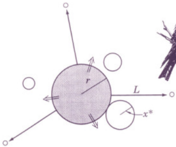
Oxford Series in Ecology and Evolution

Biological Invasions: Theory and Practice

Nanako Shigesada and
Kohkichi Kawasaki



Biological Invasions: Theory and Practice

Nanako Shigesada
Nara Women's University, Japan

and

Kohkichi Kawasaki
Doshisha University, Japan

This publication was supported by a generous donation
from the Daido Life Foundation

Oxford New York Tokyo
OXFORD UNIVERSITY PRESS
1997

Biological Invasions

This book has been printed digitally in order to ensure its continuing availability

OXFORD
UNIVERSITY PRESS
Great Clarendon Street, Oxford OX2 6DP
Oxford University Press is a department of the University of Oxford.
It furthers the University's objective of excellence in research, scholarship,
and education by publishing worldwide in
Oxford New York
Auckland Bangkok Buenos Aires Cape Town Chennai
Dar es Salaam Delhi Hong Kong Istanbul Karachi Kolkata
Kuala Lumpur Madrid Melbourne Mexico City Mumbai Nairobi
São Paulo Shanghai Singapore Taipei Tokyo Toronto
with an associated company in Berlin
Oxford is a registered trade mark of Oxford University Press
in the UK and in certain other countries
Published in the United States
by Oxford University Press Inc., New York

Reprinted 2001

A catalogue record for this book is available from the British Library

Library of Congress Cataloging in Publication Data
Biological invasions : theory and practice / Nanako Shigesada and
Kohkichi Kawasaki. — 1st ed.
(Oxford series in ecology and evolution)
Includes biographical references and index.
1. Biological invasions. 2. Biological invasions—Mathematical
models. I. Kawasaki, Kohkichi. II. Title. III. Series.
QH353.S54 1997 574.5'247—dc20 96-34591 CIP

ISBN 0-19-854851-6 (Pbk)
ISBN 0-19-854852-4 (Hbk)

Oxford Series in Ecology and Evolution

Edited by Robert M. May and Paul H. Harvey

The Comparative Method in Evolutionary Biology
Paul H. Harvey and Mark D. Pagel

The Causes of Molecular Evolution
John H. Gillespie

Dunnock Behaviour and Social Evolution
N. B. Davies

Natural Selection: Domains, Levels, and Challenges
George C. Williams

Behaviour and Social Evolution of Wasps: The Communal Aggregation Hypothesis
Yosiaki Itô

Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology
Eric L. Charnov

Quantitative Ecology and the Brown Trout
J. M. Elliott

Sexual Selection and the Barn Swallow
Anders Pape Møller

Ecology and Evolution in Anoxic Worlds
Tom Fenchel and Bland F. Finlay

Anolis Lizards of the Caribbean: Ecology, Evolution, and Plate Tectonics
Jonathan Roughgarden

From Individual Behaviour to Population Ecology
William J. Sutherland

Evolution of Social Insect Colonies: Sex Allocation and Kin Selection
Ross H. Crozier and Pekka Pamilo

Biological Invasions: Theory and Practice
Nanako Shigesada and Kohkichi Kawasaki

To the memories of
Professors Ei Teramoto and
Akira Okubo

Preface

Human activities have brought about drastic changes in the global environment, one grave consequence of which is increased incidences of biological invasions. This book provides mathematical development of ideas about biological invasions on a global scale, with emphasis on deriving general biological principles from specific biological case studies.

The present book is based on an earlier one published in Japan (in Japanese) by one of the authors (N.S.), entitled *Mathematical modeling for biological invasions* (University of Tokyo Press, 1992); this English edition, however, results from the collaboration between two authors. The original Japanese edition is aimed primarily at university undergraduate and graduate students, and its purpose is to introduce to them some of the pioneering works in biological invasion as well as some mathematical models developed by the authors. Necessarily, discussions on many relevant theories, field data, and their references were curtailed in favor of conciseness. For this English edition, we have included more field data, updated some theoretical results according to the latest findings, and rewritten much of the text with a wider audience, including field researchers and scholars, in mind.

As noted in the introductory chapter, examples of biological invasions are to be found everywhere, some of the most obvious being with common plants familiar to most of us. The actual invasion process varies depending on multiple factors such as the characteristics or behaviour of the invading species, environmental conditions of the invaded site, and interactions with indigenous species. We have limited our discussion to examples that are characteristic and typical. Furthermore, most of the models we present are constructed upon simple conditions, often leading to simple, clear-cut results. Some readers may thus find that the data on invasion which they possess do not conform to any of the propagation patterns introduced in this book. It goes without saying that the living environment of organisms varies greatly, and if one is to offer a rigorous explanation of actual propagation patterns, one must prepare a model that corresponds to the detailed reality of the species in question. Even so, the authors' hopes are that many of the cases can be explained by using as the basis a model presented in this book, and modifying the model by incorporating additional factors. Indeed, if this book can provide an initial framework for those pursuing an analytical study of invasion, then our original purpose in writing it will have been met.

The authors had hoped to dedicate this book to Dr Ei Teramoto, who was largely responsible for founding and developing the field of mathematical ecology in Japan, and to Dr Akira Okubo, who wrote the classic treatise on ecological diffusion, *Diffusion and ecological problems: mathematical models* (Springer-Verlag, 1990). Sadly, both passed away at about the same time, in February of this year. The authors' relationships with Dr Teramoto go back to their student days at Kyoto University, where as their supervisor he sparked their interests in mathematical biology, leading each of them to pursue academic careers in this field. Meanwhile, each of the authors has spent a sabbatical period at Dr Okubo's laboratory at the State University of New York, where they were given opportunities to deepen their interests in the theory and practice of biological diffusion. Clearly, the authors would not be what they are today were it not for these two *sensei*s.

The authors wish to thank Dr Joel Cohen, who created for them the opportunity to publish this English version, and Dr Robert M. May, who encouraged them to publish it as part of the Oxford Series of Ecology and Evolution. Dr Cohen visited N.S. in 1990 when she was at Kyoto University, and after looking at the Japanese manuscript which she was working on at the time, encouraged her to publish a translated version. When the Japanese volume was finally published two years later, N.S. sent him a copy as a courtesy, which he obligingly forwarded to Dr May along with his letter of recommendation. This English version, then, owes its existence to these two persons. Dr May offered many valuable suggestions and comments regarding the book's composition, as well as warm support and encouragement to speed up its publication.

In the process of writing this book, the authors were fortunate to receive from many researchers in the field their latest research findings and data as well as much advice, directly and indirectly, concerning its content. These people include, from abroad, Drs David Andow, Peter Kareiva, Simon Levin, Jim Murray, Hal Caswell, Eli Holmes, Sandy Liebhold, and Hans Metz. Within Japan, many people pointed out corrections and offered constructive suggestions against the already published Japanese version. In particular, Drs Yasushi Harada, Masahiko Higashi, Kazuro Iwata, Yoh Iwasa, Masae Shiyomi, Fugo Takasu, and Nobuyuki Tuji carefully read the entire text and offered invaluable comments. Incorporating their comments, the original Japanese manuscript was extensively rewritten for the English translation, hopefully improving its readability. The authors gratefully acknowledge all those who offered assistance or support in the writing of this book, including many whose names are not mentioned here.

The authors also wish to thank Dr Toshitaka Hidaka, who originally recommended to N.S. that she publish the Japanese edition, and their editor, Mr Yoshifumi Komyo of the University of Tokyo Press. Thanks are further due to Ryu Takeguchi for his unfailing and invaluable help in producing the English translation, and to the editorial staff of Oxford University Press for their unceasing and expert support.

The authors are grateful for a generous donation from the Daido Life Foundation. They also acknowledge that their research presented in this book was supported by Grants-in-Aid for Scientific Research from the Ministry of Education, Science and Culture.

Last but not least, K.K. thanks his wife Tomoko for her wonderful personal support. N.S. expresses her gratitude to her husband, Katsuya Shigesada, for his great understanding and constant encouragements.

September 1996 N.S.
K.K.

Contents

1 Introduction **1**

2 Invasion of alien species **6**

2.1 Mammals 6
2.2 Birds 12
2.3 Insects 18
2.4 Plants 22
2.5 General features and classification of expansion patterns 26
2.6 Appendix: measurement of range distance 30

3 Diffusion models and biological waves **35**

3.1 Fisher's model 35
3.2 Diffusion equation 36
3.3 Logistic equation 39
3.4 Skellam's model 41
3.5 Fisher equation and travelling frontal wave 46
3.6 Travelling waves in general models 49
3.7 Match between theory and observation 51
3.8 Appendix 1: derivation of diffusion equation 56
3.9 Appendix 2: travelling wave solution and its speed 57

4 Travelling waves in heterogeneous environments **61**

4.1 Patch models 61
4.2 Travelling periodic waves 63
4.3 Condition for successful invasion 64
4.4 Speed of travelling periodic wave 66
4.5 Travelling irregular wave 69
4.6 Effects of environmental fragmentation on biological conservation 72
4.7 Appendix: derivation of invasion condition, eqn (4.4) 77

5 Invasion by stratified diffusion 79

5.1 Short-distance dispersal and long-distance dispersal 79
5.2 Scattered colony model 80
5.3 Coalescing colony model 85
5.4 Application: European starling and house finch 93
5.5 Mechanistic models 96
5.6 Appendix: the coalescing colony model—derivation of eqns (5.12)–(5.15) 102

6 Invasion of competing species 104

6.1 Competition between resident and invading species 104
6.2 The competition equation 105
6.3 Retreat of resident species 107
6.4 Competition between grey and red squirrels 109

7 Competition for open space 114

7.1 Disturbance and open space 114
7.2 Competition for large open spaces 116
7.3 Disturbance and species diversity 122
7.4 Appendix: range expansion of a later invading species: an approximate solution 130

8 Invasion of predators 133

8.1 Invasion of a predator and biological control of pest species 133
8.2 Travelling wave in prey–predator system 134
8.3 Host–parasitoid systems and self-organized spatial structures 137
8.4 Retreat of travelling wave by sterile insect release 140

9 Epidemic models and propagation of infectious diseases 144

9.1 Epidemics in history 144
9.2 Kermack–McKendrick model 149
9.3 Epidemics of measles 152
9.4 Spatial spread of the Black Death 158
9.5 The effects of epidemics on population demography 161
9.6 Evolution of myxoma virus in the European rabbit 162

9.7 Appendix: threshold population for epidemic occurrence—derivation of eqn (9.6) 165

10 Invasion of rabies in Europe **166**

10.1 Recent epidemics in Europe 166
10.2 Red fox and rabies 167
10.3 Spatial propagation 172
10.4 Control of expansion 180
10.5 Appendix: speed of range expansion of rabies 184

References **186**

Index **201**

1

Introduction

In nature, all organisms migrate or disperse to some extent. This can take a diversity of forms as in walking, swimming, flying, or being transported by wind or flowing water. Among organisms that have the ability to move, many possess the habit of moving back and forth within a definite range on a regular basis. For instance, zooplankton repeat diurnal vertical movements in which they float to the water's surface during the daytime, while sinking to the bottom at night. Many birds and mammals return to their nests or dens at the end of an active day spent in their respective home range. The most commonly identified return migrations are those with a yearly periodicity. Migratory birds such as swallows return regularly to the same breeding area year after year. Some fish and whales migrate between the equatorial zone and polar regions in their search for feeding or breeding grounds. However, a species' range cannot expand beyond fixed ranges by such return migrations alone. It can expand only if there are certain individuals who disperse to new areas without returning to their original places.

Dispersive movements become noticeably active when an offspring (or seed) leaves its natal sites, or when an organism's habitat deteriorates from overcrowding. Many marine organisms, such as reef-dwelling shrimp or shellfish that spend their larval period floating in the open seas, and most insects have within the individual's life cycle a built-in period of dispersion. Among vertebrates, exploratory migration is a characteristic of the dispersal patterns of immature animals, often called post-juvenile dispersion. If a new suitable habitat is found by such dispersal, the range can expand; if not, the dispersion ends up being wasted. 'Invasion' occurs when a species colonizes and persists in an area which it previously had not inhabited.

In an area where the environment remains virtually unchanged and which is isolated from the external world, inhabiting organisms are considered to expand their range as much as their dispersive capacities allow, after which a stable, balanced state is maintained. In reality, however, not only is an organism's living environment spatially and temporally changing, it is also an open system into which various species are moving.

Seen from a geological time scale, the geographical distribution of species on the earth's surface has changed each time a large-scale climatic or geomorphological change has taken place (Cox and Moore, 1993). These changes have resulted in geographical separations in a species' range, at times causing further speciation. For example, with glacial expansions the flicker, which inhabited the central forests in North America, shifted its range southward and spent the glacial period as two separate groups, east and west, divided by the Rocky Mountains. Eventually, when the climate became warmer again, the two groups moved back north to meet once again, but they had become different enough from each other so as to be classified as distinct species (Udvardy, 1969).

As an example of a large-scale invasion caused by geographical changes, fossil records show that when an upheaval at the present Panama canal site bridged the North and South American continents in the Pleistocene epoch some two million years ago, it caused organisms from both sides to intermix with each other. Because they had not been directly connected for a long period, the two continents shared no mammalian species that belonged to the same family groups; once the Panama land bridge initiated faunal mixing, the number of families on each continent increased drastically. Due to the competition between existing and invading species, however, many of them subsequently became extinct, and in the biota that eventually resulted after reorganization, the number of families had fallen to about the same level as before intermixing had occurred (25 in North America, 30 in South America) (May, 1978; Cox and Moore, 1993). This is often cited as supporting evidence for the dynamic-equilibrium theory of MacArthur and Wilson (1967), which states that in a certain area (particularly an island) the number of invader species and of those that become extinct balance each other, thus achieving equilibrium in the number of species. Most South American species that moved into North America eventually died out, which is thought to be the result of the superior competitive strength of North American species. This is explained by the fact that the North American continent had previously been connected to other continents in the northern hemisphere, making its ecosystems less susceptible to invasion by alien species than in South America.

More recently, when Krakatau, a volcanic island located between Java and Sumatra, erupted in 1883, the biota on the island was wiped out under a rain of hot volcanic ash. Systematic studies of the subsequent rehabitation process have obtained valuable data on invasion. These results show that the island was recolonized by plants and animals from the adjacent lands, and after fifty years had already a rich and maturing jungle of forest inhabited by epiphytic plants and many kinds of animals; particularly, the number of bird species has already reached equilibrium. However, the number of plant species is still growing and outbreaks of certain insect species often occur, showing that even 100 years later a stable, steady state has not been reached (Elton, 1958; Simkin and Fiske, 1983).

The examples given so far are of invasions accompanying environmental fluctuations caused by nature. When the Quaternary glacial period ended and mankind arrived on the scene, human activities began causing various organisms to be transported to new areas, sometimes purposefully, at other times inadvertently. With the European discovery of the New World (1492) and its subsequent colonization, many Old World plants and animals invaded the Americas or Australia and rapidly drove native species to extinction. In one episode, when Captain Cook revisited the islands of New Zealand four years after his first landing in 1769, the botanist who was accompanying his voyage found to his surprise that Canary grass, a plant native to the Mediterranean, had already established itself in several places (Crosby, 1986). As another notable example, in the tropical insular fauna of Mauritius, prior to colonization in the 17th century, there were at least 23 taxa of endemic landbirds, 12 reptiles, and two fruit bats. Currently only nine endemic landbirds, four geckos, one skink and one fruit bat survive on the mainland of Mauritius (di Castri, 1989).

> A hundred years of faster and bigger transport has kept up and intensified this bombardment of every country by foreign species, brought accidentally or on purpose, by vessel and by air, and also overland from that used to be isolated.... The real thing is that we are living in a period of the world's history when the mingling of thousands of kinds of organisms from different parts of the world is setting up terrific dislocations in nature. We are seeing huge changes in the natural population balance of the world.

The above excerpt is from Elton's *The Ecology of Invasion by Animals and Plants* (1958). Even though some 40 years have passed since the publication of this classic work, this description still retains its original relevance. Although most countries today practise a quarantine system as a line of defence against biological invasions, more and more people are travelling and intermixing on an international scale and this creates increasing opportunities for invasions by organisms or diseases. There is also the danger that new life forms which were created artificially through bioengineering may escape from the laboratory and spread. Meanwhile, artificially disturbed areas, such as forests and rivers destroyed by human activities or cultivated land and pastures, are rapidly increasing, and this has increased the number of cases in which organisms which had hitherto been unsuccessful are now succeeding in invading and inhabiting new areas.

As we have seen so far, the issues of invasion and propagation are not only of academic interest but have been age-old concerns to humans because of their relevance to human society. Particularly with the accumulation of quantitative data in recent years, momentum has been building to obtain a mathematical understanding of these issues.

Much of the literature on invasion has dealt with three themes (Roughgarden, 1986; Williamson, 1989; Hengeveld, 1994):

(1) the conditions necessary for an invasion to take place,
(2) the way the invasion progresses through space,
(3) the properties of the fauna that is assembled by successive invasions.

The main goals of these works are to predict:

(1) which species will become an invader;
(2) what kind of habitat is susceptible to invasion by a particular species;
(3) if an invasion occurs, how fast it will spread;
(4) after an invasion has spread, what biological impact the invader will have on the native biota.

Recently, these questions have actively been addressed by many investigators either individually or in groups for a variety of ecosystems seen worldwide (see the publications, asterisked in References, of the SCOPE Program on the ecology of biological invasions). Among such efforts, the mathematical modelling of the spatial spread of invaders is a relatively well-developed area which has been extensively tested as well. In this book, instead of treating invasions as local events, we look at the process of invasions occurring on a global scale, and examine how mathematical models have been constructed and applied to understanding the various aspects of range expansion of invading species.

As we introduce in the next chapter, mathematical modelling of the spatial propagation of invasions was initiated by J. G. Skellam in 1951. By using the diffusion equation combined with population growth, he discovered that the range front of an invader species advanced at a constant velocity. This result was subsequently found to apply to many invader organisms, and so research in this field is widely considered as one of the most successful examples of modelling. However, some recent data have uncovered cases for which this principle does not apply. For instance, there are cases when movement takes place not only by random diffusion but also through long-distance dispersal or when environmental conditions of the invaded area are constantly changing in both time and space; such cases cannot be treated within the framework of Skellam's model. This book attempts several new approaches to such problems.

First, in Chapter 2, we introduce typical spatial expansion patterns for some well-documented cases of invasion. In Chapters 3 to 5, we discuss mathematical models that explain the characteristic features of these expansion patterns and explore the mechanisms by which invasion progresses. In particular, Chapter 3, centring on Skellam's model, will discuss the expansion pattern caused by random diffusion associated with reproduction. Chapter 4 derives conditions for successful invasions when the environment is changing in patchwork fashion, and also attempts applications to environmental issues. Chapter 5 develops a stratified diffusion model which describes invasions by organisms that extend their range by random diffusion as well as long-distance movements. Chapters 6 and 7 deal with cases when invading and native species compete for space, and show how the range of native species is pushed back by the invasion. In particular, Chapter 7 deals with disturbances that cause the environment to change in both time and space, and explores principles of coexistence between the invading and native species. Chapter 8 presents several analyses on the invasion of a predator or parasite, as well as a model of biological control by sterile insect release. Chapters 9 and 10 turn to invasions and the spread of diseases. We first introduce basic theories of epidemiology and then apply them to epidemics, such as measles and bubonic plague, among human populations. We also discuss the effects that diseases have had on human demography. Chapter 10 discusses the spread of rabies currently occurring in Europe; we will make predictions on the periodic occurrences of its epidemics and on their rate of expansion, and also discuss measures to control its spread.

Since this book's primary purpose lies in explaining how to construct models, the presentation of mathematical derivations from the models has been minimized, while diagrams have been used to maximum effect to obtain an intuitive understanding. For those readers interested in the analytical methods of mathematics, sections presenting simple derivations of the major equations are placed at the end of some chapters. By doing so, we hope to make this book largely self-contained.