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Epilogue

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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.