Population and Community Biology

FOOD WEBS

Population and Community Biology

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The study of both populations and communities is central to the science of ecology. This series of books will explore many facets of population biology and the processes that determine the structure and dynamics of communities. Although individual authors and editors have freedom to develop their subjects in their own way, these books will all be scientifically rigorous and often utilize a quantitative approach to analysing population and community phenomena.

FOOD WEBS

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LONDON NEW YORK
CHAPMAN AND HALL

First published 1982 by
Chapman and Hall Ltd
11 New Fetter Lane, London EC4P 4EE
Published in the USA by
Chapman and Hall
733 Third Avenue, New York NY 10017

J. W. Arrowsmith Ltd., Bristol

British Library Cataloguing in Publication Data

Pimm, Stuart
Food webs.—(Population and community biology)
1. Food chains (Ecology)—Mathematical models
I. Title II. Series
574.5′3 QH541.15.M3

ISBN-13: 978-94-009-5927-9 e-ISBN-13: 978-94-009-5925-5
DOI:10.1007/978-94-009-5925-5

Library of Congress Cataloging in Publication Data

Pimm, Stuart L. (Stuart Leonard)
Food webs.
(Population and community biology)
Bibliography: p.
Includes index.
1. Food chains (Ecology) 2. Biotic communities.
I. Title. II. Series.
QH541.P56 1982 591.5′3 82-1306
AACR2

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Preface

Often the meanings of words are changed subtly for interesting reasons. The implication of the word 'community' has changed from including all the organisms in an area to only those species at a particular trophic level (and often a taxonomically restricted group), for example, 'bird-community'. If this observation is correct, its probable cause is the dramatic growth in our knowledge of the ecological patterns along trophic levels (I call these horizontal patterns) and the processes that generate them. This book deals with vertical patterns – those across trophic levels – and tries to compensate for their relative neglect. In cataloging a dozen vertical patterns I hope to convince the reader that species interactions across trophic levels are as patterned as those along trophic levels and demand explanations equally forcefully. But this is not the only objective. A limited number of processes shape the patterns of species interaction; to demonstrate their existence is an essential step in understanding why ecosystems are the way they are.

To achieve these aims I must resort to both mathematical techniques to develop theories and statistical techniques to decide between rival hypotheses. The level of mathematics is likely to offend nearly everyone. Some will find any mathematics too much, while others will consider the material to be old, familiar ground and probably explained with a poor regard for rigour and generality. However, a British student with 'A' level mathematics or his American counterpart with two semesters of college calculus will find nothing beyond his training and much that will be a revision of familiar ideas. It is for these students – who need to understand the biological assumptions in mathematical ecology and for whom texts on differential equations and linear algebra are too daunting – that this book is designed.

Developing theory using mathematical techniques is only one aspect of this book. The research programme that we call the field of population dynamics has not only clarified our ideas (e.g. those on the stability–complexity question) but has synthesized much existing knowledge. Most importantly, the theory has suggested new phenomena, including ones that we can observe or demonstrate experimentally in the field. The importance of theory to the field ecologist is clear, but what does the field ecologist offer to the theoretician? I shall argue that the possibilities available to the theoretician are so many that only by considering the field can he prevent his time being wasted in extensive investigations of theoretically possible yet biologically bizarre phenomena. My intent has been to place this book firmly on the interface between theory and observation.

In developing my ideas I owe a particular debt to John Lawton and Michael Rosenzweig. Much of the original work is based on joint papers with John, many of the ideas are his, and very few, if any, of the ideas have not been hotly debated over ale under the shadow of York Minster or while consuming tamales in the mountains of New Mexico. Only John's prior writing commitments prevented him from co-authoring this book, and it is poorer as a consequence.

Michael Rosenzweig, in addition to editing the book, has been a particularly close colleague. He has markedly shaped my ideas on ecology and provided encouragement without which I would have produced many fewer papers, no books, and certainly no grant proposals.

I am also in debt to those who reviewed all or part of this book. Michael Rosenzweig and John Coulson reviewed the entire document. Detailed chapter reviews were undertaken by W. Atmar, T. S. Bellows, J. E. Cohen, D. L. DeAngelis, M. P. Hassell, R. L. Kitching, J. H. Lawton, R. T. Paine, E. R. Pianka, P. W. Price, W. M. Post, R. D. Powell, R. J. Raitt, S. C. Stearns, N. C. Stenseth, and M. Williamson. Students in my classes (particularly, A. W. King, M. P. Moulton and M. E. T. Scioli) also provided useful comments. Errors no doubt remain, but the book would have been much the poorer without their advice. Much of the original work in this book was carried out under the tenure of grants from the National Science Foundation to Texas Tech University and from grants from the National Science Foundation and Department of Energy to Oak Ridge National Laboratory. My colleagues and the staff at Oak Ridge have been particularly supportive of my research on food webs.

I dedicate this book to my wife, June, and my parents, Hannah and Leonard.

Portal, Arizona

Acknowledgements

I gratefully acknowledge the authors and publishers of the original material that has been reproduced or modified to give the figures and tables in this book for their permissions. Full citations are given in the figure and table legends and at the appropriate places in the text together with the relevant entry in the bibliography. Figures 3.3, 3.4, 3.5, 4.9, 4.10, 4.11, 4.12, 4.13, 4.14, 4.15, 6A. 1, 8.1, 8.3, 8.4, and 8.5 and Tables 5.4, 6.1, 6A.1, 7.2, 7.3, 8.3, 8.4, 8.5, 8.6, and 8.7 are from papers produced while I was supported by the Oak Ridge National Laboratory (operated by the Union Carbide Corporation for the United States Department of Energy). Figure 4.3 is also reproduced with their permission. Figure 4.1 is modified from figures by R. T. Paine and is reproduced by permission from *The American Naturalist* (copyright 1966 The University of Chicago Press). Figure 4.4 is by R. M. May and reproduced by permission of Dr W. Junk, BV Publishers. Figure 6.3 is modified from Figure 2.6 in J. Phillipson's monograph in The Institute of Biology's *Studies in Biology* series published by Edward Arnold (Publishers) Ltd. Figure 6.5 is by permission of Blackwell Scientific Publications Ltd and includes material from a figure by T. R. E. Southwood. Figures 6.1 and 6.2 are based on figures by T. M. Zaret and R. T. Paine, Figure 7.1b on a figure by D. C. Force and Table 5.3 is a table by L. E. Hurd, M. V. Mellinger, L. L. Wolf and S. J. McNaughton and are reproduced from *Science* (copyrights 1973, 1960 and 1971 respectively, by the American Association for the Advancement of Science). Figure 6.10 is from a paper by R. L. Kitching in a volume published by Plexus Publishing, Inc. Figure 6.8 is modified from a paper by S. L. Pimm and J. H. Lawton in *Nature* (Volume 268, page 329), Figure 7.2 and Table 7.1 are from a similarly authored paper in *Nature* (Volume 275 page 542), and Figure 4.2 is modified from a paper by M. R. Gardner and W. R. Ashby in *Nature* (Volume 228, page 784) copyright 1977, 1978 and 1970 respectively by MacMillan Journals Ltd. Tables 5.1 and 5.2 are from a paper by S. J. McNaughton and are reproduced with permission from *The American Naturalist* (copyright 1977, The University of Chicago Press). Tables 9.1 and 9.4 are excerpted from Tables 5 and 9 in *Food Webs and Niche Space* by J. E. Cohen (copyright 1978 by Princeton University Press).

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Conventions and definitions

X_i	The *i*th species *or* its density.
$\dot{X}_i$	The rate of change of X_i, that is, dX_i/dt.
X_i^*	The non-trivial equilibrium density of X_i, that is, where $\dot{X}_i = 0$ and $X_i \neq 0$.
a_{ij}	The interaction coefficient between X_i and X_j; the effect of one individual of X_j upon the growth rate of an individual of X_i.
b_i	The *per capita* rate of increase or decrease of X_i in the absence of any other species.
c_{ij}	Elements of the Jacobian matrix.
x_i	$X_i - X_i^*$.
$f(x), g(x)$	Functions of the variable(s) within parentheses.
$\lambda_i, \lambda_{\max}$	Eigenvalues, the maximum eigenvalue. For their calculation see Chapter 2.
$\sum_{i=1}^{n} X_i$	$X_1 + X_2 + \ldots + X_n$.
$\exp(a)$	e^a, where e is the base of natural logarithms.
$\ln(a)$	*a* expressed as a natural logarithm.
$X_{1,t}$	The density of X_1 at time *t*.
$\partial y/\partial x_i$	The partial derivative of *y* with respect to x_i; obtained by differentiating *y* with respect to x_i and keeping all the other possible variables ($x_j, j \neq i$) constant.
n	The number of species in a system; sometimes the number of species of prey in a system.
m	Usually, the number of species of predators in a system.
C	See connectance.
P	A proportion (usually obtained by Monte-Carlo simulations and involving the proportion of random webs that exceed an observed web in some character).
α	The probability of a hypothesis given an observed result.
autotroph	Species which can obtain energy directly from sunlight and/or chemical sources and which do not require other organisms as food.
basal species	Species which feed on no other species in a food web.
connectance	The proportion of the possible interspecies interactions that are nonzero.
determinant	See Chapter 2, page 32.
detritus	Dead animal and plant matter.

detritivore	Animals or plants that feed on detritus.
ectotherm	Animals which do not usually maintain a constant body temperature.
endotherm	Animals which usually maintain a constant body temperature.
feasible	A model where all $X_i^* > 0$.
heterotroph	Animals which must feed on other organisms to survive.
Jacobian matrix	See Chapter 2, Appendix 2C.
loop	A pattern of species interaction where species A feeds on species B which feeds on species A, or A feeds on B, B on C, C on A, etc.
monophage	A species which feeds on only one other species.
oligophage	A species which feeds on few other species.
omnivore	A species which feeds on more than one trophic level.
phytophage	A species which feeds on plants.
polyphage	A species which feeds on many different species.
predator	A species (animal or plant) which feeds on other species.
prey	A species (animal or plant) on which other species feed.
return time	See Equation (2.42). The time it takes perturbations to reach 1/e (about 37%) of their initial value in a stable system.
saprophage	A species which feeds on decaying plant material.
singular	A system whose determinant is zero; see Chapter 2, page 32.
top-predator	A species on which nothing else feeds.