Integrodifference equations in spatial ecology

Frithjof Lutscher

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Preface

Ecosystems are marvellous assemblages of individuals that grow, reproduce, interact with one another, move about in space, and eventually die. Spatial ecology aims to understand the role that individual movement, population interaction, and landscape characteristics play in generating the patterns of species distributions that we observe in space and time. The seemingly most basic question is: what conditions are necessary for a particular species to be present at a particular location? This deceptively simple question is at the heart of modern conservation biology: how do we design nature reserves to preserve a particular species? Its economic cousin, which arises for example in fisheries, is the question: how much can we harvest, and where, without jeopardizing the survival of that species and the others that depend on it? And a planning perspective on the same question is: where should we place infrastructure to minimize negative effects on ecosystems? These are all inherently spatial questions. Whether a population persists in a given environment depends on how individuals move about, use the available resources and avoid existing dangers.

Another striking example of spatial processes in ecology are biological invasions. The spread of alien species can disrupt ecosystem function, diminish biodiversity, and require massive investments in remediation measures. Human activities such as travel or international trade facilitate the arrival of alien species and their spread in new environments. Spatial ecology aims to provide theory to predict the speed of spatial spread of a species from its various underlying reproductive and dispersal mechanisms. In other situations, we would like to introduce certain species in new habitats as biological control agents, and we need to predict and assess their spread and efficiency. In a world of climate change, species will have to move and colonize new territories to keep up with their preferred climatic conditions. Spatial ecology aims to predict which species will be able to do so, and develop mitigation measures for those who will not.

The sheer scope of these problems, their spatial and temporal extent, make mathematical models indispensable tools to answer some of the questions. Such models provide fundamental insights about the processes at work; they serve to process the increasingly growing amount of available data; and they allow to test management strategies in simulations before implementation in the real world. My goal is to provide a mathematical framework to study and understand how individual dispersal characteristics and interactions within and between populations interact to generate spatio-temporal patterns of population distribution and abundance. My particular focus is on species with distinct growth and dispersal phases, which include many plant, insect and bird species in temperate climates. I envision this book to be a new opportunity for ecology and mathematics to meet and create synergies that lead to deeper understanding of ecological phenomena and create better tools and guidelines for management of ecosystems.

Mathematical models in the form of dynamical systems served ecological theory well for over a century and, in turn, spurred the development of mathematical theory. Ordinary differential equations for the growth of individual populations and for population interactions in continuous time go back to Lotka and Volterra and are now found in many textbooks of ecology as well as mathematics. The seminal work by Fisher (1937) in population genetics and by Skellam (1951) in ecology began to combine these population growth models with spatial movement of individuals, modelled as random diffusion. The resulting reaction-diffusion equations have yielded many deep insights into spatial phenomena in ecology as well as the mathematical structure of infinite-dimensional dynamical systems (Cantrell and Cosner, 2003).

Dynamical systems models for populations in discrete generations rose to fame with the discovery that simple density-dependent growth functions could generate complex and chaotic dynamic behaviour (May, 1975). These discrete-time dynamical systems are sometimes easier to formulate, typically easier to simulate, and almost always more difficult to analyze than their continuous-time counterparts. The two foundational works that combined discrete-generation population dynamics with spatial dispersal of individuals are by Weinberger (1982) in genetics and by Kot and Schaffer (1986) in ecology. After the discovery of the mathematical phenomenon of ‘accelerating invasions’ (Kot *et al.*, 1996), ecologists quickly embraced these so-called integrodifference equations as their framework of choice to test models against data for species invasions (Lewis *et al.*, 2006). Meanwhile, mathematicians took up the challenge to study the qualitative behaviour of these infinite-dimensional recursions. This book provides the first comprehensive exposition and review of the mathematical and ecological literature on integrodifference equations.

The Introduction serves as an overview of some of the fundamental questions of spatial ecology, some recent challenges in the face of global change and human disturbances, and their relation to current challenges in ecosystem management. The first part of the book (Chapters 2-8) develops all aspects of the theory of integrodifference equations from model derivation to basic mathematical analysis and numerical implementation. The guiding principle is to explain every new aspect with the simplest possible example and motivate the more general study with it. Chapter 2 carefully derives the basic model, discusses its assumption and limitations, and summarizes some of the mathematical background required to proceed. Chapter 3 deals with the so-called ‘critical patch size’, the question of how much space a population needs to persist. Chapter 4 looks at the steady-state problem and the spatial profile of the population distribution. Chapters 5-6 deal with spatial spread and biological invasions in the absence and presence of an Allee effect. A typical integrodifference equation contains only the outcome of the dispersal process, but in many cases it is helpful and necessary to model the actual process itself (Chapter 7). Chapter 8 contains recipies and warnings about numerical implementations of integrodifference equations.

In the second part of the book, I present many applications of the theory from the first part to more realistic ecological problems. Including more realism often requires minor modifications of the models and sometimes new theory to understand their behaviour. In Chapters 9 and 10, I present various techniques for how to approximate population dynamics and spatial spread characteristics when only partial information about dispersal is available. Chapter 11 examines the intricate shapes that the fronts of invading species can take. Chapter 12 reviews many applications of integrodifference equations to date, for example, to river ecosystems, to global change scenarios, to Reid's paradox and more.

The third part of the book contains extensions of the theory that represent the current edge of the theory and its applications. Chapter 13 considers population stage-structure and presents the most recent literature connecting models to data for invasive species. Chapter 14 includes the interaction of two species and studies phenomena such as spatial pattern formation. Chapters 15 and 16 deal with population dynamics in spatially and temporarily (stochastically) varying environments. The final chapter summarizes the most recent developments in various directions and includes a review of connections of this theory to related approaches.

While the focus of this book is on the mathematical aspects, I include real applications to ecological questions throughout – in fact, they serve as a constant source of motivation and illustration of the mathematical approaches and results. I strongly believe that the greatest progress is made where ecology and mathematics come together to inspire each other towards deeper understanding in each discipline and their interplay.

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