Ecology of Populations

The theme of the book is the distribution and abundance of organisms in space and time. The core of the book lies in how local births and deaths are tied to emigration and immigration processes, and how environmental variability at different scales affects population dynamics with stochastic processes and spatial structure, and it shows how elementary analytical tools can be used to understand population fluctuations, synchrony, processes underlying range distributions, and community structure and species coexistence. The book also shows how spatial population dynamics models can be used to understand life history evolution and aspects of evolutionary game theory. Although primarily based on analytical and numerical analyses of spatial population processes, data from several study systems are also dealt with.

ESA RANTA is Professor in Animal Ecology at the University of Helsinki, Finland.

PER LUNDBERG is Professor in Theoretical Ecology at the Lund University, Sweden.

VEIJO KAITALA is Professor in Population Biology at the University of Helsinki, Finland.

ECOLOGY, BIODIVERSITY, AND CONSERVATION

The world's biological diversity faces unprecedented threats. The urgent challenge facing the concerned biologist is to understand ecological processes well enough to maintain their functioning in the face of the pressures resulting from human population growth. Those concerned with the conservation of biodiversity and with restoration also need to be acquainted with the political, social, historical, economic and legal frameworks within which ecological and conservation practice must be developed. This series will present balanced, comprehensive, up-to-date and critical reviews of selected topics within the sciences of ecology and conservation biology, both botanical and zoological, and both 'pure' and 'applied'. It is aimed at advanced final-year undergraduates, graduate students, researchers, and university teachers, as well as ecologists and conservationists in industry, government and the voluntary sectors. The series encompasses a wide range of approaches and scales (spatial, temporal, and taxonomic), including quantitative, theoretical, population, community, ecosystem, landscape, historical, experimental, behavioural, and evolutionary studies. The emphasis is on science related to the real world of plants and animals, rather than on purely theoretical abstractions and mathematical models. Books in this series will, wherever possible, consider issues from a broad perspective. Some books will challenge existing paradigms and present new ecological concepts, empirical or theoretical models, and testable hypotheses. Other books will explore new approaches and present syntheses on topics of ecological importance.

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ESA RANTA
University of Helsinki

PER LUNDBERG
Lund University

VEIJO KAITALA
University of Helsinki

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Preface

The ecology of populations is the study of the patterns of distribution and abundance of organisms. It also goes beyond mere description and seeks the evolutionary forces that might produce such patterns, and their ecological constraints. This book is on the ecology of populations but it is not a population ecology textbook. Therefore, there will be much standard textbook material left out. This book does not attempt to establish a new field, or summarize or synthesize an old one. Neither does it provide the student of population biology with all the necessary tools for further exploration, nor does it review the entire discipline, or parts of it. So what does this book do? As with most books, it presents an idiosyncratic world-view. We hope that some well-known problems and phenomena are getting a fresh and novel approach. We also hope that applying basically the same analytical tool to a number of seemingly disparate problems in population biology will be convincing enough to make others do likewise. By using rather simple models of population change to a large number of problems, we hope that conceptual unification will be promoted. Science becomes more and more specialized with the risk of losing track of the bigger picture. Although no bigger picture is presented here in a coherent way, the approach we have taken to address problems in population ecology aims at getting to that more synthetic understanding. We start by investigating simple and well-known models of population change and the extent to which they are reasonable representations of the population phenomena we can observe in natural or laboratory systems. By doing so, we also emphasize the link between evolutionary change, ultimately altering the life history of organisms, and changes in population size in time and space. The spatial dimension in population ecology is such a fundamental one that we have cast many of the problems in one spatial setting or another. In fact, simple assumptions about local births and deaths coupled by the movement of individuals across space (i.e., immigration and emigration) make so much sense, and has indeed the power of explaining a wide range of problems from life

history evolution to the management of harvested populations. Including more than one species (or life history strategy), i.e., to move into the field of community ecology, is not a particularly big step. Approaching this wide range of problems with these methods, we believe, is a fruitful way of doing population biology.

Although we have tried to show that the theoretical constructs dealt with here also have a lot to do with actual phenomena in nature, we have not emphasized examples and empirical evidence. Rather, this is more a book on how to approach scientific problems in (evolutionary) population ecology. It does not say anything on how to test models, or how to build models. It emphasizes that it is possible to use rather simple building blocks, the per capita rates of births, deaths, immigration, and emigration, to model and therefore hopefully better understand population processes from an ecological and evolutionary point of view.

Doing theoretical ecology is a hazardous cruise between the formal and rigorous mathematical SCYLLA, and the overwhelmingly rich empirical CARYBDIS. Too many equations and too few examples make an empiricist suspicious, uneasy, and sometimes even hostile. Too little rigor and a good deal of careless talking of things we do not *really* understand make the mathematician bored and a disbeliever as well. So, the best pedagogic trick would then be, of course, to show how beautifully the models and theories match the data ecology so painfully has collected over so many years. But our purpose here is not to show that theory works according to some suitable standard. We want to show that if some of the very basic and easily accessible concepts in ecology are taken seriously, and adding some spatial structure, much of what we can observe of the distribution and abundance of organisms can be explained and understood. If we also leave the deterministic world-view and let the processes of concern be the stochastic variables they inevitably are, then even more is gained.

This book should thus be read as a starting point for further explorations rather than a summary of the field. We have probably erred when omitting much of the classic and rather far-reaching knowledge in many of the areas covered here. This is both a consciously biased selection and a flaw in our knowledge and thinking. Hopefully the novelty and in some parts state of the art material compensate for that.

The self-evident, yet joyful fact that science is a collective process does not stop us from acknowledging the contributions from a number of people and organizations to this and other projects of ours. The whole idea of writing this book emerged at a meeting in Møls, Denmark, at a workshop funded by the Nordic Academy for Graduate Teaching

(NorFA) in 1996. We organized a number of workshops and symposia after that, and all the students and colleagues contributing to those meetings have also contributed to this book in various ways. That tradition continued as we launched a network of researchers and graduate students funded by the Finnish Academy (the MaDaMe program). The financial support from NorFA and the Finnish Academy (ER, VK), the Spatial Ecology Program (Ecology and Evolutionary Biology, University of Helsinki), Center of Excellence in Evolutionary Ecology (Department of Biological and Environmental Science, University of Jyväskylä (VK)), the Swedish Research Council (PL), and the Swedish FORMAS Research Council (PL) has been crucial for our joint efforts. Parts of this work were conducted while PL was a Sabbatical Fellow at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-0072909), the University of California, and the Santa Barbara campus. We owe all students and colleagues that have participated in those activities a heartfelt thank-you. People in our immediate neighborhoods have been wonderful friends, colleagues, inspirers and teachers, and hence important throughout the production of this book. Others have influenced our scientific journey more subtly. Many thanks to Sami Aikio, Susanna Alaja, Joel Brown, Katja Enberg, Torbjörn Fagerström, Anna Gårdmark, Mikko Heino, Bob Holt, Peter Hudson, Jouni Laakso, Harto Lindén, Niclas Jonzén, Jörgen Ripa, Nils Christian Stenseth, Stuart Pimm and Peter Turchin. Finnish Game and Fisheries Research Institute has allowed us to use their long-term records of game animals. The Nordic Centre of Excellence Programme by the "Nordiska Ministerrådet" supported the final phase of the manuscript preparation.

The entire manuscript of the book was read and commented upon by Tim Benton and Hannu Pietiäinen. Jordi Bascompte, Mikko Heino, Stuart Humphries, Niclas Jonzén, Hanna Kokko, Jouni Laakso, Elina Lehtinen, Kate Lessells, Jan Lindström, Jari Niemilä, Jörgen Ripa, Graeme Ruxton, Richard Solé, Bill Sutherland, and Erik Svensson have read one or several chapters. We are very grateful to all these people for insightful comments and suggested corrections. We have probably taken their advice too lightly and – of course – all errors or omissions are ours alone.

Finally, we are indebted to our close friends and families for letting us do what we are doing, at times even supporting it!