BIOGEOGRAPHY

BIOGEOGRAPHY

E.C. PIELOU

BIOGEOGRAPHY

E. C. PIELOU

Dalhousie University
Halifax, Nova Scotia

A Wiley-Interscience Publication
JOHN WILEY & SONS
New York • Chichester • Brisbane • Toronto

Library of Congress Cataloging in Publication Data:

Pielou, E C 1924–
Biogeography.

"A Wiley-Interscience publication."
Bibliography: p.
Includes index.
1. Geographical distribution of animals and plants.
2. Evolution. I. Title.

QH84.P53 574.9 79-13306
ISBN 0-471-05845-9

Printed in the United States of America

10 9 8 7 6 5 4 3 2

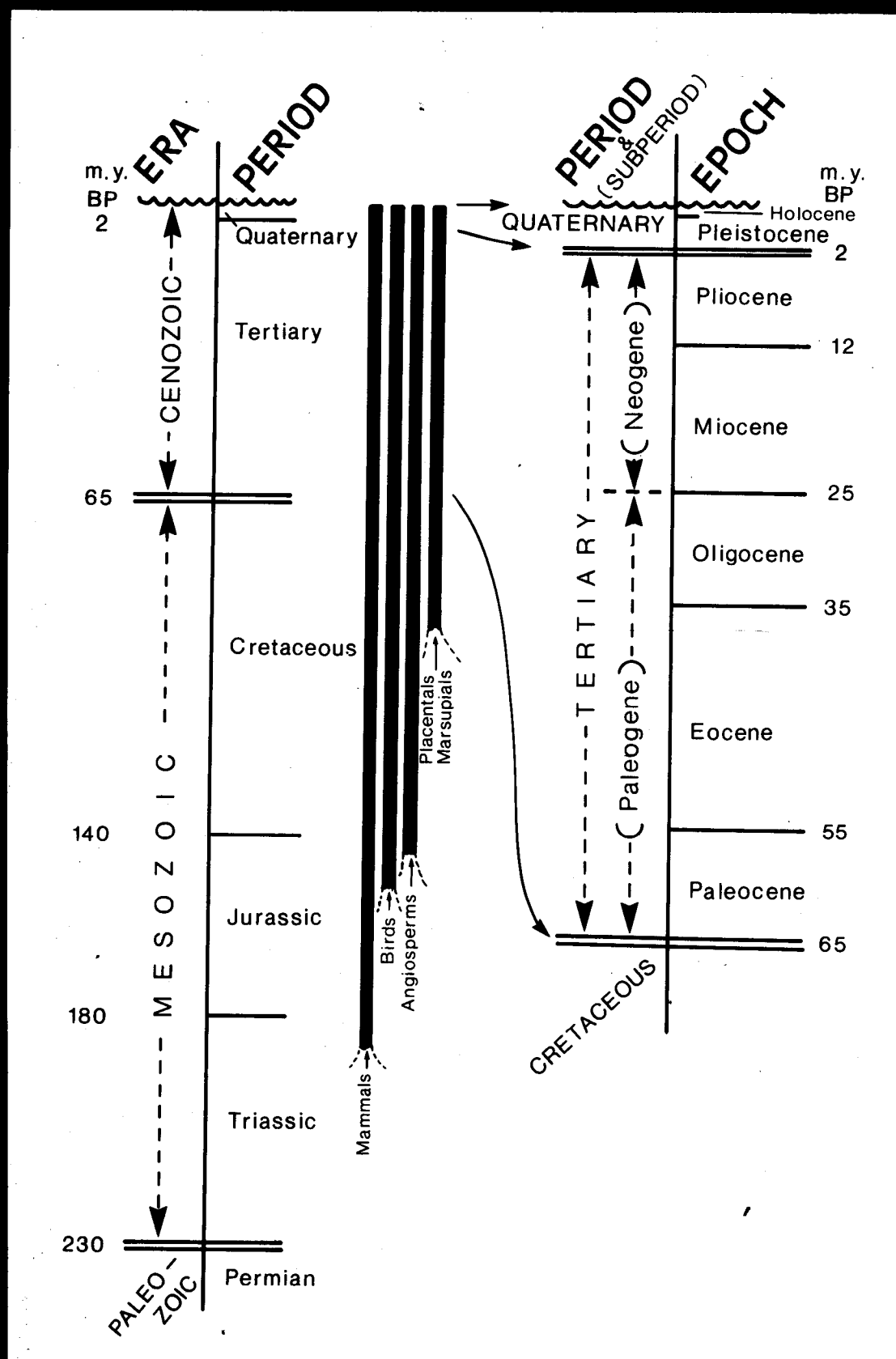
The evolution of life on a constantly changing planet, and the results of the process as we see them now, are the topics of this fascinating book. There have been many recent advances in our understanding of the development of life on Earth. New insights have come from plate tectonics; from investigations of life in the deep oceans; from island biogeography; from rapidly growing knowledge about the geography, climates, and ecology of the past; and from (sometimes controversial) developments in evolutionary theory. These new insights have come to shape biogeography into a newly unified subject at the forefront of the combined life and earth sciences.

Since biogeography is a subject of such enormous breadth, few attempts have previously been made to deal with more than a few facets of it in a single volume. This authoritative and comprehensive book discusses every aspect of biogeography, summarizing an enormous range of topics with both clarity and insight and presenting both sides of several current fierce controversies. It will interest 'outdoor' biologists of all kinds, ecologists, students of evolution, oceanographers, paleontologists, and geographers, and will broaden the knowledge of a great variety of specialists.

The solution of any biogeographic problem requires a holistic approach following a great many varied lines of inquiry. Thus, although the chapters could be treated as a series of essays, there is considerable cross-referencing. The mathematical sections (which can be skipped by non-mathematical readers) form about one-fifth of the book. They introduce serious students to many new research projects of great promise. The text includes numerous maps and diagrams and an extensive bibliography of over 300 references.

About the Author

DR. E.C. PIELOU is a professor of biology at Dalhousie University, Halifax. She was formerly professor at Queen's University at Kingston, Ontario, and has been a visiting professor at North Carolina State University, at the Yale School of Forestry and the University of Sydney, Australia. Dr. Pielou is a Fellow of the Royal Society of Arts and is the author of several books including, POPULATION AND COMMUNITY ECOLOGY (Gordon & Breach, 1974), ECOLOGICAL DIVERSITY (Wiley-Interscience, 1975), and MATHEMATICAL ECOLOGY (Wiley-Interscience, 1977). Dr. Pielou received a Ph.D. and a D.Sc. from the University of London.


m.y. BP
ERA
PERIOD
2
Quaternary
Tertiary
CENOZOIC
65
Cretaceous
MESOZOIC
140
Jurassic
180
Triassic
230
PALEO-ZOIC
Permian
Mammals
Birds
Angiosperms
Placentals
Marsupials
PERIOD & (SUBPERIOD)
EPOCH
m.y. BP
QUATERNARY
Holocene
Pleistocene
2
Pliocene
12
Miocene
(Neogene)
25
Oligocene
35
TERTIARY
(Paleogene)
Eocene
55
Paleocene
65
CRETACEOUS

THE QUATERNARY PERIOD

Years B P	EPOCH	GLACIALS & North America	Interglacials Europe
10,000	Holocene	(The present interglacial)	
	Pleistocene	WISCONSIN	WÜRM
		Sangamon	Riss-Würm
		ILLINOIAN	RISS
		Yarmouth	Mindel-Riss
		KANSAN	MINDEL
		Aftonian	Gunz-Mindel
		NEBRASKAN	GUNZ
			Donau-Gunz
		?	DONAU
		(Pre-glacial)	
? 2,000,000			

PREFACE

The word "biogeography" denotes a subject of enormous breadth, so enormous that attempts are rarely made to deal with more than a few facets of it in one book. It can be subdivided on the basis of regions, organisms, or concepts. For example, marine biogeography has been treated by Ekman (1953) and Briggs (1974); vertebrate zoogeography by Darlington (1957); phytogeography from an ecological point of view by Dansereau (1957); phytogeography from a taxonomic point of view by Good (1974); ecological biogeography by Watts (1971); paleobiogeography by Simpson (1953), Kurtén (1971), and Valentine (1973); island biogeography by MacArthur and Wilson (1967) and Carlquist (1974). In addition there are symposium volumes devoted to the biogeography of various regions such as the Pacific Basin (Gressit, 1963), the Bering Strait region (Hopkins, 1967), the North Atlantic (Löve and Löve, 1963) and the southern continents (Keast, Erk, and Glass, 1972). And these are only a few representative examples.

This book attempts (probably rashly) to cover the whole field, at a more advanced level than that of a survey for beginners. It is intended for senior undergraduates, and for interested biologists and earth scientists of all kinds. My purpose in writing it is to make students aware of the tremendous range and diversity of biogeography. The subject is so large that a research worker cannot hope to be expert in more than one or two branches of it, but at the same time cannot afford to be ignorant of the multitude of other branches. In biogeography perhaps more than in any other subject, a holistic approach is necessary. The solution of any biogeographic problem, no matter how small, requires the following of a great many varied lines of inquiry.

Although no one person can weigh all the diverse bits of evidence bearing on a particular problem, he should at least be conscious of their existence and relevance. It therefore seems worth while to bring together in one book a set of "samples" of biogeography's many branches. The chapters can be treated as a series of essays but there is much cross-referencing. The need for cross-referencing brought home to me, as I wrote, the degree to which the threads of the subject are interwoven. The desirability of ample cross-referencing is the justification I offer for presuming to write on so broad a range of topics.

I am very grateful to Peter Raven, Director of the Missouri Botanical Garden, for wise and useful advice (I took most of it). I am also indebted to Marjorie Willison of Halifax for considerable help in gathering and collating material, and to Terry Collins of Halifax who did the drawings and most of the diagrams.

E. C. PIELOU

Halifax, Nova Scotia
May 1979

CONTENTS

(Starred sections are mathematical)

INTRODUCTION

A book, or a series of lectures, is a one-dimensional stream of words. This fact constrains all scientific writers, whatever their topic. Any branch of science has, in reality, a multidimensional framework of concepts, and the task of projecting this framework onto a single line in such a way that the inevitable distortions do not obliterate the intricacies of the structure is the hardest part of scientific writing. In the case of so-called interdisciplinary subjects (and biogeography is preeminently one of them), the difficulties are compounded. Where best to begin the subject, and how best to divide it into compartments, are debatable problems with no unique answers.

The work of a biogeographer consists in observing, recording, and explaining the geographic ranges of all living things. These ranges are not static. Their salient feature is that they are continually expanding, contracting, fragmenting, and coalescing. Moreover, these changes are occurring over a whole hierarchy of different time scales. Obviously the causes and effects of short-term changes, those taking a few decades, differ fundamentally from those taking tens or hundreds of millions of years.

Changes in the geographic range of a biological species-population, just as much as changes in the morphology and physiology of its member individuals, are all part of the evolution of that species. Range-changes influence, and are influenced by, changes in a species' biology. Thus biogeography should not be thought of as a fringe subject, an optional supplement to a biologist's training for students whose timetables have room for it. It is, in truth, right at the heart of biology, an integral part of the study of evolution.

The current upsurge of interest in biogeography follows, and is part of, the scientific revolution undergone by the earth sciences in the late 1960's. This revolution consists in the reversal of opinion of the great majority of geophysicists on the reality of continental drift. Before it, most geophysi-

cists regarded drift as physically impossible (Wilson, 1963a). The switch in consensus coincided with the development and widespread acceptance of the theory of plate tectonics, according to which the earth's crust is formed of a number of thin, rigid plates that are constantly in motion relative to each other. They are forced apart, along various lines of separation, by the process of sea-floor spreading. With the demonstration by geophysicists that this process can and does occur, a belief in continental drift suddenly gained respectability. Before the revolution, only a few biologists were tough-minded enough to maintain, in the teeth of opposition, that drift *must* occur since it is the only reasonable explanation of a great many well-known biogeographic patterns. Since the revolution, they have been joined by most of their more timid colleagues, who had previously allowed their opinions to be formed for them by geophysicists. Perhaps the moral has now been perceived: biological evidence for continental drift is as weighty as geophysical evidence. Biologists who denied this, and who deferred to geophysicists on the subject, were undervaluing their science.

The changes in biogeographic range-patterns caused by plate movements are, of course, long-term changes, and are only one of the scales of change discussed in this book. A synopsis of its contents will show how I have dismantled the multidimensional structure of the science of biogeography so as to present it in a sequence of chapters.

To begin (Chapter 1) we consider modes of biogeographic classification: the subdivision of the present-day earth into faunal and floral realms and provinces.

The biogeographic consequences of plate tectonics and modern interactions between biogeography and geophysics are the subjects considered in Chapter 2.

Chapter 3 stresses the evolutionary consequences of biogeographic change, and the conclusions about evolutionary processes that may be derived from biogeographic evidence. These are topics of heated controversy.

In Chapter 4 we concentrate on a much shorter time interval in earth history than that covered in Chapter 2 and discuss the biogeographic effects of the last ice age.

Chapter 5 describes aspects of biogeography that are peculiar to marine organisms. The continuity of the world ocean, and the effects of ocean currents, obviously lead to some fundamental differences between terrestrial and marine biogeography.

Chapter 6 discusses island biogeography, the subject founded by MacArthur and Wilson (1963). It forms a distinct field of study. Large-scale events in earth history (such as the opening of the Atlantic Ocean)

and large-scale units of the earth's surface (the continents and oceans) are unique and have no replicas. Small islands, in contrast, are so numerous that biological events occurring in them can be thought of, in the statistical sense, as samples from larger, parent populations. This contrast sets "island" theory in a class by itself.

Chapter 7 deals with geoecology. This includes (among other things) a study of the recurrence, in geographically similar areas, of ecologically similar communities composed of taxonomically different members.

Chapter 8, on biological dispersal and diffusion, brings together much that has already appeared, in scattered form, in earlier chapters.

Chapter 9, likewise, is a synthesizing chapter. Biogeographic range-disjunctions are always thought-provoking and have many different causes. Examples are described, in a wide array of different contexts, throughout the earlier chapters of the book. Chapter 9 brings them together in brief, summary form.

Chapter 10 deals with geographic patterns in polymorphic species, and geographic variations in polyploidy.

Deciding which chapter was the appropriate home for a topic was often difficult. Many topics have an equal claim to inclusion in two, three, or more chapters and the choice was arbitrary. This merely illustrates the multidimensional linkages that characterize the framework of the body of knowledge known as "biogeography."

Statistical and mathematical reasoning and methods are gradually seeping into biogeography. The few sections of the book that presuppose some knowledge of mathematics and statistics are marked with asterisks. The reader who wishes to omit these sections can be assured that without them the book still forms a connected whole. But to skip them is to miss a taste of the direction in which biogeography seems most likely to advance.

In Chapters 2, 3, and 4 are repeated references to geological time intervals of different ranks (eras, periods, epochs, and smaller units), and to the times, in millions of years (m.y.) before the present (BP) of various events in earth history. As an aid to those whose background is chiefly in neobiology, two tables are printed on the endpapers. One shows the major divisions of geological time since the start of the Mesozoic era about 230 m.y. ago. The other, on a larger scale, shows the estimated dates and durations of the various glacial episodes of the Quaternary ice age.

Chapter One

THE BIOGEOGRAPHIC SUBDIVISIONS OF THE EARTH

Biogeography is concerned with plant and animal species and also, from the very nature of the science, with entities such as biogeographic realms, regions, and provinces. The biogeographic classification of the modern earth is therefore the first topic to consider in a study of biogeography, and is the subject of this chapter.

There are three sections. The first discusses the units into which the whole earth has been divided, on the basis of accumulated knowledge of floras and faunas, carefully, but subjectively, weighed and considered. Section 2 describes one of the many possible ways of performing an objective classification, using multivariate statistical methods, of a comparatively small area; that is, an area small relative to the whole earth. In the example given, Australia is the area classified. Section 3 deals with methods of delimiting biogeographic provinces in a rather special case, when the region to be subdivided can be treated for all practical purposes as one-dimensional. This is true of a shoreline, inhabited along a very narrow strip by a biota of strictly littoral organisms.

1. BIOGEOGRAPHIC REALMS, REGIONS, AND PROVINCES

A "biological" subdivision of the earth's surface can take account either of the terrestrial or the marine biosphere. Obviously, the results are very

different. In a terrestrial subdivision, boundary lines are drawn through the oceans which are treated as "lifeless" for the purpose at hand; and *mutatis mutandis* for a marine subdivision. In what follows, we consider the terrestrial biosphere first.

Further, a "biological" subdivision of the earth's surface can be based on taxonomic or ecological criteria. A biogeographic subdivision, as the term is ordinarily used, is one using taxonomic criteria. Of course no biologist can afford to ignore the ecological differences between different areas, and a list of the world's ecological units of highest rank, the biomes, is given in a later subsection.

A Taxonomic Classification of the Terrestrial Biosphere

A "perfect" biogeographic classification of the terrestrial world is, of course, an unattainable ideal. Disagreements over the ranks to be assigned to the recognized units, and over the exact locations of their boundaries, are inevitable. Somewhat different subdivisions are obtained depending on whether a classification is based on the floras or the faunas of the different areas.

The following classification (Table 1.1) and map (Figure 1.1) will serve as bases for the following discussion.

Table 1.1 is the classification of Schmidt (1954; see Sylvester-Bradley, 1971). As may be seen, units of four different ranks are recognized: the realm, the region, the subregion, and the province. This is a zoogeographic classification. In order to arrive at a map of the world's biogeographic divisions which, as far as possible, gives equal emphasis to animals and plants, I have combined Schmidt's provinces, as shown by the boxes in Table 1.1, into eight "biogeographic regions" which are mapped in Figure 1.1.

Examination of the table and the map naturally leads one to ask how, and why, the subdivisions were arrived at. To say that the flora and fauna of any one region exhibit uniformities that set it off from all other regions is to beg the question. It would, in any case, be truer to say that biogeographic units are marked more by the differences between them than by the resemblances within them. It is by their boundaries that they are best defined. These boundaries could be more precisely described as transition zones. Some are narrow, others wide; some are clear and definite, others ill-defined. They merit careful study in their own right and we return to the topic below.

First it is worth considering how we might characterize the different regions shown in Figure 1.1. One way is to list the families of mammals that are endemic to each region. (Mammals are useful for illustrative