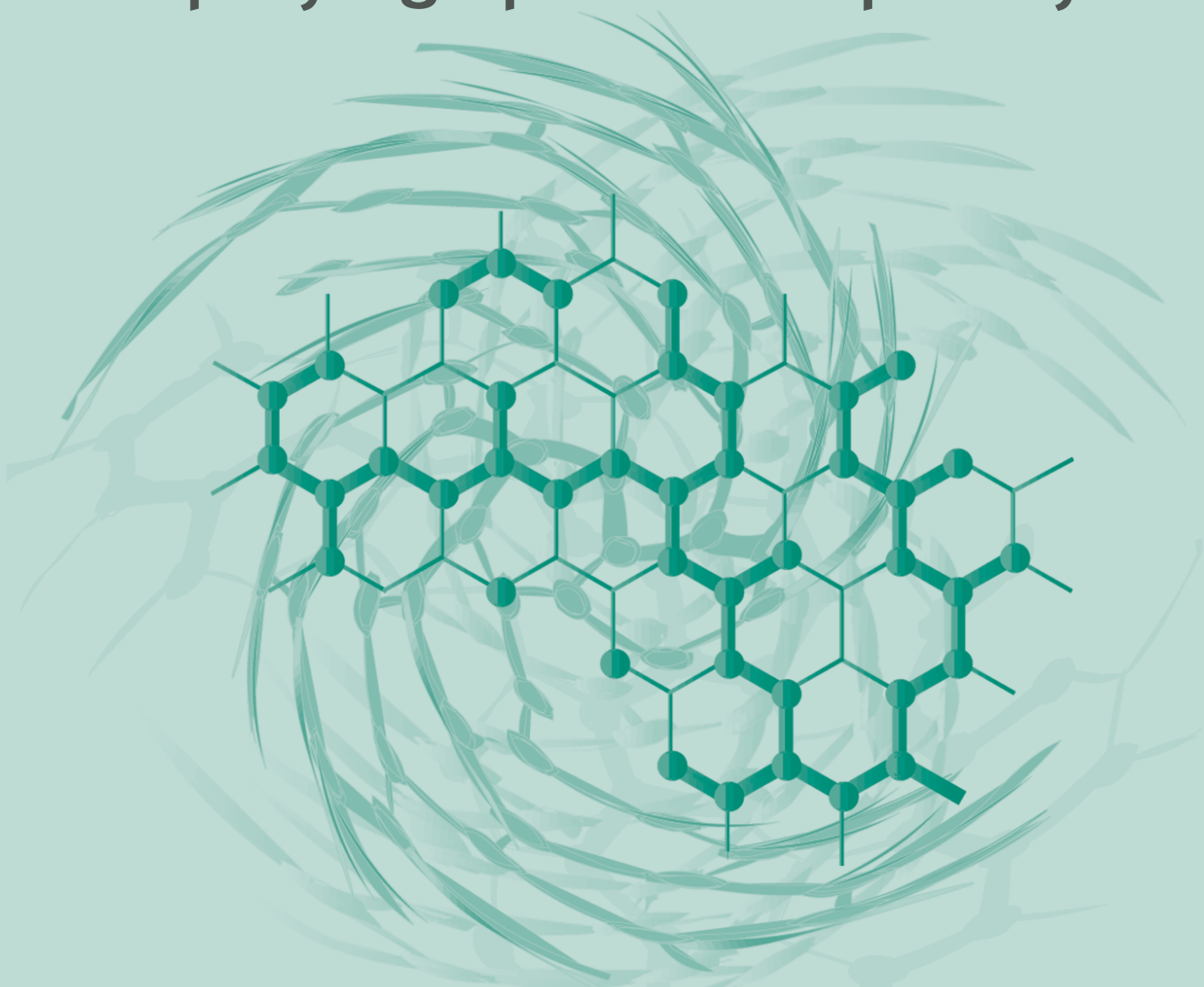


Cambridge Studies in Adaptive Dynamics

The Geometry of Ecological Interactions

Simplifying Spatial Complexity



Edited by

U. Dieckmann, R. Law, and J.A.J. Metz

The Geometry of Ecological Interactions: Simplifying Spatial Complexity

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Ulf Dieckmann, Richard Law, and Johan A.J. Metz



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1

Introduction

Richard Law, Ulf Dieckmann, and Johan A.J. Metz

Species form different kinds of patches; these patches form a mosaic and together constitute the community. Recognition of the patch is fundamental to an understanding of structure. Patches are dynamically related to each other. But there are also departures from this inherent tendency to orderliness. At any given time, therefore, structure is the resultant of causes which make for order, and those that tend to upset it. Both sets of causes must be appreciated.

*Abbreviated from Watt (1947, p. 2)
Pattern and process in the plant community*

A sea change has come over theoretical ecology in the past 10 years. The era of the simple general model that tries to capture the elusive essence of an ecological community is rapidly fading from sight. This is the age of the individual-based, spatially explicit, computer-based model (Huston *et al.* 1988; DeAngelis and Gross 1992; Judson 1994).

Why has this transformation taken place? First there is the simple matter of practicality: desktop computing power has reached a level at which it is quite feasible to simulate individuals as they move across a landscape, interact, reproduce, and die. Second is the issue of language: for many ecologists, rules encoded in computer algorithms are much more accessible than the formal mathematical language of dynamical systems. Third is the appreciation that important ecological intricacies, such as the mechanisms by which organisms interact in communities, often cannot be incorporated sufficiently faithfully into simple models. Fourth is an awareness that the simple models traditionally used in ecology have not always proved very successful in accounting for phenomena observed in natural systems.

Individual-based simulations are most realistic when they encompass the randomness of individuals in births, deaths, and movements (e.g., Pacala *et al.* 1996). Our computer screens then give realizations of complex spatio-temporal stochastic processes. The simulations have their own intrinsic interest; they can be a valuable aid in defining and characterizing the processes involved and can lead to the discovery of new and interesting phenomena. But we should not to infer too much from a few realizations of a

process: it is not the location and behavior of each individual that matters, since the stochasticity will ensure that every realization is different at least in detail. It is the gross properties of the stochastic process that are likely to be of interest in the long run.

Helpful though simulations are, they can be no more than a step toward understanding properties of the stochastic process. When you next look at such a realization as it unfolds on the screen, ask yourself the following questions:

- Can you distinguish between the random variation intrinsic to any stochastic process and the ecological signal that characterizes the system's representative behavior?
- What spatial and temporal patterns come about in the long run? In other words, can you characterize the asymptotic states of the system?
- Can you identify different kinds of patterns that develop as the initial configuration of the community is changed? Are there alternative metastable states that depend on the starting conditions?
- Can you work out how many different kinds of patterns could develop from different starting conditions?
- Can you understand what happens when you change the environment in which the organisms live by altering the parameters of the process?
- How readily can you sample the parameter space and determine the effects of parameters on the qualitative and quantitative properties of your system?

These are important questions, but ones that are very difficult to answer from individual-based simulations. The heterogeneity of natural environments in time and space provides a strong imperative for such analyses, but dealing with such heterogeneity, always a major undertaking in ecology, is especially demanding in the context of a stochastic process.

As a result of developments in theoretical ecology over the past decade, enormously complex models have replaced simple ones. If you doubt this, imagine a community being modeled on a spatial lattice of, say, 100 cells. To keep matters simple, suppose population sizes in the cells are large enough for stochasticity to be ignored. If you have 10 species in the community, your dynamical system comprises 1000 equations. Can it really be that community dynamics need a state space of such staggering dimensionality? We believe that very often the dynamics can be adequately represented in a more parsimonious set of equations. It should be possible to project the dynamics into a low-dimensional space which carries the essential information. This is more than wishful thinking: Rand and

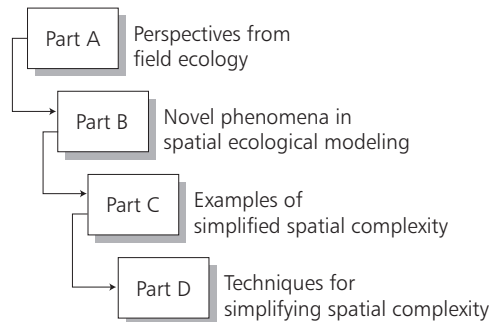


Figure 1.1 Structure of the book.

Wilson (1995) found a spatial resource–predator–prey model that has effective dynamics in a four-dimensional embedding space. The problem is, what simplified state space would be an appropriate target for projecting the dynamics? Can projections be found that properly hold in place the main effects of spatial structure?

Ecology needs new ideas and methods to deal with dynamics of processes in a spatial setting (Wiens *et al.* 1993; Hastings 1994; Levin *et al.* 1997; Tilman and Kareiva 1997). This book points to and explains some possible ways forward (Figure 1.1). In the first place, there is obviously much to be learned from individual-based modeling of ecological communities. Such models can be motivated by direct observations of individuals in the field, and they force precise thinking about the processes involved. They help in developing intuition about how ecological systems behave. They show us repeatedly how new, unexpected phenomena emerge when spatial structure is introduced.

Spatially explicit, individual-based models contrast with models that lack spatial structure, widely used in theoretical ecology in the past. These earlier models make an assumption that the effects of neighbors are proportional to their density averaged across a large spatial domain (the so-called mean-field assumption, see Box 1.1). In communities where individuals interact with their neighbors, the presence of nonrandom spatial pattern, for which there is abundant evidence in nature, will most likely lead to major departures from the mean-field dynamics. The world is full of spatial structure, and this has fundamental consequences for many ecological processes. Individual-based models are an important step toward seeing what happens when the mean-field assumption is abandoned, and Part B gives some striking illustrations of the remarkable behavior that can then emerge.

Box 1.1 The mean-field assumption in ecology

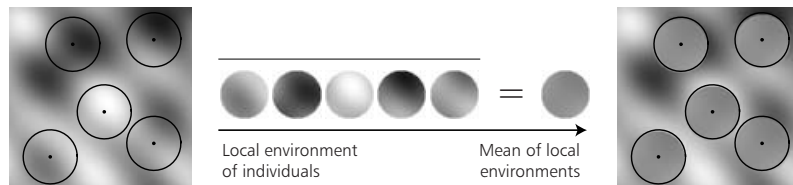
At the heart of much ecological theory lies an assumption that individual organisms encounter one another in proportion to their average abundance across space. You find this assumption in, for instance, the Lotka–Volterra equations for two interacting species i and j , expressed as the product of their mean densities $N_i N_j$.

Before being applied to ecological problems, assumptions of this type were used in physics and chemistry (Weiss 1907). Examples are collisions between molecules in a well-mixed gas, the electrical field experienced by electrons within an atom, and the magnetic field around elementary magnets of a solid. In the last two cases, all electrons in an atom (all elementary magnets in a solid) are assumed to be locally surrounded by the same electric (magnetic) field, called the “mean field.” This is why, even in ecology, the assumption is widely referred to as the mean-field assumption.

The mean-field assumption is most likely to hold as a good approximation when the physical environment of organisms is homogeneous and

- physical forces exist that cause strong mixing of organisms,
- organisms themselves are highly mobile, or
- organisms interact with others over long distances.

As conditions depart from those above, the mean-field assumption becomes less and less appropriate. A lack of mixing, whether due to the external environment or immobility of the organisms, generates neighborhoods around individuals that deviate from the spatial averages. Differences in local environmental conditions become especially important if organisms only interact over short distances (integrating over large neighborhoods can give spatial averages quite close to the mean field). The local environment organisms experience can then be quite different from the mean environment, averaged across the entire ecological habitat (see figure). Such departures from the mean field can feed through to the vital rates of individuals and can have fundamental effects on their dynamics.



Constructing the mean field. Spatial variation in environmental conditions (e.g., measuring a resource’s availability) is shown by gray scales; individuals are depicted as points, and their local environments, as circles. Constructing the mean field by averaging over local environments shows why the mean-field assumption may break down: a population’s response to a spatially heterogeneous environment is often different from its response to the mean field.

However, theoretical ecology needs to move on from simulations of individual-based processes to manageable approximations that give a better understanding of the generic properties of these processes. This is already being done with some success, as can be seen from the examples in Part C and the methodological chapters in Part D. When the patterns we are interested in have a large spatial extent, the methods include diffusion approximations using partial differential equations. These methods have been available for many years (Okubo 1980) but still have much to offer ecologists. In addition, novel methods, such as pair approximations and correlation dynamics, are being developed that concentrate on dynamics of small-scale spatial structure. Analysis of the resulting deterministic equations can deal with many of the issues left unresolved by stochastic simulations, including

- overall qualitative features buried in the processes;
- the attractors that are present and whether they correspond to spatially homogeneous systems or indicate the presence of spatial structures;
- the effect on eventual states of communities of changes in the environment and ecological interactions, using bifurcation analysis in moderately large parameter spaces;
- the fate of newly introduced mutants and immigrant species, whether they will invade or be driven to extinction by the resident system.

There is much for the theorist to do here and a great deal to challenge the ecologist. But a major factor hindering progress is the difficulty ecologists and theorists have had in developing an effective dialogue. We think it is essential to develop theory that is demonstrably relevant to real ecological systems and to show how it illuminates our understanding of ecology. We begin with several chapters in Part A that explain what ecologists have learned about spatio-temporal processes in ecological communities to provide some guidelines for developing theory.

The book covers a much wider span of knowledge from ecology to mathematics than is usual in a single textbook, and we recognize that you may not want to read it from cover to cover (although of course we hope you will!). But we hope that you will be encouraged to build bridges from the parts of the book that lie in your own area of expertise – whether ecology, computation, or mathematics – to other, less familiar parts and that the book will aid your understanding of these different areas.

In a sense, the path mapped out in this book – from field observations, to individual-based simulations, to deterministic approximations of stochastic processes, and back again – is how ecological theory might have developed

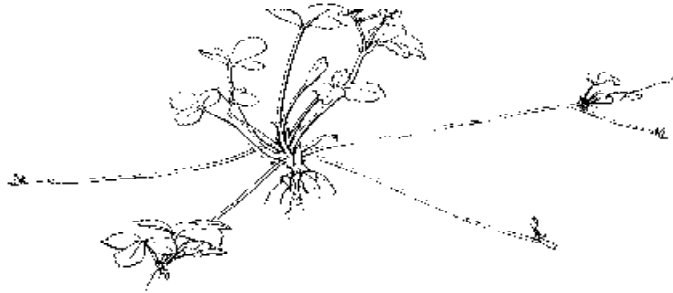
in an ideal world. But progress in research has its own imperative, and scientists work on the problems that appear promising at the time. Although the simple models from an earlier age of theoretical ecology may now look somewhat *ad hoc*, their importance should not be underestimated: there certainly are circumstances where spatial structure is less important, and in these circumstances the earlier theoretical framework will prove helpful. Our focus on spatio-temporal processes tries to extend the formal framework of ecology, not to replace one paradigm with another. As theoretical ecology develops, the broader framework that emerges should place earlier theory in its proper context within the structure of our expanding understanding.

Acknowledgments This book was conceived while two of the editors, Ulf Dieckmann and Richard Law, were working with Tomáš Herben at the Institute for Advanced Study, Wissenschaftskolleg zu Berlin, in the academic year of 1995/1996. It became evident during the course of our discussions that there was a real possibility of moving on from individual-based models, currently at the center of much theoretical ecology, toward a more rigorous and elucidating treatment of spatial dynamics. The Institute for Advanced Study provided ideal conditions in which to develop our ideas, and we are very grateful to the staff for the welcome they gave us and for providing such a good working environment. Special thanks go to Wolf Lepenies, Joachim Nettelbeck, Hans Georg Lindenberg, and Andrea Friedrich.

Subsequent stages in development of the book took place at the International Institute of Applied Systems Analysis (IIASA), Laxenburg, Austria, where IIASA's current director Gordon J. MacDonald and former director Peter E. de Jánosi provided critical support. We organized two workshops in which authors were brought together to discuss their contributions to achieve as much continuity across subject areas as possible. The success of a book of this kind depends very much on cooperation of authors in dealing with the many points editors are bound to raise, and we thank our authors for their patience over the past two years. The book has benefited greatly from the support of the Publications Department at IIASA; we are especially grateful to Ellen Bergschneider, Anka James, Martina Jöstl, and Eryl Maedel for the work they have put into preparing the manuscript. Any mistakes that remain are our responsibility.

Part A

Empirical and Statistical Background: A Plant Ecological Perspective



Introduction to Part A

What have ecologists learned about spatio-temporal processes in natural communities? The first part of the book gives some answers to this question and is intended to provide ecological background to which theorists can turn. We believe such a basis is necessary if we are to achieve a constructive and enlightening dialogue between ecologists and mathematicians. The information in Part A indicates how ecologists think about spatio-temporal processes and sets boundaries on the kinds of spatio-temporal models likely to be of lasting interest in ecology. This part of the book is a small step in an iterative process of mutual education of theorists and ecologists.

Ecologists study many kinds of communities, and from this large set we have chosen to focus on plant communities living on land. The link between spatial structure and dynamics is particularly strong in these communities for two main reasons. First, plants in terrestrial communities are relatively immobile in space. Dispersal of propagules does less than one might expect to compensate for such immobility because most seeds do not travel far, even if they have structures that aid dispersal. Second, interactions occur primarily between immediate neighbors. Plants respond to the state of a small spatial neighborhood in their immediate vicinity, not some large-scale spatial average of the whole community (the so-called mean field). If there are circumstances in natural communities under which local spatial pattern should be important, they are in these terrestrial plant communities. The variation in spatial pattern from one location to another is both sensed and partially generated by the plants; such plant communities are therefore an obvious place to start looking for dynamics in which space plays an important part. This is not to suggest that it is only in plant communities that spatial structure can play a major role – several chapters later in the book point to the importance of spatial structure in other ecological and evolutionary processes.

Part A concentrates on temperate grasslands. Here, nonrandom spatial pattern is particularly evident. One reason for this pattern is that many plant species in such communities reproduce by clonal growth, which greatly restricts dispersal of propagules and gives rise to clumps of conspecifics. What is less obvious, but equally important, is that these spatial structures are in a continual state of flux, and the time scale on which this flux occurs is short enough for changes in spatial pattern to be observed over a few

years. Grassland communities are about as close as ecologists can get to systems in the field in which (1) spatial structure should play a major role and (2) turnover rates are great enough to make it feasible to study the dynamics.

The first three chapters follow a sequence from small to large spatial and temporal scales. The sequence starts in Chapter 2 at the microscopic scale, with the concept of a neighborhood around an individual plant within which local interactions take place, resulting in overlapping zones of influence. Stoll and Weiner consider the mechanisms of competition within this neighborhood through limited resources such as light and mineral nutrients. They discuss how ecologists have tried to characterize the neighborhood as an area around an individual plant and the assumptions implicit in this work. They also point out some of the main issues that remain open, such as how to deal with the modular structure that many plants have, and how to allow the neighborhood to expand as plants grow. Last but not least, they express a viewpoint about the role of theory in ecology, quite widely shared by ecologists.

Chapter 3 moves up a step in the scale of time to tackle the turnover of individuals as they interact in small neighborhoods. A detailed mechanistic view of neighborhoods of the kind described in Chapter 2 is difficult to distill from ecological data. Silvertown and Wilson take a more phenomenological approach, integrating over the known (and unknown) mechanisms of interaction by means of a single measure of neighborhood dependence, often given as a competition coefficient for a pair of species. They describe how such coefficients are estimated in the field and the information that can be gleaned from matrices of these coefficients for several coexisting species. Rather little has been done to develop these ideas explicitly in a spatial framework. The authors discuss the state of this art, together with the work that they and their colleagues have done in estimating parameters for spatial invasion of grasses in the field. Their work leads to a cellular automaton model of the spatial dynamics.

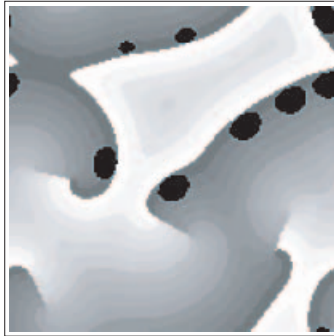
Chapter 4 moves up a step further in the scale of both time and space to the spatio-temporal patterns observed in grassland communities. In the long run, the success of spatio-temporal models of plant communities will be judged by their capacity to capture these macroscopic features from the underlying microscopic (neighborhood-dependent) processes of birth, death, and movement. Nonrandom spatial patterns are certainly typical of grassland communities. In Chapter 4, Herben, Dalling, and Law discuss the extent to which these patterns can be said to be self-generating

or imposed from outside by heterogeneities in the external environment. Several informal theories can be found in the ecological literature that foster an understanding of how spatial structure of plant communities develops through time. The models include cyclic sequences of community states (mosaic cycles), random sequences of states (carousel model), non-allowable states (guild proportionality), and community states that are “frozen” through time by space preemption.

The last chapter in Part A provides a link between what ecologists can do in the field and what theorists can do at their desks. It is essential to have in place a formal statistical framework for analysis of the spatio-temporal processes taking place in nature. Chapter 5, by Cox, Isham, and Northrop, gives an introduction to the armory of methods that statisticians have available for treating empirical data associated with spatio-temporal processes. First, the chapter covers descriptive methods for preliminary inspection of data collected over time, space, or both time and space together. Second, it deals with stochastic models for describing spatial data, in particular, Poisson-based models and Markov random fields. Third, it considers methods by which the parameters of such models can be estimated, notwithstanding the complex interdependencies that spatio-temporal data typically exhibit.

Part B

When the Mean-field Approximation Breaks Down



Introduction to Part B

Part B of the book turns from the field to models of ecological processes in spatially structured environments. We hope eventually for a seamless transition from field-based rules of interaction among neighboring plants and animals to computer simulations. The results given in Chapter 3 illustrate how far plant ecologists have gotten in the field, and Chapter 6 shows what theorists can do by listening carefully to ecologists. But at the present state of the art, most models, while motivated by ecological and evolutionary phenomena, are based on assumptions about spatial processes in nature. From study of these models, there is a clear and exciting message: new phenomena, unexpected from mean-field models, are very often evident.

Why should spatially extended models of population and community dynamics differ so much from their mean-field counterparts? A major reason is the existence of spatial variation in local environments. As Part A emphasizes, organisms very often interact with their neighbors, and it is the density of these neighbors that matters, not the density averaged over some large spatial region. Deviations of local neighborhoods from the global average are of two kinds: systematic and random.

- Systematic deviations often arise from previous interactions between neighbors. For example, if individuals of species A and B interact antagonistically and reproduce locally, fewer individuals of A will be found around those of B than expected from their global densities (and vice versa). Such deviations are described by local correlations, and dealing with them becomes a major theme later in the book (Chapters 13, 14, and 18 to 21).
- Random deviations are due to the finite number of neighbors. These local fluctuations play an important role when organisms respond nonlinearly to different local environments because the individuals' response, averaged across environments, is not equivalent to their response to the average environment. In such cases, chance fluctuations do not cancel out, and they may have macroscopic consequences (Chapters 7, 19, and 21).

The separation of systematic and random deviations does depend to some extent on the approach used; yet both types of deviation are often present, and the distinction is a useful aid to understanding the dynamics. The aim

of Part B is to illustrate and emphasize the phenomena that can result from these local correlations and fluctuations.

To construct models of spatio-temporal processes, researchers have to make some basic choices about space, time, and state variables. Each of these quantities may be continuous or discrete, giving eight combinations, underpinned by different kinds of mathematics. Some approaches are more commonly used than others, and the chapters in Part B illustrate two of the more widely adopted approaches. Most popular among biologists are cellular automaton (CA) models. These are usually stochastic and update discrete states of cells (typically representing individuals) on a discrete spatial lattice according to the state of cells in some neighborhood in discrete time (Chapters 6 to 8). The popularity of CA models is well deserved: as they are rule based, biologists can readily turn them into algorithms for numerical simulation of individuals interacting in some spatial region, as discussed in Chapter 6.

In another widely used approach, models take state to be a continuous variable, envisaged as a locally well-mixed density or concentration, with dynamics that are continuous in space and time. These models are written as partial differential equations (PDEs), most commonly reaction–diffusion equations, with terms describing (1) interactions (“reactions”) that depend on locally well-mixed densities of individuals and (2) diffusion across space by random movements of individuals. Biologists often find reaction–diffusion equations more difficult than CA models to understand and turn into computer algorithms, but reaction–diffusion equations do have the potential to give important insights into the development of large-scale spatial structure, as Chapters 9 and 10 illustrate. How these two modeling paradigms are related is discussed in detail in Chapter 9.

CA and PDE models are two points in a broader spectrum of alternative approaches to spatial modeling. The relative merits of different approaches depend on the biological problem posed, and Chapter 11 illustrates how the modeling framework needs to be changed as the scale moves from the individual to the local population to the global population.

In their study of spatially extended models, theorists are motivated by a wide variety of biological phenomena, as is evident from the chapters in Part B. In Chapter 6, Wissel illustrates the insights that CA models can give into effects of space on dynamics of three ecological communities. The first deals with rabies in populations of foxes; using the CA model and given some simple rules for infection, a wavelike pattern of spread develops over space with a good match to field data. The second is a shrub community in

an arid environment; a CA model shows the importance of rainfall events, external to the community, in driving the long-term community dynamics. The third community is a boreal forest; the CA model describes the spread of fires through the forest and gives a close resemblance to the size and shape of fires observed in the field.

Chapter 7 introduces a framework for analysis of prebiotic evolution based on a set of replicators that share a common metabolism. The replicators are bound to a surface and depend on local diffusion of metabolites from other replicators within a small neighborhood to synthesize the monomers they need to replicate themselves. Comparing results of a CA model for this system with those of its mean-field counterpart, Czárán and Szathmáry show that the community of replicators depends on the absence of local correlations for survival. All replicators must be present in the same locality for successful metabolism, and a replicator that becomes rare has an advantage over those that are common. Such a system illustrates the importance of local fluctuations and has the potential to produce a stable community of replicators, notwithstanding their inherent tendency toward competition.

In Chapter 8, Nowak and Sigmund describe evolutionary games that are played with neighbors on a spatial grid. They show that interactions between neighbors have major effects on the relative success of individuals exhibiting cooperative and selfish behavior. In particular, clusters of cooperative individuals can develop and persist, even without repeated interactions between pairs of individuals. This is not possible in the absence of spatial structure, and the introduction of space thus increases the range of conditions under which cooperation is to be expected.

Chapter 9 explores discrepancies between CA and PDE models that are intended to describe the same reaction–diffusion system. Drawing examples from the interaction of polymers in early evolution, Cronhjort demonstrates the various pitfalls awaiting the unattentive modeler. He explains how different assumptions that are deeply ingrained in the two types of spatial models sometimes can result in incompatible predictions of spatio-temporal dynamics. Processes used for illustration are interesting in their own right: rotating spirals, their resistance to parasites (chemical species that accept catalysis from a member of the cycle but do not catalyze the self-replication of any other member), and self-generating clusters that can split, chase, and collapse are fascinating instances of non-mean-field behavior.

Chapter 10 elaborates on one of the biological themes broached in Chapter 9, spatial self-structuring in hypercycle models. Hypercycles are

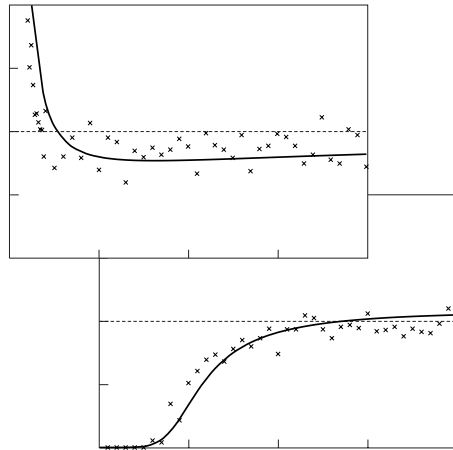
small cyclic reaction networks where each chemical species catalyzes the self-replication of the next species in the cycle. Boerlijst uses PDE models of hypercyclic reaction–diffusion systems while accounting for the discreteness of individuals by using a cut-off at low densities. He discusses how spatio-temporal patterns generated in these systems can greatly change the course of evolution. Specifically, the formation of spirals and spots can make hypercycles resistant to parasites. Such dynamics are best explained by analyses of selective pressures arising at the level of emergent spatial patterns.

Chapter 11 discusses how diffusive coupling between patches can stabilize small predator–prey cycles at the cost of large ones. Jansen and de Roos also consider the effective decoupling of fluctuations in different patches; this decoupling comes about due to demographic stochasticity as well as to the existence of a deterministic but chaotic spatial attractor. The resulting spatio-temporal processes lead to effective stabilization of overall population densities, and the message is that spatially extended predator–prey cycles are damped down relative to their mean-field counterparts.

It is evident from the examples given in Part B and elsewhere in the book that the dynamics of systems that incorporate space can be much richer than those based on mean-field approximations. Biologists and mathematicians are only just starting to chart this territory and to consider what the implications are for dynamics of living systems.

Part C

Simplifying Spatial Complexity: Examples



Introduction to Part C

Because individuals react only to their local environment, ecological interactions are intrinsically spatial. It is the local environment that affects light absorption, nutrient or food intake, and predation risk, thereby indirectly impinging on growth, births, deaths, and movements. Part A showed how, in real life, the local environment is influenced more by near neighbors than by neighbors at greater distances. Various examples presented in Part B showed that these local ecological interactions can have a dramatic influence on population dynamics. Clearly, mean-field approximations can tell only a small part of the ecological story.

Each example discussed in Part B represents an ecological or evolutionary problem worth studying in its own right. Yet it is natural to want to go further and ask to what extent the relationships that emerge apply to more general classes of ecological processes. The resulting research program aims at determining which features in the interplay of mechanisms are essential for the occurrence of particular phenomena and which are coincidental.

This agenda can be approached from two perspectives, an intuitive and a formal one. (Actually these are just extremes of a continuum of research strategies in which both components figure in different proportions.) Intuitive approaches seek appropriate metaphors drawn from our physical or geometrical imagination. If used unaided by more formal tools, these approaches have two drawbacks: their unsystematic character severely limits their scope in complicated settings, and the resulting insights are not always trustworthy. Yet, results based on intuitive reasoning are easy to communicate and have considerable immediate appeal because they engender a feeling of “real understanding.”

Currently available formal approaches cover only a rather small subset of the ecological mechanisms and phenomena of interest. In our opinion, this should not be so much a reason for experimentalists or theorists to seek other pastures as a reason to try to extend the reach of formal methods. In ecology we are unavoidably confronted with complicated patterns of interaction, and formal tools are all we have for tackling such problems in a systematic way. Part C links the surprising range of phenomena originating from the spatially localized nature of ecological interactions exemplified in Part B to the formal approaches for analysis of spatial interactions

explained in Part D. This is done by means of concrete examples showing how the tools can be brought to bear on ecological questions. Part C also illustrates additional relevant tools that are not yet well embedded in a systematic framework.

Chapter 12 shows that, from an appropriate perspective, ecological spatial complexity can be less than it appears at first sight. The chapter starts with the question of how one recognizes natural spatial scales generated by ecological interactions against the backdrop of a homogeneous physical environment. Wilson and Keeling answer this question using as examples both a static pattern generated by a genetic competition mechanism and a dynamic one generated by a predator–prey interaction, obtained by running a grid-based artificial ecology. After identifying the appropriate spatial scales, the authors show how a substantial degree of low-dimensional determinism can be found by considering spatial averages at an intermediate scale, above the scale at which the inherent demographic fluctuations dominate and below the scale at which spatial averaging reduces all spatio-temporal patterns to a homogeneous blur. The chapter's overall message is that a fair amount of formalism may be needed to extract clear signals from a spatially explicit ecological model, but that the quest for reduced descriptions of heterogeneous systems is far from hopeless.

The remaining chapters in Part C fall into one of three categories. Chapters 13 and 14 deal with small-scale patterns; Chapter 15, with intermediate-scale patterns; and Chapters 16 and 17, with large-scale patterns. Small-scale patterns are necessarily stochastic, since they involve small numbers of individuals, whereas large-scale patterns tend to be more deterministic.

Part C provides a first glance at so-called pair approximations and moment closures, recently developed formal tools for dealing with small-scale spatial heterogeneity. In grid-based models, the behavior of each individual is influenced only by a few neighboring individuals. If those neighbors are equivalent and act additively on births, deaths, and movements, mean rates for these three types of events depend only on the average number of neighbors. If we refer to individuals as singlets and to pairs of adjacent individuals as doublets, the change in the average density of singlets depends only on the average density of doublets. Unfortunately, the rate of change of the latter depends on the average density of triplets. Pair approximations and moment closures try to capture triplet densities as functions of doublet and singlet densities, for example, by assuming conditional independence: triplets behave as if they were formed from doublets by random

assemblage. Equations describing the change in singlet and doublet densities are also called moment equations. In the general case, doublet densities, or second moments, depend on the distance between paired individuals. The resulting functions are also called correlation densities, and the notion of moment dynamics is used interchangeably with that of correlation dynamics. In current practice, the term pair approximation is reserved for modeling in discrete space. In principle, however, pair approximations are just special types of moment closures that derive their simplicity from restricting attention to pair correlations at nearest-neighbor distances (a restriction that is only meaningful in discrete space). Examples in Chapters 13 and 14 show how pair approximations and moment equations can successfully describe ecological change under small-scale spatial heterogeneity. A systematic treatment of pair-approximation techniques and moment closure methods can be found in the first four chapters of Part D.

Chapter 13 demonstrates the utility of pair approximations for understanding grid-based models. Iwasa presents three successful applications, ranging from forest dynamics to bacterial competition. The first example studies plants that can reproduce both vegetatively and by seed, with a linear trade-off between the two modes. Mean-field results predict that equilibrium plant density is independent of relative investment in either mode, whereas spatially explicit simulations and pair-approximation results both predict a single maximum at intermediate levels of relative investment. The second example illustrates bistability in the spatially explicit dynamics of forest gaps; the bistability is predicted by pair approximation but is absent from mean-field equations. The model was fitted quantitatively to field data from Barro Colorado Island, Panama, using pair approximation. A third example studies competition between colicin-producing and colicin-sensitive strains of *Escherichia coli*. Whereas mean-field equations predict either bistability or success of the sensitive strain, pair-approximation results largely replace bistability with success of the colicin-producing strain, in accordance with laboratory experiments.

Chapter 14 introduces moment equations for continuous space and presents applications to two spatial Lotka–Volterra models as examples. As in Chapter 13, the quantitative match between results obtained from spatial simulations and those from a moment closure based on a conditional independence hypothesis turns out to be surprisingly good. In the first model, Law and Dieckmann pit two species against each other, one being the better competitor and the other the better disperser. Mean-field results predict survival of the better competitor, whereas moment equations correctly forecast

development of a spatial structure that causes the poorer disperser to suffer more from intraspecific competition, resulting in a reversal of the competitive outcome. The second example investigates how spatial scales of dispersal and competition affect equilibrium mean densities in a single species with local logistic density regulation. Mean-field results can only be trusted when both scales are large. For smaller, yet similar, scales, clumping causes reduced equilibrium densities. When competition neighborhoods are small relative to the scale of dispersal, more regular distributions of individuals result, allowing for increased equilibrium densities.

Chapter 15 investigates the evolution of transmission rates in a grid-based host–parasite system. In the mean-field approximation, evolution maximizes the basic reproduction ratio of parasites, which is proportional to the transmissibility and lifetime of the parasites. The fact that the basic reproduction ratio should be larger than 1 sets a lower bound to viable transmissibilities. In spatial systems accounting for the discreteness of individuals, an upper bound also exists: parasites that are too virulent quickly kill all locally reachable hosts and therefore die out. In addition to these ecological considerations, Keeling discusses evolutionary implications. In a system with spatial structure, adaptation of transmission rates stops near the upper critical value, whereas in mean-field models rates continue to increase (unless a trade-off between transmission and survival is imposed). This chapter is featured in Part C because it illustrates how to simplify complexity at intermediate spatial scales: based on a deterministic caricature that describes the frequency dynamics of spatial aggregates that differ in their numbers of hosts and parasites, the essential behavior of the full spatial model is well recovered. Although, at present, the reduction technique employed is specific to the host–parasite model investigated here, it appears to hold wider promise. One additional message of this chapter is that evolution may proceed considerably slower in a spatial setting than under mean-field conditions.

Chapters 16 and 17 analyze the dynamics of invasion waves, a class of large-scale spatial phenomena that are particularly well understood. Invasion waves are especially relevant for evolutionary considerations, as adaptive innovations often sweep through spatial populations in a wavelike fashion.

Chapter 16 investigates the expansion of epidemics in agricultural crops, ranging from the microscale, where foci with diameters of a few meters develop from single infections, to the continental scale, where an epidemic rages over a continent in one or a few growing seasons. The economic

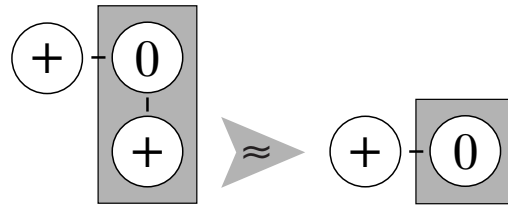
importance of epidemics has resulted in detailed quantitative experimentation and modeling. Zadoks has participated in this research from its early stages and from this perspective describes its history and results. Initial approaches used deterministic numerical simulations. Because basic reproduction ratios of fungal pathogens are very high in agricultural epidemics, their life-history characteristics cannot be neglected; consequently, reaction–diffusion models are inadequate. Early simulation models were based on delay-differential equations for pathogen density coupled with integral equations for the spatial redistribution of spores. A second generation of models taking an analytical approach were phrased in terms of integral equations in space and time; the corresponding mathematical framework is summarized in Chapter 23, including simple recipes for extracting spatial expansion rates. When supplied with real life-history data, these integral-equation models provide surprisingly accurate predictions of the speed of focus expansion. Third-generation models take better account of spatial inhomogeneities and the stochasticity inherent in long-range spore dispersal; they again rely mainly on numerical simulations.

Chapter 17 provides a link between spatial game theory, described in Chapter 8, and reaction–diffusion models, treated in Chapter 22. Ferrière and Michod show how reaction–diffusion equations can be constructed for evolutionary games and review the mathematics available for predicting outcomes of competitive spatial processes. In such settings, strategies can overcome disadvantages of rarity by forming clumps. Supported by such “base camps,” rare strategists can start to conquer space in a wavelike fashion. The chapter investigates invasion waves for the competition between *Tit For Tat* (*TFT*) and *Always Defect* (*AD*), two strategies in the iterated Prisoner’s Dilemma. In particular, the effects of mobility rates and types of memory (determining how past actions of other players are remembered) on competitive outcomes are discussed. In a spatially inhomogeneous setting, the mobility rates strongly influence the rate at which fresh meetings occur. For the *TFT* strategy to spread, *TFT* players need to encounter a sufficient number of their own kind in the front of an invasion wave and should not be suckered too often by *AD* players newly moving into *TFT* clumps.

By showcasing “methods at work” to simplify spatial complexity, Part C should provide a gentle transition to the systematic treatments of techniques offered in Part D.

Part D

Simplifying Spatial Complexity: Techniques



Introduction to Part D

Which systematic techniques can we apply for simplifying spatially explicit models in ecology? In the following chapters, we have assembled a menu of tools tailored to capturing and reducing spatial complexity. Chapters in this part are tutorials, each introducing or extending one method. They should help you to acquire the necessary skills for applying these techniques to ecological problems of your own choice.

The tools described in this part cover three complementary types of models in spatial ecology:

- Probabilistic cellular automata and pair approximations (Chapters 18 and 19)
- Dynamical point processes and moment methods (Chapters 20 and 21)
- Deterministic continuum models and analyses of traveling waves (Chapters 22 and 23)

As we have seen in previous chapters, probabilistic cellular automata discretize ecological space into sites on a regular grid or on a more general contact network. On such a geometry, ecological dynamics unfold as sites change their states depending on states of adjacent sites. In contrast, individuals in dynamical point processes occupy locations in continuous space and thus are not restricted to any given set of sites; individuals may multiply, move, or disappear in response to other individuals present in their neighborhood. Ecological models of cellular automata and point processes are typically stochastic: two realizations of the same ecological process are unlikely to be identical. Continuum models are different: while individuals here are situated in continuous space, they are assumed to be so abundant that their spatial density distributions can be regarded as continuous and their dynamics as deterministic.

For each such modeling framework, techniques have been developed to reduce its spatial complexity. Methods of choice for cellular automata are pair approximations and their refinements; point processes can be simplified by way of moment methods; and the dynamics of continuum models are often best understood by investigating the existence and propagation of traveling density waves. The various examples presented in Part C have introduced these different tools: each has its domain of utility and thus ought to be chosen according to the ecological question at stake. We believe that you will find it worthwhile to learn about these alternatives: such an

overview allows you to decide which tools are best suited to the specific ecological scenario you wish to investigate.

The first two chapters in this part introduce pair approximations. Chapter 18 reviews the fundamental concepts of this technique for grid-based models. While mean-field approaches keep track only of global spatial densities (and therefore are restricted to spatially uniform systems), pair approximations step beyond this simplified view by tracking through time probabilities of states of pairs of adjacent sites. Satō and Iwasa also present so-called improved pair approximations that allow specific *a priori* assumptions about the density of triplet configurations to be incorporated into analyses. This can be done either in a static way (constant discounting) or dynamically (variable discounting). Both refinements are designed to enhance the accuracy of pair approximations.

Chapter 19 shows how pair approximations can exploit knowledge about underlying contact structures. Triangular and square lattices are studied in detail, and other two-dimensional contact networks, resulting from local randomization of lattice links, are investigated as well. To represent ecological processes on grids, it is often helpful to consider simultaneous changes in the states of two adjacent sites (think, for example, of the consumption of a prey individual and the resulting satiation of a predator); van Baalen allows for this generalization. The chapter also emphasizes the importance of local fluctuations for refining predictions of pair approximations.

In Chapter 20, the pair-approximation method is extended to continuous space. Individuals are represented by their actual location, avoiding an artificial discretization of the habitat. With each point in a pattern corresponding to a single individual, ecological change can then be envisaged as the stochastic dynamics of point processes. Bolker, Pacala, and Levin analyze how spatial densities of pairs of individuals depend on the distance between the individuals and how these pair densities are expected to change over time. The resulting moment methods for simplifying spatial complexity successfully predict outcomes of intra- and interspecific competition, and provide analytical insight into intricacies of spatial interactions.

Chapter 21 elaborates on the method of moments in continuous space and presents a three-tiered procedure for its derivation. Ecological processes at the level of individuals are described by a spatially explicit, stochastic process. Expected dynamics of this process are then expressed in terms of correlation densities, with global densities and pair densities as special cases. A closure assumption finally yields self-contained dynamics. Dieckmann and Law discuss their method within the broader context

of relaxation projections, evaluate the relative performance of different closure assumptions, and stress the importance of fluctuation corrections complementing the correlation corrections derived from pair dynamics.

Chapter 22 gives an introduction to reaction–diffusion models – the most popular type of deterministic models in spatial ecology to date. Assuming continuous spatial density distributions, ecological interactions at each location of a habitat are described by deterministic population dynamics, defining the reaction part of the model. The model’s diffusion part allows for the coupling of different locations that results from movement processes. Hutson and Vickers explain the use of comparison methods and review analytical techniques for understanding the formation of Turing patterns and the dynamics of traveling waves. They underline the flexibility of reaction–diffusion modeling by presenting applications to mutation–selection processes and to systems with memory.

Invasion waves are empirically important and are investigated in Chapter 23. Concentrating on this specific class of spatio-temporal patterns, Metz, Mollison, and van den Bosch can incorporate more realistic movement processes and life-history details than is possible for reaction–diffusion models. While invasion waves and foci expansions occur in many different settings – ranging from epidemiological to evolutionary – their main characteristics are often determined solely by the speed of the resulting wave front. The chapter explains ways to predict this speed and discusses complications that arise when space is inhomogeneous, individuals interact (directly or indirectly), or movement of individuals occurs across different spatial scales.

Part D thus provides introductions to three major techniques for simplifying spatial complexity. The utility of these tools has been demonstrated in Part C; here, systematic treatments are given.

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Epilogue

Johan A.J. Metz, Ulf Dieckmann, and Richard Law

We would like to close this volume with a look at the future of mechanistic modeling in spatial ecology. We hope that at least some of the optimistic views sketched below come true. No doubt others, hopefully fewer, will turn out to be mirages.

Just as theory is at its best when it is demonstrably applicable to real ecological systems, field research is most important when it addresses questions that clearly transcend a particular study system. Few researchers, however, have sufficient command of both theory and experiment to actively participate at the two research fronts. It is therefore essential to extend chains of collaboration between empiricists and theorists. These chains should not become too long lest they break or the message passed along becomes too garbled. If such collaborative chains are to work effectively, each partner must have a good understanding of the others' vocabulary, basic concepts, and techniques.

One of this book's objectives is to foster dialogue between those researchers with empirical competence and those with theoretical skills in the field of spatial ecology. In practice, there is still an appreciable distance between the detailed investigations of plant interactions reported in Part A of this volume and the mathematical methods advanced in Part D. However, ecological theory is making great strides toward integrating more ecological realism into manageable models. Theorists and empiricists alike are searching for new kinds of models that are better able to account for the complex implications of spatial heterogeneity. In this context, we clearly discern an increasing appreciation for the importance of constructing ecological theory from the bottom up, starting from the level of the individual and working up to the dynamics of populations and communities. We believe that this is why there already is a close conceptual correspondence between the interaction neighborhoods considered by the plant ecologists in Part A and those used by the mathematicians in Part D (notwithstanding

the distance between the two research fields as practiced today). At a larger spatial scale, the good match between observed epidemiological foci and the theory of invasion waves is also encouraging. We may not yet have all the connections in place, but contacts are being made.

Whereas Parts A and D show some correspondence in their concepts and methods, there is substantial diversity in the intermediate realm, covered in Parts B and C of this book. Here, scientific imagination is roaming more freely, spurred by the availability of powerful computers and the multitude of novel phenomena to be discovered. Humans are visual creatures, with a fascination for spatial pattern. It is becoming increasingly clear that many important ecological phenomena can only be understood in terms of the self-generated spatial patterns found in ecosystems.

Computer simulations and resulting spatial patterns have considerable, and rightful, appeal. In the process of covering new ground in ecological understanding, simulation studies often take on the role of pioneers. In the long run, however, we hope to see the former shoals transformed into safe, fertile ground through systematic consolidation during later successional stages. Here, mathematics can provide the necessary infrastructure. Such consolidation is currently under way in spatial ecology and may eventually help us to see the pattern in the patterns.

At the moment, the pattern is clearest at the extremes of spatial scale. Current mathematical techniques are most successful at the relatively large and the relatively small scales. Moment methods and pair-approximation techniques help us to unravel some of the intricate consequences of small-scale spatial structure. Yet, these methods fail, or need to be extended, in the presence of long-range heterogeneities. On the conceptual side, moment methods alert us to the critical importance of adopting an “individual’s-eye view”: it is the (necessarily local) environments experienced by individuals that shape a population’s response. And in these local environments, neighbors are not always abundant enough to permit us to neglect sampling variance; fluctuation corrections are thus important complements of the correlation corrections that take care of small-scale structure. Reaction–diffusion and integral-equation methods, on the other hand, are tailored to describe large-scale heterogeneities. Models of these types are typically derived from so-called rapid-stirring limits, ensuring the local equivalent of mean-field conditions; for this reason, correlation and fluctuation corrections are rarely considered in such models.

Models in which space and populations are discrete (as in cellular automata) and those where they are continuous (as in partial differential equations) are often viewed as interchangeable descriptions that can be appropriately applied to the same kinds of systems. This view obscures the fact that matches between real systems and their simplified mathematical descriptions are only as good as the assumptions under which those simplifications have been derived from individual-based considerations. Putting more emphasis on formal derivations therefore is not just pedantry. The derivations unveil assumptions and help eliminate misunderstandings that otherwise would soon permeate spatial ecology.

Recent studies underline that it is the discreteness of individuals in particular that has unexpected consequences. In continuum-based descriptions, this discreteness can to some extent be fudged by applying ad hoc threshold rules, but more rigorous ways of handling are needed.

For intermediate-scale patterns, no obvious solution is on the horizon. This is mainly because, for such patterns, clear mathematical limits from which to derive suitably simplified descriptions do not seem to be available. We are more hopeful about the problem of coping with the simultaneous presence of small- and large-scale spatial structure. Here, it seems worth aiming at a merger of moment methods and reaction–diffusion techniques. One step in this direction has already been taken by incorporating fluctuation corrections into reaction–diffusion models (based on so-called hydrodynamic limits of interacting particle systems). Yet, the real challenge remains: to systematically incorporate correlation corrections into reaction terms. We expect some rapid progress on this problem will be possible in the near future.

We believe that all of these developments together will lead to a third generation of models in spatial ecology. After the drastic oversimplification that has compromised mean-field models and, to a lesser extent, reaction–diffusion models, and following the bewildering intractability of many of the contemporary individual-based simulation models, a bridge will be established, constructed from elaborate but manageable models of intermediate complexity.

We expect that this third generation of models will have the following features:

- They will be intimately linked to individual-based models by sound approximation schemes that make explicit the underlying assumptions.

- In particular, new approaches will respect the discreteness of individuals by putting into place fluctuation corrections that go beyond current threshold heuristics.
- They will entail the merging of the insights and techniques already available for small- and large-scale patterns.
- Some will address spatial heterogeneity at intermediate scales. Development of a suite of spatial statistics, geared to particular types of intermediate-scale structure, will allow more systems to be approximated by relaxation projections.
- Based on such advances, evolutionary implications of spatial structure will receive more attention. A theory of spatial adaptive dynamics, in which descriptions of local mutant growth are translated into predictions of phenotypic change, is in the making.

Yet there are many reasons for modesty. More powerful methods generally impose steeper learning curves on their practitioners. Unfortunately, no amount of effort will ever result in models of spatial complexity possessing the simplicity that mean-field approximations once offered. Nonetheless, we believe that the new methods presented in Parts C and D of this book have enticing cost-to-benefit ratios, and we hope that this volume makes those benefits accessible. If the new methods can successfully be applied to an increasing number of relevant ecological questions, then some of them, stripped down to their essentials, may eventually become part of the standard ecological repertoire.

One should be aware, though, that spatial processes have an inexhaustible potential for dynamical complications, and that it will never be possible to deal with this complexity through just one method. Instead, we need inspired combinations of a range of techniques for constructing helpful simplifications. Spatial systems of realistic complexity need to be approached from many angles to achieve the greatest understanding.