Theoretical Systems Ecology

ADVANCES AND CASE STUDIES

Efraim Halfon

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ACADEMIC PRESS
New York San Francisco London 1979
A Subsidiary of Harcourt Brace Jovanovich, Publishers

ACADEMIC PRESS, INC.
111 Fifth Avenue, New York, New York 10003

United Kingdom Edition published by
ACADEMIC PRESS, INC. (LONDON) LTD.
24/28 Oval Road, London NW1 7DX

Library of Congress Cataloging in Publication Data
Main entry under title:

Theoretical systems ecology.

Includes bibliographies.
1. Ecology—Mathematical models. I. Halfon,
Efraim. II. Title.
QH541.15.MdT43   574.5'01'84   78-27014
ISBN 0-12-318750-8

PRINTED IN THE UNITED STATES OF AMERICA

79 80 81 82 83 84 9 8 7 6 5 4 3 2 1

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Preface

After many years of development, systems ecology is having a large impact upon all aspects of environmental research. The system approach with its body of concepts and techniques has broadened the ecologists' perspectives and has attracted students into ecology from other disciplines. Their common ground is systems science and ecological theory. Their goals have been the establishment of a sound theoretical basis and the development of mathematical models. Unfortunately, there has been a lack of communication between theoreticians, and modelers and field ecologists. Modelers have dealt almost exclusively with difference and differential equations to model ecosystems and to produce simulations, computer solutions of the equations, that could be used for forecasting. They approached the problems of model development, simplification, identification, and analysis on an *ad hoc* basis. Theoreticians worked on a theory of modeling, but their concepts seldom were used in complex modeling exercises. Perhaps the language of system theory was too mathematical for many ecologists to understand and apply.

The purpose of this book is to try to bridge this gap. It is to present to theoretical systems ecologists and other theoreticians in systems science recent advances in the field. Since the language of system theory is mathematics, many chapters are mathematically sophisticated. It is also a purpose of the book to present to scientists, who do not have the background to follow mathematical concepts, some aspects of systems ecology with which they are not familiar in a way they can understand and apply. The examples at the end of each chapter have this function. They show how theory can be used successfully and fruitfully to improve the development and analysis of models.

Notation has been kept uniform as much as possible, given the difference in topics included in the book. References have been spelled out to allow easy access to information complementary to that presented here. To demonstrate that a set of data contains information that can be extracted with system techniques and used at different stages of model construction and usage, three authors (Beck, Ivakhnenko, and Singh), have used data from the river Cam in England. To show how systems ecology has evolved in places other than North America, authors from nine countries contributed to this effort.

Three classes of problems are analyzed in the book: (1) Selection of components comprising the system model. The first two sections deal with theory of modeling, formalisms, classes, and properties of models. (2) Definition of the relationships and interactions between the system variables. The section on Identification deals with the problem of extracting information from data for the purpose of deriving the model structure. (3) Model analysis. Several sections cover this aspect. To represent current trends, several chapters on stability and control theory are included.

This book was conceived in the stimulating research environment of the Canada Centre for Inland Waters, and I am grateful to Floyd C. Elder and Theodore J. Simons who provided a sheltered climate for unencumbered research. I am grateful to Lawrence R. Pomeroy, Bernard C. Patten, and Rolf E. Bargmann, who directed me and helped to bring out and develop my true research interests. I have come to appreciate the theoretical aspects of systems ecology during the several years I spent with the systems ecology group at the University of Georgia. Together with Bernard C. Patten, Jack B. Waide, Jack R. Webster, and William G. Cale provided me with guidance in the difficult art of ecological modeling.

I thank all the authors for writing, and rewriting the chapters until the referees and myself were satisfied. It was a pleasure to act as their editor. Many persons contributed their ideas, talent, and time. Most of the following also acted as referees: L. J. Bledsoe, W. G. Cale, M. Conrad, J. J. Duffy, J. T. Finn, B. S. Goh, J. Harte, A. G. Ivakhnenko, C. Jeffries, D. P. Lettenmaier, S. H. Levine, M. McLean, J. Orava, B. C. Patten, D. Sahal, D. Siljak, R. V. Thomann, R. E. Ulanowicz, V. Watson, J. R. Webster, and B. P. Zeigler. Ms. J. Fleet, Ms. V. Hamilton, and Ms. N. Snelling helped with the typing and other clerical tasks.

My wife Silvia gracefully put up with all the pressures during the organization of the book.

Efraim Halfon

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1. INTRODUCTION

A system may be defined as a set of elements standing in an interrelation among themselves and with the environment. It is generally agreed that a "system" is a model of general nature, that is, a conceptual analog of certain rather universal traits of observed entities. In other words, system-theoretical arguments pertain to, and have predictive value, inasmuch as general structures are concerned (von Bertalanffy, 1972). As researchers in other disciplines have done before, ecologists have turned to the system approach (e.g., Van Dyne, 1969; Patten, 1971; Odum, 1971).

The system approach is based on the evidence that certain system properties do not depend on the specific nature of the individual system, that is, they are valid for systems of different nature as far as the traditional classification of science (physical, biological, social) is concerned (Klir, 1972). Therefore, sophisticated procedures developed for the analysis of complex systems, mainly electrical, can now be applied to ecological

THEORETICAL SYSTEMS ECOLOGY

ISBN 0-12-318750-8

systems where analytical methodology is far less advanced. When quantitative formalisms such as algebraic or differential equations are used, the similarity of different systems becomes a subject of interest. A model is a conceptualization of the real system; they are similar. Usually a model cannot be considered a unique representation of the real system. Indeed an infinite number of models may be conceptualized. When a model is built, the similarity relation must be understood and quantified.

Compartmental analysis is a phenomenological and macroscopic approach for modeling physicochemical process. A compartment (or state variable, object, element, etc., according to the different terminologies common to systems theory) is a basic unit of functional interest. It may be a species of algae in a lake, all plankton, or the whole lake itself, depending on the study goals. The choice of the compartment may be arbitrary, but any decision made at the early stages of model development will influence all of the other results. This choice of the compartment defines the relation between models and systems. This is the *aggregation problem.*

The second main topic of interest in model development is the *system identification problem*; the study of relations among compartments. The formulation of a correct model structure is as important as the solution to the aggregation problem. Most of the volume (13 out of 20 chapters) is dedicated to these problems of model development. It is my belief that a solid theoretical foundation is important if we want to continue to progress in the systems analysis of ecosystems. The concept of similarity is crucial to any form of general systems theory and thus crucial to the understanding of a theory of modeling of all systems and, particularly in this instance, of ecological systems.

This volume contains four major parts and their sequence follows the usual course of thinking in system science.

Part I discusses some fundamental system problems and focuses on the aggregation problem and its relation to sampling activities. Here some theoretical foundations are laid. Problems related to model development are analyzed.

Part II includes information on modeling approaches and philosophy. The emphasis here is on model structure and includes formalisms, classes, and model properties. Three main topics in this part are hierarchical models, structure properties, and the relation of causality to model structures.

Part III introduces methodologies and computer techniques of system identification. These methods, however, cannot be separated from the modeling philosophies of their originators: Klir and Ivakhnenko present their inductive approaches to general systems theory and their identification methods reflect their respective beliefs.

Part IV contains studies on model analysis, and the focus is on structural properties, such as stability, flow analysis, and general systems properties. The other topic of interest in this part is the applicability of control theory to ecological models. Goh presents the basics in Chapter 15, followed by more sophisticated applications (Chapters 16 and 17).

2. AGGREGATION AND ORGANIZATION

"A model which must be capable of accounting for all the input–output behavior of a real system and be valid in all allowable experimental frames can never be fully known" (Zeigler, 1976). This model, which Zeigler calls the *base* model, would be very complex and require such great computational resources that it would be almost impossible to simulate. For ecosystems, the base model can never be fully known because of the complexity of the system and the impossibility of observing all possible states. However, given an experimental frame of current interest, a modeler is likely to find it possible to construct a relatively simple model that will be valid in that frame. This is a *lumped* model. It is the experimenter's image of the real system with components lumped together and interactions simplified (Zeigler, 1976).

Modeling an ecosystem requires knowledge of the real system, obtained with experiments, and its abstraction within a mathematical framework. Systems methods can be used effectively in the latter phase of model development. Indeed, when coupled with experimental work, system-theoretic concepts can help in the development of an ecologically realistic mathematical model. The *state space approach* is the most widely used in modern systems analysis because it allows description of both observable and unobservable variables. The models are memoryless and nonanticipatory and the state of the system is predicted using information on the present state and inputs to the system.

How do we choose the state variables and what kind of errors originate when we develop a homomorphic model? The problem is that ecosystem models have been developed *a priori* as aggregations without regard to the consequences of that aggregation. According to Zeigler (Chapter 1), the organization of simulation models is accomplished by considering several elements and their relationships. These elements are a collection of experimental frames, the real system, and the domain of possible models. The experimental frames specify the restrictions on experimental access to the real system. The models are assumed to be transition systems which are specifiable at various levels of structure and behavior and within short-hand conventions (e.g., sequential machines,