado, and J. Bascompte. 1995–96. Phase transitions and complex systems. *Complexity* **1**(4):13–26.
- Taylor, G. I. 1950. The formation of a blast wave by a very intense explosion. I. Theoretical discussion. *Proceedings of the Royal Society Series A* **201**:159–174.
- Volterra, V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animale conviventi. *Mem. R. Accad. Nazionale del Lincei (Ser. 6)* **2**:31–113.
- Wilson, K. G. 1983. The renormalization group and critical phenomena. *Reviews of Modern Physics* **55**:583–600.

