

The mechanisms of macroevolutionary change have long been a contentious issue. Palaeoecological evidence, presented in this book, shows that evolutionary processes visible in ecological time do not build up into macroevolutionary trends, contrary to Darwin's original thesis.

The author discusses how climatic oscillations on ice-age time-scales are paced by variations in the Earth's orbit, and have thus been a permanent feature of Earth history. There is, however, little evidence for macroevolutionary change in response to these climatic changes, suggesting that over geological time macroevolution does not occur as a result of accumulated short-term processes. These conclusions are used to construct a post-modern evolutionary synthesis in which evolution and ecology play an equal role.

Written by a leading palaeoecologist, this book will be of interest to researchers in both ecology and evolutionary biology.



Evolution and Ecology: The Pace of Life

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 artifical boundaries within the science of ecology.



Cambridge University Press

0521399211 - Evolution and Ecology: The Pace of Life

K. D. Bennett Frontmatter More information

CAMBRIDGE STUDIES IN ECOLOGY

Series Editors

H. J. B. Birks Botanical Institute, University of Bergen, Norway, and Environmental Change Research Centre, University College London, UK J. A. Wiens Department of Biology, Colorado State University, USA

Advisory 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, UK

ALSO IN THE SERIES

H.G. Gauch, Jr

R.H. Peters

C.S. Reynolds

Multivariate Analysis in Community Ecology
The Ecological Implications of Body Size
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

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

C. Little The Terrestrial Invasion: An Ecophysiological Approach

to the Origins of Land Animals

P. Adam Saltmarsh Ecology

M.F. Allen The Ecology of Mycorrhizae

D.J. Von Wilbert et al. 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.J. Whelan The Ecology of Fire

R.C. Mac Nally Ecological Versatility and Community Ecology



Evolution and Ecology: The Pace of Life

K.D. BENNETT

Department of Plant Sciences, University of Cambridge, UK





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, United Kingdom
40 West 20th Street, New York, NY 10011-4211, USA
10 Stamford Road, Oakleigh, Melbourne 3166, Australia

© Cambridge University Press 1997

This book 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 1997

Typeset in 11/13 Bembo Roman.

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

Library of Congress Cataloguing in Publication data

Evolution and ecology: the pace of life / K.D. Bennett p. cm. – (Cambridge studies in ecology)
Includes bibliographical references. (p.) and index.
ISBN 0 521 39028 1 (hardback). – ISBN 0 521 39921 1 (pbk.)
1. Evolution (Biology). 2. Paleoecology – Quaternary.
I. Title. II. Series.
QH 366.2.B4635 1997
575 – dc20 96-13368 CIP

ISBN 0 521 39028 1 hardback ISBN 0 521 39921 1 paperback

Transferred to digital printing 2004



All the business of war, and indeed all the business of life, is to endeavour to find out what you don't know by what you do; that's what I called "guessing what was at the other side of the hill" Arthur Wellesley, Duke of Wellington, 1852, quoted by J.W. Croker (Jennings 1884, vol. 3, p. 274).



Contents

Tables		page xi
Illustrations		xiii
Pre	eface	xvii
1	Introduction	1
	Outline	3
	Terms and Definitions	3
2	Development of ideas	6
	Evolutionary processes	6
	Ecological processes	35
	Quaternary research	39
	Discussion	42
3	Orbital-forcing of climatic oscillations	44
	Orbital parameters	45
	Insolation	48
	Climate models	51
4	Geological evidence for orbital-forcing	65
	Cenozoic	66
	Mesozoic	74
	Paleozoic	82
	Proterozoic	84
	Continental glaciation in Earth history	85
	Discussion	89
5	Biological response: distribution	92
	The physical background	92
	The terrestrial record	94
	The marine record	145
	Discussion	148



X	· Contents	
6	Biological response: evolution	154
	Geological time	155
	Ecological time	168
	Discussion	173
7	Biological response: extinction	178
	Animals	178
	Plants	181
	Discussion	183
8	Evolution and ecology: synthesis	184
	Biological responses	184
	Post-modern evolutionary synthesis	184
	Difficulties	195
Re	eferences	199
Index		226



Tables

1.1	Simplified geological time-scale	4
2.1	Darwin's model of evolution by natural selection	21
2.2	Main modes of evolution	23
3.1	Effect of Earth-Moon distance on the periodicity of palaeo-	
	climatic parameters	47
4.1	Earth's pre-Quaternary glacial record	88
5.1	Holocene rates of increase for tree populations	151
5.2	Interglacial rates of increase for tree populations	152
6.1	Stratigraphical ranges of deer in the Quaternary of the British	
	Isles	156
6.2	Mean species duration in geological time	175
8.1	Expanded model of evolution	187
8.2	Temporal hierarchy of processes controlling evolutionary	
	patterns	189



Illustrations

2.1	Stages of speciation	17
2.2	Speciation and trends in lineages	28
2.3	Species response to environmental change	32
2.4	Effect of changing environments on sympatric distributions	33
3.1	Variations in the Earth's eccentricity, obliquity, and precession	
	of the equinoxes since 1 Ma	46
3.2	Orbital variations of Mars	48
3.3	Precession of the equinoxes	49
3.4	0-100 ka deviations of solar radiation from modern values	50
3.5	GCM-simulated climatic variables for 18 ka and the present	52
3.6	GCM-simulated climatic variables for 9 ka and the present	57
3.7	Reconstructed climates of Pangaea	61
3.8	Reconstructed climatic variations with Cretaceous continental	
	configuration	63
3.9	Reconstructed January surface temperatures during the	
	Cretaceous	64
4.1	Geological time-series from deep-sea sediment of the South-	
	ern Indian Ocean	68
4.2	High-resolution spectra of orbital, insolation, and geological	
	variations in the late-Quaternary	69
4.3	Orbitally-based chronostratigraphy for the late-Quaternary	71
4.4	Composite variance spectrum for oxygen isotope datasets	73
4.5	Carbonate oscillations from South Atlantic sediments	74
4.6	Miocene pollen record from Wyoming, USA	75
4.7	Sediment properties, Cretaceous, Italy	76
4.8	Power spectra of sediment variables, Cretaceous, Italy	77
4.9	Facies of the Ladinian Latemar Limestone, Triassic, northern	
	Italy	79
4.10	Extent of detrital cycles, Lockatong Formation, Triassic,	
	northeastern USA	80



xiv · Illustrations

4.11	Correlations and fish distributions across Newark Basin,	
	Triassic, northeastern USA	81
4.12	Carboniferous sea-level curve	83
4.13	Thickness of calcium sulphate layers, Permian, southern USA	84
4.14	Salt content and time-series, Ordovician-Silurian, Western	
	Australia	86
4.15	Proterozoic shelf palaeogeography, northern Canada	87
5.1	Distribution of ice-sheets at the last glacial maximum	93
5.2	Quaternary pollen record at Valle di Castiglione, Italy	97
5.3	Quaternary pollen record at Tenaghi Philippon, Greece	98
5.4	Quaternary pollen record at Ioannina, northwest Greece	101
5.5	Late-Quaternary distribution change for European Quercus	104
5.6	Late-Quaternary distribution change for European Tilia	105
5.7	Reconstructed late-Quaternary 'vegetation' units for Europe	106
5.8	European no-analogue vegetation in Europe since 13 ka	108
5.9	Changing areal extent of tree taxa in the Holocene of the	
	British Isles	109
	Quaternary pollen record from Clear Lake, California, USA	110
	Late-Quaternary spread of trees in eastern North America	112
5.12	Numerical comparison of fossil and modern pollen spectra in	
	the late-Quaternary of northwestern Canada and Alaska, USA	116
5.13	Modern and full-glacial ranges of trees and shrubs, Nevada,	
	USA	118
	Zonation of vegetation since 20 ka, Great Basin, USA	119
	Zonation of plant communities since 24 ka, Arizona, USA	120
5.16	Numerical comparison of late-Quaternary and modern plant	
	remains, Grand Canyon, USA	121
5.17	Generalized late-glacial and present plant zonation on the	
	Colorado Plateau, USA	122
	Late-Quaternary pollen record, El Valle, Panama	123
	Late-Quaternary pollen record from Guatemala	124
	Late-Cenozoic pollen record from Bogotá, Colombia	125
5.21	Quaternary stratigraphic ranges of pollen types from Bogotá,	
	Colombia	127
	Late-Quaternary pollen record from Kashiru, Burundi	128
	Locations of Holocene pollen records, eastern Sahara	129
	Holocene pollen record at Selima, Sudan	130
5.25	Quaternary pollen and charcoal record from Lynch's Crater,	
	northeastern Australia	131



	Illustrations ·	XV
5.26	Quaternary record of pollen and charcoal from Lake George,	
	eastern Australia	134
5.27	Late-Quaternary pollen record from New Guinea	136
5.28	Quaternary intermingled fauna: European beetles	139
	Quaternary intermingled fauna: North American beetles	140
5.30	Quaternary intermingled fauna: European land mollusca	141
5.31	Quaternary intermingled fauna: North American vertebrates	142
5.32	Quaternary intermingled fauna: North American mammals	143
5.33	Quaternary intermingled fauna: Eurasian and Australian	
	mammals	144
5.34	Full-glacial-modern distribution changes of North Atlantic	
	coccolithophores	146
5.35	Changing Quaternary coastlines between southeast Asia and	
	Australia	149
6.1	Last interglacial red deer from Jersey and Great Britain	155
6.2	Modern distribution of the beetle Helophorus aquaticus and its	
	races	158
6.3	Morphological stasis in ostracodes of eastern North America	160
6.4	Quaternary phyletic history of the Bermudan land-snail	
	Poecilozonites bermudensis	161
6.5	Comparison of fossil and recent samples of the Bahamian	
	land-snail Cerion agassizi	162
6.6	Cenozoic molluscan sequence, Turkana Basin, Kenya	163
6.7	Morphological change in Pliocene foraminiferal clades of	
	Globoconella	165
6.8	Pliocene evolution of equatorial Pacific radiolarians	166
6.9	Late-Cenozoic morphological change in Pacific diatom	
	lineage Rhizosolenia	167
6.10	Idealized changes in interglacial distributions and abundance	
	of European trees	169
6.11	Darwin's finches	170
6.12	Changing abundance and morphology of the finch Geospiza	
	fortis, Galápagos	172
6.13	Lyellian curve for bivalve molluscs	174
7.1	Late-Cenozoic extinction episodes for North American land	
	mammals	179
7.2	Patterns of change for North American Plio-Pleistocene	
	mammals	180
7.3	Late-Quaternary pollen record from Easter Island	182



Preface

In July and August 1988 I spent time in Australia, partly on a study visit to the Australian National University, and partly attending a conference in Brisbane. After a conference field trip in northern Queensland, I had some time to spare in Cairns, and, as one does, took a day-trip snorkeling on the Great Barrier Reef. As the catamaran returned into Cairns, I noticed an osprey idly flying over. I had just spent much of the day watching fishes on the reef, and I had previously seen ospreys in northern Scotland, coastal Maine, and in the North American Great Lakes area (including, memorably, one flying over Exhibition Stadium, Toronto, during a ball game). I had long known that ospreys were cosmopolitan. The Cairns osprey reminded me of all of this. Whatever that bird was feeding on, whatever other organisms it interacted with, it had a different biotic environment, at least, from the Scottish or Canadian birds. I, like the rest of my generation, was brought up scientifically on the Neo-Darwinian paradigm, and had not thought too much about it in my day-to-day activities. But what, if anything, are ospreys 'adapted' to? This book is not about ospreys or their evolutionary history, but the Cairns bird has remained in my mind as a symbol for the relationships between organisms and their environments on ecological through evolutionary time-scales, including the crucial intermediate time-scales (10⁴-10⁵ years) typified by the Quaternary (the last 1.6 Myr).

The relationship between palaeoecology and ecology has been a topic of concern to many Quaternary workers for some time. This book was written partly as a result of a feeling of frustration that much of the ecological excitement of Quaternary events was not penetrating into mainstream ecological thinking, and partly as a result of realizing that these same events held considerable significance for processes of evolution, also untapped. The original scheme was for a book written jointly with Donald Walker on the subject of time in ecology. It evolved into this solo effort after a few years of little joint progress during which I developed the central theme of the book as it now is. Donald has been



xviii · Preface

a significant source of support, ideas, and encouragement, particularly when I visited Canberra in 1988, and during the writing. His comments on an early draft convinced me to complete the thing. I am deeply indebted to him.

I began palaeoecological research under the supervision of John Birks, and I am very grateful to him for his continuing encouragement and discussion of the topics presented here, and many others, during and since those days. Many of the ideas in this book were initiated when I was an NSERC postdoctoral fellow working with Jim Ritchie while we were both in Toronto, and I thank him for his help and encouragement then and subsequently. It is an especial pleasure to thank Kathy Willis for her positive and helpful comments on several drafts, and for the many free and frank discussions that helped to shape the book. Janice Fuller allowed me to cite unpublished data from her thesis (Table 5.1) and, together with Jane Bunting, Alex Chepstow-Lusty, Simon Haberle, Susie Lumley, Maria Fernanda Sánchez Goñi, Julian Szeicz, Rebecca Teed, and Chronis Tzedakis, provided helpful discussions and made many suggestions for improvement. I also thank Nick Butterfield and Jim Ritchie for comments on a later draft, and Sylvia Peglar for allowing me to use Fig. 5.1. At CUP, I am grateful to Alan Crowden for his interest in the project, Barnaby Willitts for guiding it through the Press, and Sharon Erzinçlioğlu for carefully checking the text. John Birks and John Wiens made many helpful comments on behalf of CUP. Finally, but not least, I am grateful to Alison, Graham, and Hugh for their patience in the face of considerable neglect. If there is any merit in the book, they should all share the credit, but I alone take responsibility for omissions (it became impossible to include everything) and other failings.

The preparation of the text was greatly facilitated, and even made enjoyable, by Donald E. Knuth's wonderful type-setting program TEX, together with the macro package Lamport (by Leslie Lamport) and the bibliography program BibTEX (by Oren Patashnik). I also gratefully acknowledge the provision of computing resources in the Department of Plant Sciences, University of Cambridge.

Keith Bennett Cambridge 24 April 1996