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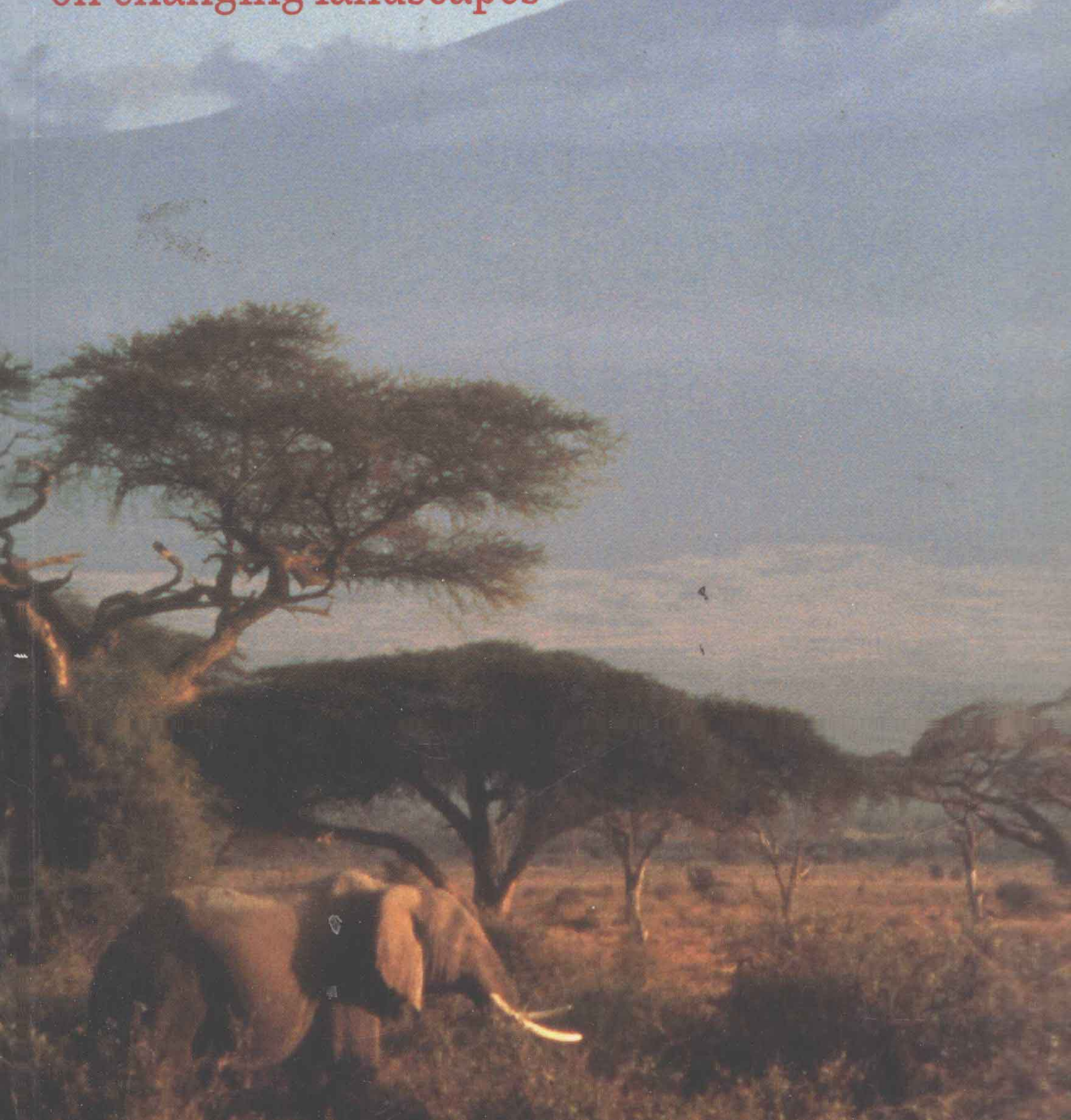
The coexistence of species on changing landscapes



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The coexistence of species on changing landscapes

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CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge CB2 1RP, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK http://www.cup.cam.ac.uk
40 West 20th Street, New York, NY 10011–4211, USA http://www.cup.org
10 Stamford Road, Oakleigh, Melbourne 3166, Australia

First published 1994
Reprinted 1995, 1996 (twice), 1998

Printed in the United Kingdom at the University Press, Cambridge

Typeset in 10/13 Monotype Times

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

Library of Congress Cataloguing in Publication data available

ISBN 0 521 36093 5 hardback
ISBN 0 521 36930 4 paperback

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Preface

The endeavor of writing a book, particularly one on a topic as broad as biological diversity, quickly brings one face-to-face with one's own limitations, in terms of time, energy, memory, and ability. I realize that my ambitious goal at the outset of this effort, of creating a comprehensive synthesis of the information and ideas about biological diversity, is still far from being realized. I am left with every author's hope, that the second edition (if there is one) will be much better than the first.

A cursory review of any subfield of ecology, or any science for that matter, reveals that the literature is vast. Not only are current publications overwhelming in their number, but the past century of research and publication has left an extensive history of important and insightful work that should not be overlooked. My approach has been to look more carefully at the past literature than the current literature, undoubtedly at the cost of missing important recent work. Part of this bias stems from my impression that many of us are ignorant of the past accomplishments and ideas in the field of ecology, and often expend great effort (and publish many papers) rediscovering something that was well-known fifty years ago, or perhaps even making errors of interpretation that were corrected long ago.

While I hope that most readers will find some surprising data and exciting ideas in this book, I suspect that Frederick Clements, Arthur Tansley, S.A. Forbes, or H.C. Cowles would find little that they didn't already know or hadn't already considered (as well as various errors of fact and interpretation that they would tactfully point out). I believe that many of the 'pioneers' in the field of ecology had a much broader and clearer understanding of basic ecological processes than many of us today. It is very difficult to come up with an idea that is genuinely new.

On the premise that 'there is nothing new under the sun,' I have conscientiously tried to trace major concepts as far back into the history of ecology as possible (given my own limitations of knowledge and time), and to give credit to the originators of the ideas I discuss in this book. Undoubtedly, I have not always succeeded. It is also likely that I have missed many important recent contributions, both theortical and empirical, to the issues I attempt to address. I am hopeful that my colleagues will inform me when I have overlooked their important contributions that are relevant to issues in this book, and that they will pardon me for concentrating on the work of those who can no longer speak for themselves.

While I am interested in data that are consistent with the ideas I have developed, I am particularly anxious to try to understand data or patterns of diversity that contradict the predictions and generalizations in this book. Although I have made an honest effort to find results that do not fit the theories outlined in this book, I suspect that I will be informed of many phenomena that are inconsistent with these ideas.

Oak Ridge, Tennessee *Michael A. Huston*

Acknowledgements

While there are many individuals throughout my academic career and personal life who have in some way contributed to this book, it would not have been written without the encouragement and support of my wife, Mary Ann. Over the much-longer-than-expected gestation of this work, with periods of intense effort and frustrating inactivity, she has kept the rest of our life functioning, encouraged me to keep going, and borne two beautiful children. It is my hope that this book will contribute to a wiser use of the world's natural resources, and a better future for many people, especially our family.

John Birks also deserves special mention, since I wouldn't have tried to write a book if he hadn't asked me to write one on biological diversity, over six years ago. I am also indebted to John, and to Robert McIntosh, for reading and carefully commenting on the entire first draft of the manuscript, an unenviable task which no one else even attempted. I did receive many valuable comments on sections of the book from my Oak Ridge colleagues Don DeAngelis, Mac Post, Antoinnette Brenkert, Jackie Griebmeier, and Kirk Winemiller, and I appreciate their help.

Since my interest in biological diversity stems from my days as graduate student at the University of Michigan, I want to acknowledge my fellow students who supported and stimulated me in the early days of my interest in this topic, and encouraged me to pursue my ideas in spite of pressure to the contrary. Those whose time and arguments were especially valuable include Doyle McKey, Tom Getty, Diane DeSteven, Lissy Coley, Hank Howe, Jim Affolter, Cathy Pringle, and George Sugihara. I was fortunate to have the opportunity of first visiting the tropics as an assistant to Dan Janzen and John Vandermeer, who did not necessarily agree with the 'insights' I gained under their tutelage. During those years the University of Michigan offered a course that brought some of the major figures in ecology to campus for two-week seminar series. I am grateful for the opportunity to have discussed some of my early ideas with these scientists, especially Henry Horn and Robert Whittaker.

As is evident from the figures and citations, this book draws heavily on past work I did as a graduate student as well as with colleagues at Oak Ridge National Laboratory. I am grateful to these friends for our many stimulating interactions and the (I believe) important papers we published together. In particular, Don DeAngelis, Tom Smith, Mac Post, John Pastor, and Phil Robertson were especially valuable in helping me to refine and express my (our) ideas, as well as educating me about a great variety of topics.

I am fortunate to have had many outstanding teachers, from elementary school through the present, who have stimulated and encouraged me. But it was my mother and father who first encouraged, then supported and tolerated my interest in natural history and later ecology. My siblings have always been very supportive and have helped me collect data in some beautiful, and sometimes uncomfortable, places. During my childhood in Newton, Iowa, Neal Deaton helped me view the world from his perspective as a naturalist and artist, from Cambrian seas to Guatemalan rain forests and African savannahs. During my graduate research, Napoleon Murillo and his wonderful family taught me about life in a tropical country and made possible my forest succession experiments in Costa Rica. Throughout my graduate career Joe Connell shared many of my interests and encouraged me to pursue career opportunities outside of traditional academia.

There are certainly many others who, as friends and teachers, have contributed to the development of my ideas and the overall course of my life. I hope they will take some satisfaction in this book, and not blame themselves for the mistakes I have made.

Portions of this book are expansions of work that I, and my colleagues, have published elsewhere, and I want to express my gratitude to the publishers of these papers for permission to use them here. In particular, the University of Chicago Press has generously allowed me to use material from my publications, with Don DeAngelis and Tom Smith, in *The American Naturalist*, specifically volume 113, 81–101, volume 129, 678–707, and volume 130, 168–198, as well as figures and tables from numerous important papers in that journal. I thank Annual Reviews, Inc. for permission to include and expand portions of my paper on coral reefs from the *Annual Reveiw of Ecology and Systematics*, 16, 149–77. I have also used major portions of a paper by Tom Smith and myself, from

Vegetatio, 83, 49–69, and I thank Kluwer Academic publishers for permission to use and expand this material. I hope that inclusion of material from these publications will help clarify the connections between these works, and increase appreciation for each of the individual contributions.

Some of the effort of writing this book has been supported as part of my activities with the Walker Branch Watershed Project at Oak Ridge National Laboratory. The Walker Branch Watershed Project is supported by the U.S. Department of Energy's Office of Health and Environmental Research as part of their Program for Ecosystem Research. While biological diversity has not traditionally been a major concern of the Department of Energy, I want to thank Dr. Clive Jorgensen of the Program for Ecosystem Research for his support, and express my appreciation to my supervisors at Oak Ridge National Laboratory who encouraged me to pursue this effort, especially Bruce Kimmel and Webb Van Winkle.

M. A. H.

For Ann and Thomas

Open, O Lord, the eyes of all people to behold thy gracious hand in all thy works, that, rejoicing in thy whole creation, they may honor thee with their substance, and be faithful stewards of thy bounty.

The Book of Common Prayer, 1979

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1
Introduction

The extinctions resulting from human activities throughout the world have caused great concern in the scientific community and among the general public. This disappearance of species has been decried as a loss of plants and animals with potential agricultural and economic value, as a loss of medical cures not yet discovered, as a loss of the Earth's genetic diversity, as a threat to the global climate and the environment for human existence, and as a loss of species that have as much inherent right to exist as does *Homo sapiens*. The attention given this issue has led to the addition of a new word to the English language, biodiversity (a contraction of 'biological diversity', Wilson and Peter (eds.), 1988). Biological diversity is more than a scientific or economic issue. Biological diversity, in all of its manifestations, is an essential component of the quality of human existence, summarized in the ancient aphorism: 'variety is the spice of life.'

Biological diversity encompasses all levels of natural variation from the molecular and genetic levels to the species level, where we have most of our interactions with biological diversity through enjoyment of the common, strange, and beautiful forms of life or through suffering caused by the effects of pests, parasites, and diseases. Beyond the species level, biological diversity includes patterns in nature up to the landscape level. These components of biological diversity are not independent. The many flowers that form spots of color in a meadow, the songbirds that give forests a different music than fields, the various forest types that create zones of color on a mountain that we see from twenty miles away, or the variations in greenness that can be detected from satellites in space, are all ultimately the consequence of genetic diversity interacting with environmental conditions to produce differences between organisms.

There is little hope of understanding any phenomenon with as many complex components and scales of spatial and temporal variability as biological diversity, *unless* it can be divided into components within which repeatable patterns and consistent behavior occur. One central premise of this book is that biological diversity can be broken down into components that have consistent and understandable behavior. The other central premise is that the various components of biological diversity are influenced by different processes, to the extent that one component may increase, while another decreases in response to the same change in conditions. If these premises are true, it is impossible to completely understand 'total biodiversity' until the regulation of each of its components is understood.

The subdivision of biological diversity into tractable components is essential for developing and testing hypotheses about its regulation. The focus of this book is on those components of biological diversity that are influenced by the number and identity of species present in a given area. My goal is to explain the regulation of species diversity and why the number of co-occurring species varies under different conditions. I will not deal with the issue of the regulation of genetic or molecular diversity within species or populations, and only note that the total genetic diversity within any area is primarily a consequence of the number and identity of species that are present. This book is about the ecological regulation of species diversity, the interaction of ecological processes with geological and evolutionary processes, and the consequences of these interacting processes for the large-scale spatial and temporal patterns on landscapes that are generally considered to be components of biological diversity.

Functional Classifications of Organisms

To apply the two premises outlined above to understanding the regulation of species diversity, the ideal components would be groups of species within which consistent patterns appear, and within which a given process will always produce the same pattern. Such groups of species could be defined on the basis of properties of the areas in which they occur, which has been a common approach in ecology and biogeography. However, with the goal of developing explanations of species diversity that are as broadly applicable as possible, my approach will be to classify species based on attributes that they have in common, such as size and physiological properties, rather than on the attributes of their environment, such as the successional stage or moisture conditions of the habitat in which they are usually found. In particular, I attempt to develop classifications that are based on 'functional' attributes, that is, attributes related to how organisms interact with each other and with their environment, rather than on phylogenetic attributes and genetic relatedness.

One very general classification scheme, which applies to many species is that of species being either 'structural' or 'interstitial'. By structural species I mean those species that create or provide the physical structure of the environment. Obvious examples include trees, reef-forming corals, giant kelp and other multicellular algae, and sessile animals such as oysters, mussels, barnacles, tubeworms, etc. These organisms create the physical structure of their environment, produce variability in physical (e.g., microclimatic) conditions, provide resources, and in general create the habitat used by many other, generally smaller, 'interstitial' organisms. Interstitial organisms would include most insects, other arthropods, birds, mammals and other vertebrates, microbes and fungi, as well as plants such as epiphytes and understory herbs.

'Structural' organisms have a major influence on the diversity of 'interstitial' organisms: in most cases the interstitial organisms would not be present in a particular area without the structural organisms. The direct influence of interstitial organisms on structural organisms and their diversity is usually minor, although the indirect effects of interstitial organisms through evolutionary and biogeochemical processes can be very important. While this size-based functional classification could be used to further subdivide interstitial organisms into smaller structural organisms and their interstitial dependents, the main point I wish to make is that the diversity of these two general types of organisms is likely to be influenced by different factors and processes.

Although the effect of structural species on the diversity of interstitial species is a major contributor to the total species diversity of virtually all communities, this explanation does not address the critical issue of the diversity of the structural species. A second and more general classification scheme provides a framework for dealing with the diversity of both structural and interstitial species, and also allows total species diversity to be broken into two components that (I will argue) operate according to different rules, and/or according to the same rules at very different temporal and spatial scales.

The total diversity of any community, or any subset of a community, can be broken into two hierarchical components: 1. the number of different *functional types* of organisms (i.e., 'guilds', Root, 1967); and 2. the number of *functionally analogous species* within each functional type