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MODELING RANGE EXPANSIONS IN BIOLOGICAL INVASIONS

Shigesada, Nanako, and Kohkichi Kawasaki. 1997. **Biological invasions: theory and practice**. Oxford Series in Ecology and Evolution. Oxford University Press, New York. xiii + 205 p. \$75.00 (cloth), ISBN: 0-19-854852-4; \$32.95 (paper), ISBN: 0-19-854851-6.

Biological invasions have emerged in the last decade as one of the most pressing and challenging ecological issues associated with human expansion and global change. This issue has led to a strong increase in awareness by field biologists and has resulted in a plenitude of anecdotal data on the occurrences, impacts, and consequences of invasions. However, even the most basic questions—which species will invade, what habitat is susceptible, how far and fast an invasion might spread, what will happen to the existing community or ecosystem—go largely unanswered. This might be a direct result of the strong emphasis on case studies within the invasion literature, where each invading organism and each invaded ecosystem are considered unique, and where it seems impossible to generalize and even less to predict invasions. Or it might result from deep difficulties inherent in the complexity of invasions. Predicting which small subset of a vast collection of potential invaders will actually be successful in a specific case may be as difficult as predicting the future course of evolution. Indeed, models can consider some aspects of evolution to be the invasion, spread, and establishment of new phenotypes. However, in spite of difficulties, we must try to generalize, and must try to predict which species invade and how they invade. A theoretical framework can provide a way to understand the crucial factors controlling an invasion and also might increase our ability to predict invasions. This is largely lacking from the invasion literature, except for an extensive literature on the actual spread of specific invasions.

Now, for readers hoping to find simple prescriptions for answering specific questions on invasions, this book may be a disappointment. It contains numerous fascinating examples of invasions, like classic studies on starlings, muskrat, house finch, gypsy moth, cheatgrass, rinderpest, etc. But this book does not pinpoint specific components of an invasion and how to test them with real data. It also does not emphasize questions on which species will be an invader and which ecosystems are invulnerable. Readers expecting direct answers to such questions will come away disappointed from this book.

But for readers looking to find a state-of-the-art discussion of the mathematics of invasions—deriving general principles from specific case studies—this book can be a joy. Graduate students will find a reference work for the most common modeling approaches in the spread of invasions, and re-

searchers constructing mathematical models of invasions will find this essential reading, and will find the material developed in a clear and coherent manner. The main emphasis is on the spread of populations, both under simple and complex dispersal, but the authors expand their emphasis by examining invasion under the influence of competition and predation, under disturbance, and so forth.

The book includes chapters on diffusion models (e.g., Fisher's equation of logistic population growth under random walk and Skellam's model of Malthusian growth), stratified diffusion, biological waves in homogeneous or heterogeneous environments, invasion of competing species or predators, competition for open space, and epidemics. Throughout, the authors apply broad theoretical models (largely partial differential reaction-diffusion equations) to uncover basic ecological principles. Do not expect to find complex simulation programs with an abundance of parameters. Nor to find much discussion of other approaches to modeling invasions, such as integro-difference and integro-differential equations, nor of stochastic models. But do expect to find basic mathematical models consolidated into one volume and made accessible to a rather wide audience, with the fundamental equations nicely derived from biological premises in appendices.

The book ends with epidemic models of well-studied invasions by infectious diseases. These models build on some of the best studied and documented invasion cases like measles, the black death, myxoma virus in rabbits, and rabies, and show the potential of models to generate a better understanding of the crucial factors controlling the spread of these diseases. They also offer the hope that models might be able to point a way to understand and possibly control the spread of invaders, at least for well-known invaders. From here theoretical researchers can try to explain what help they need from empirical observational or experimental data to test the factors that influence or control the range expansion of organisms. This approach could lead to a theory that may be able to understand invasions mechanistically and to make recommendations on how to limit invasions, both on a continental scale and a more local scale. This, however, will have to take present theory to the next step, which has to be beyond the process of matching models to documented invasions. This challenge is out there, and as the current awareness of invasions shows, such a theoretical framework is urgently needed. This book nobly advances the cause, but—as is often true in ecology—a lot more work remains.

JOHANNES M. H. KNOPS AND CLARENCE L. LEHMAN

*University of Minnesota
 Department of Ecology, Evolution and Behavior and
 Cedar Creek Natural History Area
 1987 Upper Buford Circle
 St. Paul, Minnesota 55108*