

## 1

## Introduction

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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

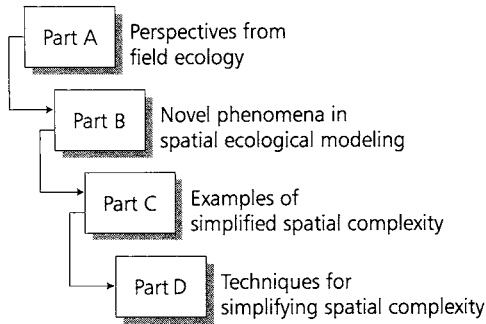
process: it is not the location and behavior of each individual that matters, since the stochasticity will ensure that every realization is different at least in detail. It is the gross properties of the stochastic process that are likely to be of interest in the long run.

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

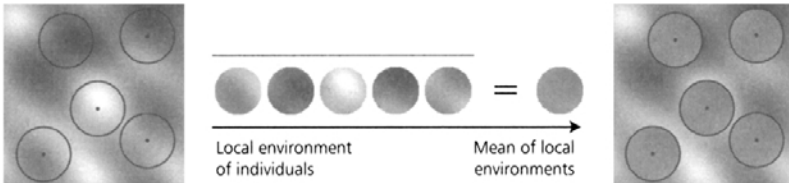
At the heart of much ecological theory lies an assumption that individual organisms encounter one another in proportion to their average abundance across space. You find this assumption in, for instance, the Lotka–Volterra equations for two interacting species  $i$  and  $j$ , expressed as the product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

Cambridge University Press

0521642949 - The Geometry of Ecological Interactions: Simplifying Spatial Complexity

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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.

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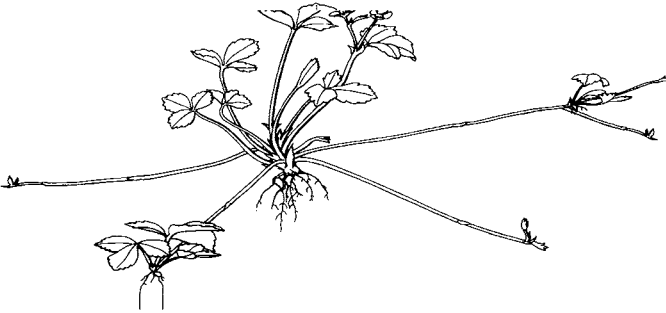
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## Part A

# 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, During, and Law discuss the extent to which these patterns can be said to be self-generating

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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.