Preface

Mathematical models and concepts have been important in ecology since its inception as a discipline. However, symbiosis between the disciplines of mathematics and ecology on any appreciable scale is a far more recent phenomenon. Fortunately, in the last few decades, there has been a growing recognition among many theoretical and empirical ecologists and mathematical scientists that they can and should work together to the benefit of both disciplines, science more broadly, and society at large. Promoting this kind of interaction and integration was the theme of a conference we helped organize here at the University of Miami in January 2005, along with colleagues from the Department of Biology and the Rosenstiel School of Marine and Atmospheric Sciences. The title of the meeting was "Workshop in Spatial Ecology." The choice of topic was deliberate and two-fold. First of all, space and spatial features are now solidly established as essential considerations in ecology, both in terms of theory and practice. Second, the mathematical challenges in advancing understanding of the role of space in ecology are substantial and mathematically seductive. We believed that the benefits of bringing together a select group of top-flight ecologists and mathematicians, many of whom would not have heretofore met each other, would be enormous, and if the atmosphere at the meeting is any indication, we were correct. Not long into our interactions, the suggestion arose for some kind of a follow-up volume to the workshop; not a conference proceedings per se, but something more substantial, more thoughtful, that would promote the kind of interplay between mathematics and ecology, and between theory and data, that we so enjoyed during the workshop. We immediately thought of two volumes of essays on ecological theory that have greatly influenced our development as mathematical scientists interested in serious ecological questions: *Perspectives in Ecological Theory*, edited by J. Roughgarden, R. M. May, and S. A. Levin, Princeton University Press, 1989; and *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*, edited by D. Tilman and P. Kareiva, Princeton University Press, 1997. We thought that a volume along those lines that considered emerging challenges in spatial ecology could be highly valuable to a new generation of mathematical scientists and ecologists, especially if the choice of contributors to the volume reflected the current trend toward increased interaction of mathematical and ecological scientists and the resulting trend toward integration of the two disciplines. It was in that spirit that we arrived at the current volume.

We have identified emergent challenges in spatial ecology: understanding the impact of space on community structure, incorporating the scale and structure of landscapes into mathematical models, and developing the connections between spatial ecology and the three other disciplines of evolutionary theory, epidemiology, and economics. This volume is divided into sections focused on those topics. Many of the authors of essays in this volume spoke at the Workshop in Spatial Ecology, but quite a number did not attend. Nevertheless, all of them share a commitment to the advancement of ecology as a truly quantitative science, particularly as it touches upon the role of space.

One of the fundamental problems in spatial ecology is to understand how spatial effects influence the dynamics of populations and the structure of communities. There has been significant progress in recent years on developing and analyzing spatial models for a single population in a temporally constant environment, and at least some on models for two competitors or a predator and its prey, but there has been much less work on models for spatial effects in communities involving several species or trophic levels or environmental variability in both space and time. On the mathematical side, much of the progress on understanding spatial models has been related to the development of a theory that can give criteria for unconditional persistence or extinction, that is, determining when a model has some sort of globally attracting set with certain species present and others absent. There has been some progress, but not as much, on methods for treating models that have multiple attracting sets so that their predictions are conditional on factors such as the initial state of the system. The chapter by DeAngelis et al. describes how models and simulations can provide insight into community and food chain structure in assemblages of fish species in wetland environments where the area of fish habitat is seasonally fluctuating. The chapter by Amarasekare presents results from models that illuminate how dispersal and spatial heterogeneity influence the mechanisms and patterns of species coexistence in multi-trophic communities with intraguild predation or predator-mediated coexistence. The chapter by Jiang and Shi describes recent progress on the mathematical theory for treating models where Allee effects, strong competition, or other mechanisms give rise to "bistability," that is, to multiple stable equilibria.

Classical modeling approaches in spatial ecology typically treat space as homogeneous and isotropic. For example, most spatially explicit models based on partial differential equations envision that organisms disperse through a uniform environment via simple diffusion. However, many ecological processes occur in spatial structures that display various sorts of heterogeneity and/or directionality at various scales, and the nature of the spatial structure of populations themselves is not always obvious. Organisms may disperse via nonrandom mechanisms that arise directly from the physical environment, for example by advection, and may decide whether or how to move in nonrandom ways based on environmental cues. The idea of connecting spatial scale and structure and dispersal behavior to phenomena in population dynamics, evolution, epidemiology, and economics is a recurring theme that is present in many of the chapters in this collection, and it is the specific focus of several of them. The chapter by Ovaskainen and Crone discusses how diffusion models can be extended and refined to describe dispersal in heterogeneous landscapes consisting of patches and corridors of various types, and to account for dispersal behavior that may involve effects such as habitat preferences. The next three chapters are motivated or partly motivated by the problem of understanding ecological processes in river systems. Those systems present a branching spatial structure that is different from that of typical terrestrial environments, and dispersal in them is influenced by physical advection. The chapter by Fagan et al. addresses the issue of formulating metapopulation models for river networks and examines the effects of the "branchiness" of the network on metapopulations inhabiting it. The chapter by Hadeler et al. treats a variety of effects related to models for populations with quiescent phases. One particular problem that is discussed in that chapter is the "drift paradox," that is, the problem of understanding how populations in streams can resist being washed out by advection. Shifting into a quiescent phase is one possible mechanism by which a population can resist washout. The chapter by Nisbet et al. treats population dynamics in advective media, reviews the drift paradox, and identifies characteristic length scales related to population dynamics in such media. The final chapter in this section, by Hinrichsen and Holmes, addresses the problem of determining the spatial structure (or absence thereof) of a population from measurements at different sites. Specifically, it treats the application of state-space models to the problem of determining whether multi-site data correspond to independent populations with independent environmental drivers, independent populations with a shared environmental driver, a collection of populations with the same growth rate but independent environmental drivers, or a single population. Each of those cases would call for a distinct modeling approach, so determining which one represents the actual situation is important for connecting models with data.

The remaining chapters in the collection treat topics related to space and ecology, but do so relative to the perspectives of evolutionary theory, epidemiology, or economics. These areas are related to ecology by both direct connections among the phenomena they examine and philosophical similarities in the issues they address. Ecology describes the framework in which the natural selection that drives evolution occurs. In a sense, epidemiology describes the population interactions between microbes and other organisms, and may involve other aspects of ecology in the contexts of vector-borne or zoonotic diseases. The economics of harvesting resources such as fish or forests are tied to the ecology of those resources. More broadly, all of these disciplines aim to describe the large-scale emergent behavior of systems consisting of many interacting independent agents that may cooperate, compete, or exploit each other. For that reason modeling ideas and approaches that have worked well in the context of one of them may be relevant to others. Finding unifying approaches to these disciplines may be one of the grand intellectual challenges of current scientific thought.

At our present level of understanding, the conclusions about spatial aspects of evolution that can be drawn from models seem to depend to a considerable extent on the detailed assumptions built into the models. The chapters on topics related to evolution in this volume provide a guided tour through a number of scenarios and modeling approaches that represent active areas of current research, and suggest some paths toward conceptual unification. The chapter by Hanski discusses how realistic metapopulation models may provide a unifying approach to ecological and evolutionary theory in fragmented habitats. Those models account for the areas of patches and the connectivity among patches. Hanski discusses how metapopulation models can be used to study the evolution of migration rates in fragmented environments. The chapter by Holt and Barfield also connects metapopulation theory to evolution. It specifically addresses the problem of understanding how environmental heterogeneity influences the evolution of species' niches. The chapters by Cantrell et al. and Bolker, in contrast, treat problems related to the evolution of dispersal in continuous environments. Both of those chapters take the viewpoint of adaptive dynamics as a starting point. The key assumption behind adaptive dynamics is that the strategies which can be expected to be successful in an evolutionarily sense are those that allow populations using them to successfully invade resident populations using other strategies. Although Cantrell et al. and Bolker use similar philosophical approaches based on adaptive dynamics, they use different types of models to study different scenarios. Cantrell et al. use reaction-advection-diffusion models in spatially heterogeneous environments to examine the evolution of dispersal mechanisms arising from local movement behavior that may be responsive to environmental conditions. Bolker uses spatial moment equations to examine how the nature and scale of spatial autocorrelation in environmental suitability influence the evolution of the shape of nonlocal dispersal kernels. Taken together the chapters treating spatial aspects of evolutionary theory show how strongly assumptions about the nature of dispersal and the scale and structure of the environment influence the conclusions that can be drawn about the evolutionary causes and effects of dispersal.

Recent concerns about the emergence or resurgence and global spread of infectious diseases have motivated renewed interest in epidemiology. Many potentially dangerous pathogens are zoonotic or vector-borne and thus have aspects that are directly related to ecology. Some similar problems arise in both disciplines, and often these can be addressed by similar modeling approaches. That point is well illustrated by the chapters on epidemiology. The chapter by Lloyd and Sattenspiel uses a metapopulation approach to examine how nonlinear disease dynamics interact with seasonal forcing to determine spatiotemporal patterns in disease dynamics. The chapter by Potts and Kimbrell describes how simulation models can be used to compare different control strategies for vector-borne diseases. The chapter by Ruan and Wu reviews a selection of reaction-diffusion models for the spread of diseases with animal hosts. In each case the modeling approach is reminiscent of ideas that are widely used in ecology, but is modified by the specific features of the epidemiological system it describes.

As human populations increase they put increased pressure on natural resources, which makes it crucial that we learn how to use them in sustainable ways and if possible to optimize the benefits derived from them. To do that it is necessary to understand how economics interacts with ecology and then apply ideas from optimal control theory. The chapter by Sanchirico and Wilen addresses the problem of optimal fisheries management from the viewpoint of metapopulation modeling. The chapter by Olson explores the general issue of constructing models that describe the dynamics of resources, human factors in harvesting them, and the flow of capital investment needed to support the harvesting. The chapter by Herrera and Lenhart reviews some results on optimal control in metapopulation models and shows how to extend the approach to reaction-diffusion models and related models based on partial differential equations.

Our friend and colleague Alan Lazer once remarked: "It is better to open up an area of research than to close one down." As the chapters in this volume show, there is a great deal more to be done before the discipline of spatial ecology is ready to be closed down. We hope that this volume will inspire readers to open up new areas of research in the mathematical theory of spatial ecology and its connections with evolutionary theory, epidemiology, and economics.

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