

Change is an omnipresent aspect of the environment, so that the practical problem of predicting how terrestrial ecosystems might respond in the future to large-scale human-generated changes is a major challenge for ecologists. In *Terrestrial Ecosystems in Changing Environments*, Hank Shugart describes the fundamental ecological concepts, theoretical developments and quantitative analyses involved in understanding the responses of natural systems to change.

The key ecological concepts described include the ecosystem paradigm, niche theory, vegetation—climate relationships, landscape ecology and ecological modelling. A variety of ecological models are presented, and their applications in predicting responses to change are considered. The challenge of producing ecological models capable of predicting long-term and large-area ecosystem dynamics is reviewed and several examples are provided. Finally, a review of some of the exciting new findings regarding terrestrial landscapes and their feedback with their climatic setting are discussed in the context of human land-use and global change.



Terrestrial ecosystems in changing environments

Cambridge Studies in Ecology presents balanced, comprehensive, up-to-date, and critical reviews of selected topics within ecology, both botanical and zoological. The Series is aimed at advanced final-year undergraduates, graduate students, researchers, and university teachers, as well as ecologists in industry and government research.

It encompasses a wide range of approaches and spatial, temporal, and taxonomic scales in ecology, experimental, behavioural and evolutionary studies. The emphasis throughout is on ecology related to the real world of plants and animals in the field rather than on purely theoretical abstractions and mathematical models. Some books in the Series attempt to challenge existing ecological paradigms and present new concepts, empirical or theoretical models, and testable hypotheses. Others attempt to explore new approaches and present syntheses on topics of considerable importance ecologically which cut across the conventional but artificial boundaries within the science of ecology.



CAMBRIDGE STUDIES IN ECOLOGY

Editors

H. J. B. Birks Botanical Institute, University of Bergen, Norway, and Environmental

Change Research Centre, University College London

J. A. Wiens Department of Biology, Colorado State University, USA

Advisory Editorial Board

P. Adam University of New South Wales, Australia R. T. Paine University of Washington, Seattle, USA

R.B.Root Cornell University, USA

F.I. Woodward University of Sheffield, Sheffield, UK

ALSO IN THE SERIES

H. G. Gauch, Jr

R. H. Peters

Multivariate Analysis in Community Ecology

The Ecological Implications of Body Size

C. S. Reynolds

The Ecology of Freshwater Phytoplankton

K. A. Kershaw Physiological Ecology of Lichens

R. P. McIntosh

The Background of Ecology: Concepts and Theory

A. J. Beattie

The Evolutionary Ecology of Ant–Plant Mutualisms

F.I. Woodward Climate and Plant Distribution

J.J. Burdon Diseases and Plant Population Biology

J.I. Sprent The Ecology of the Nitrogen Cycle

N. G. Hairston, Sr Community Ecology and Salamander Guilds

H. Stolp Microbial Ecology: Organisms, Habitats and Activities

R. N. Owen-Smith Megaherbivores: The Influence of Large Body Size on Ecology

J. A. Wiens The Ecology of Bird Communities:

Volume 1 Foundations and Patterns Volume 2 Processes and Variations

N. G. Hairston, Sr Ecological Experiments
R. Hengeveld Dynamic Biogeography

C. Little The Terrestrial Invasion: An Ecophysiological Approach to the

Origins of Land Animals

M. F. Allen The Ecology of Mycorrhizae

P. Adam Saltmarsh Ecology

D. J. Von Wilbert, B. M. Eller, M. J. A. Werger, E. Brinckmann & H. D. Ihlenfeldt Life Strategies of Succulents in Deserts
J. A. Matthews The Ecology of Recently-deglaciated Terrain

E. A. Johnson Fire and Vegetation Dynamics
D. H. Wise Spiders in Ecological Webs
J. S. Findley Bats: A Community Perspective

G. P. Malanson Riparian Landscapes

S. R. Carpenter &

J. F. Kitchell (Eds.) The Trophic Cascade in Lakes R. C. MacNally Ecological Versatility

R. J. Whelan The Ecology of Fire

K. D. Bennett Evolution and Ecology: The Pace of Life



Terrestrial ecosystems in changing environments

HERMAN H. SHUGART

Department of Environmental Sciences, The University of Virginia, USA





CAMBRIDGE UNIVERSITY PRESS
Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore,
São Paulo, Delhi, Dubai, Tokyo, Mexico City

Cambridge University Press
The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org Information on this title: www.cambridge.org/9780521565233

© Cambridge University Press 1998

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 1998

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

ISBN 978-0-521-56342-0 Hardback ISBN 978-0-521-56523-3 Paperback

Additional resources for this publication at www.cambridge.org/9780521565233

Cambridge University Press has no responsibility for the persistence or accuracy of URLs for external or third-party internet websites referred to in this publication, and does not guarantee that any content on such websites is, or will remain, accurate or appropriate. Information regarding prices, travel timetables, and other factual information given in this work are correct at the time of first printing but Cambridge University Press does not guarantee the accuracy of such information thereafter.



Contents

Preface	page xi
PART 1 INTRODUCTION	1
1 The importance of understanding eco	system change 3
2 The omnipresence of change	9
Long-term variations in climate	10
Changes in the Quaternary Period	14
Changes in the Holocene Epoch	20
Concluding comments	31
3 Temporal scale, spatial scale and the ed	cosystem 33
Roots of the ecosystem concept	33
The biogeocoenosis and the ecosystem	45
Temporal scale, spatial scale and the ecosy	ystem 50
Concluding comments	56
PART 2 BASIC CONCEPTS	59
4 Ecological modelling	61
Finite-state automata	63
State variable representations of dynamic	systems 68
Change in state space: a geometrical repr	esentation of
system dynamics	69
Compartment models and material flow	84
Formulation of compartment models for	ecosystem studies 85
Applications of compartment models	92
Common concepts used in ecological me	
Concluding comments	99



viii · Contents	
5 Niche theory	103
The Grinnellian niche	105
The Eltonian niche	108
The Eltonian niche and the competitive exclusion principle	110
Attempts to synthesise Elton's and Grinnell's niche concepts	120
Quantification of the Grinnellian niche	122
Patterns of species abundance along environmental	
gradients: the continuum concept	137
Concluding comments	140
6 Vegetation-environment relations	144
Historical roots of relating large-scale vegetation pattern	
to the environment	147
Global classifications of vegetation-environment relations	156
Adaptation of plants to the environment	170
Concluding comments	177
7 The mosaic theory of natural landscapes	178
The mosaic concept of vegetation dynamics	178
Roles of species on mosaic landscapes	187
Gap dynamics in the forest mosaic	190
Concluding comments	203
PART 3 ECOSYSTEM MODELS	205
8 Individual-based models	207
Development of individual-based models in ecology	208
Individual-based models of plant and animal populations	209
Gap models	217
Tests of gap models	232
Comparisons of different gap models	243
Concluding comments	245
~	

Mosaic landscape models	295
Interactive mosaic models and spatial models	310
Homogeneous landscape models	321
Concluding comments	336
·	

Ecological consequences at the population level

Consequences of gap models at the landscape level

10 Landscape models

9 Consequences of gap models

Concluding comments

248

248

274

291 294



Co	ontents ix
PART 4 EVALUATION OF GLOBAL CHANG	GE 341
11 Mosaic landscape models The application of phytogeographical models to asses	343
climate change effects The application of Grinnellian niche concepts to asse	344
climate change effects The application of gap models to assess change on me	353
landscapes Simulating patterns of vegetation change under altere	360
climates with gap models	371
Consistency comparisons of gap models with other approaches to modelling environmental change	376
Concluding comments	380
12 Spatially interactive landscape models	382
Effects of landscape scale in interactive landscapes	383
Ecotone dynamics under environmental change	390
Modelling interactive landscape dynamics The global carbon budget including potential spatial	394
dynamics	408
Concluding comments	410
13 Homogeneous landscape models	413
Initial results using material transfer models	416
Material transfer models applied at continental scales	420
Canopy process models at continental scales	425
Continental-scale changes in terrestrial ecosystems: a performance comparison among homogeneous	
landscape models	435
Concluding comments	442
14 Global change	445
Effects of global environmental change on the Earth's	}
terrestrial biota	446
The terrestrial surface and its interactions with the	450
atmosphere	452 463
Human society's adaptability to global change Concluding comments	466
References	469
Index	523



Preface

For the past decade or more, I have had the opportunity to be involved with one of the most exciting research areas in ecology and the geosciences: the efforts to understand the interactions of the major Earth systems of atmosphere, oceans and the terrestrial surface. This research area is sometimes referred to as 'global change biology' or 'global change ecology'. For research scientists, interest in this area has been stirred by the actions of international scientific co-ordinating committees (notably the IPCC (the Intergovernmental Panel on Climate Change) and the IGBP (the International Geosphere–Biosphere Programme)) and by public concerns as to the eventual effects of human alterations of the composition of the atmosphere, ocean and land. My own work in this area has focused mostly on the application of ecological models in an attempt to project the possible consequences of changes in climate and other conditions on forests and other terrestrial ecosystems.

A few years ago, it occurred to me that the opportunity for today's students to gain background for studies in global change ecology was rather limited. The scientists with whom I collaborated had arrived at their interest in studying global change by different and often circuitous routes. Some were palaeontologists or palaeoecologists interested in past ecosystems. The Earth has been highly variable climatically during its recent geological history and palaeoecological research leads naturally to wanting to understand better ocean—climate—vegetation interactions. Others have been drawn into global ecology by a desire to comprehend better the patterns of plants, animals and habitats over large areas. These scientists often applied a diverse array of technologies that are unique to our times: notably, the computational power to statistically interweave larger ecological and climatological data sets, the satellite technology to allow large surveys of the Earth's surface from space, instruments to measure fluxes of water, carbon dioxide, heat, chemicals to and from ecological systems, etc.



xii · Preface

Still others with an interest in conservation of unusual plants and animals saw the destruction and damage of essential habitat for these organisms by a wide variety of large-scale causes (climate change, human land-use, human alteration of the environment) as the motivation to understand better Earth systems function. Even with these and other diverse avenues for becoming interested in global change, the availability of a text that could provide necessary background for a student potentially interested in the area seemed to me to be lacking.

There are a large number of excellent books that are technical compendia on the subject of global change. They often feature chapters written by particular experts on topics in global change and whole Earth system dynamics. These represent a rich source of information for the advanced scholar with some background in the area, but there was still a need for a text that would provide access to the field for students with a basic background in ecology and sciences. During a sabbatical leave from the University of Virginia in the 1993–4 academic year, I had the good fortune to serve as a Visiting Scientist with Australia's Commonwealth Scientific and Industrial Research Organisation, Division of Wildlife and Ecology and, at the same time, to be a Visiting Fellow with the Research School of Biological Sciences, Environmental Biology Department, Australian National University. These two outstanding Australian institutions are among the world leaders in the ecological aspects of global change. Among old friends, I set about writing this book.

During the time in Australia and additional time working at the University of Virginia in the summer of 1994, I produced a first draft of this book. Several colleagues and students were dragooned into reading all or part of the text. I taught a course to about 50 students per year in the Department of Environmental Sciences at the University of Virginia beginning in the fall of 1994. This course ('Issues in Global Change' EVSC 493/795) was taught to third- and fourth-year undergraduate/introductory graduate student level and has been taught every fall since. I used the draft as a photocopied text-book for this class and revised sections according to student comments. Eventually, I produced the book that follows.

This book is not solely intended to be a textbook (although it has worked as a text in my own teaching and could serve this purpose for others) and it is to some degree idiosyncratic. My own research career has moved from ornithology to plant ecology and now to global ecology. Having already mentioned that there are several rather different routes taken by research professionals to arrive at an interest in global ecology, it



Preface · xiii

seems appropriate to outline the path most familiar to me - which I have done. Any lecturer using this book as a text would indubitably draw heavily from his or her own experience in developing a course syllabus. There are some larger, pedagogical points that I hoped to demonstrate in developing this text. I wanted to stress the changing, non-equilibrium nature of the biosphere. I hoped to show that global ecological studies were not a new invention, rather they derived naturally from basic ecological constructs (niche theory, plant geography, the mosaic nature of landscapes). I wanted to use ecological models as examples in a discursive manner and to discuss model formulation and model results generally. With respect to this latter point, I have included a discussion on the history and basics of ecological modelling that is strongly derived from a course taught by Professor B. C. Patten at the University of Georgia (Athens) when I was a student there. Some may find even this rather gentle taste of mathematics daunting, but modelling is an essential part of prediction of the consequences of past or future environmental changes. I also wanted to provide some of the many results that reflect the potential impact of the changes that humankind has wrought on the Earth. These are found mostly in the later chapters of the book.

Funding from grants from US Federal Agencies, particularly the National Science Foundation (DEB-90202041: Coupling of Ecosystem Process and Vegetation Pattern Across Environmental Gradients), NASA (NAG 5-2295: Multidiscipline Integrative Models of Forest Ecosystem Dynamics for the Boreal Forest Biome; NAG 5-1018: Forest Ecosystem Dynamics) and the Environmental Protection Agency (CR-81627-01: Implications of Climate Change on Forests: the Development of Forest Simulation Models for Evaluating Climate Change in Global Forest Ecosystems), supported major parts of the research work of my students and I over the years. Substantial parts of the later chapters of the book draw on this work as examples. A pair of Academic Enhancement grants from the Board of Visitors of the University of Virginia (Global Systems Analysis Program and Global Environmental Change Program) were invaluable in the development of this project and most appreciated. Travel to Australia was supported, in part, by a travel grant from the Australian CSIRO Division of Wildlife and Ecology. I have many friends and colleagues to thank for their help and patience during the development of this project. M. P. Austin, H. J. B. Birks, R. B. Carlson, F. Daria, T. E. Dennis, W. R. Emanuel, L. Gu, B. P. Hayden, B. M. McIntyre, M. W. Palace, B. R. Rizzo, G. Shao, W. L. Steffen, L. Von Schill, B. H. Walker, J. A. Wiens and F. I. Woodward read all or part of the book and provided helpful comments and encouragement. Two



xiv · Preface

classes at the University of Virginia in 'Ecological Issues in Global Change' used earlier drafts of the book as a reference text. In particular and along with several others, A. W. Farmer, K. K. Caylor, W. J. Faubert, A. J. Hill, N. D. Kaufman, J. M. Owens, S. U. Seddon-Brown, R. R. Shah, P. C. Shahani, A. M. Thomson and K. E. Winterson from these classes were kind enough to provide frank advice from a student's perspective. Part of the draft text was also used in a training course on 'Modelling Land-use and Forest Dynamics' at the BIOTROP-GCTE Southeast Asian Impacts Centre, Bogor, Indonesia. Thanks to Louis Lebel, Daniel Murdiyarso, Habiba Gitay, Ian Noble and Ian Davies, who were involved with me in developing part of this and an earlier workshop, M. L. Merriam and J. R. Montambault, both undergraduate students at the University of Virginia, read an early draft for clarity. R. L. Smith, Jr drafted illustrations and Jane Ward of Cambridge University Press provided much-appreciated text editing. Finally and certainly not least, I would like to express my gratitude to my wife, Ramona Jeanne Kozel Shugart, to whom this book is dedicated.

> H. H. Shugart March 1997