

# Biogeography

THIRD EDITION

MARK V. LOMOLINO

BRETT R. RIDDLE

JAMES H. BROWN





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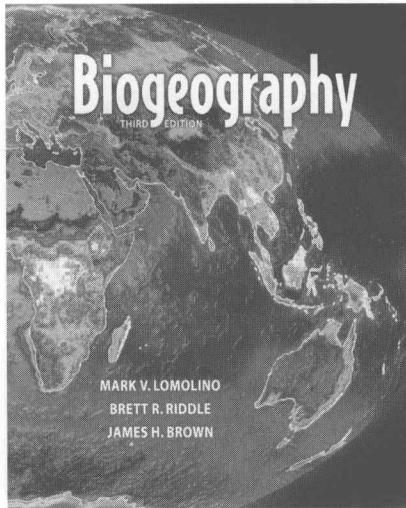
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**Sinauer Associates, Inc.** • Publishers  
Sunderland, Massachusetts



### The Cover

Average annual net primary productivity of the Earth during 2002. This map displays carbon metabolism—the rate at which plants absorbed carbon out of the atmosphere to produce organic matter during photosynthesis. Courtesy of NASA's Earth Observatory.

### The Endpapers

(Front) Wallace's (1876) scheme of biogeographic regions, which attempts to divide the landmasses into classes reflecting affinities and differences among terrestrial biotas. Numbers identify subregions. (Back) Map of the world illustrating many of the ocean basins, island chains, mountain ranges and other topographic features discussed in this text.

### Biogeography, Third Edition

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For information, address:

Sinauer Associates, Inc., 23 Plumtree Road, Sunderland, MA 01375 U.S.A.

Fax: 413-549-1118

E-mail: [publish@sinauer.com](mailto:publish@sinauer.com)

Internet: [www.sinauer.com](http://www.sinauer.com)

### Library of Congress Cataloging-in-Publication Data

Lomolino, Mark V., 1953-

Biogeography / Mark V. Lomolino, Brett R. Riddle, James H. Brown.—  
3rd ed.

p. cm.

Rev. ed. of: Biogeography / James H. Brown, Mark V. Lomolino. 2nd ed.  
c1998. Includes bibliographical references (p. ) and index.

ISBN-10: 0-87893-062-0

ISBN-13: 978-0-87893-062-3

1. Biogeography. I. Riddle, Brett R. II. Brown, James H., 1942 Sept.  
25- III. Brown, James H. 1942 Sept. 25- Biogeography. IV. Title.

QH84.B76 2005

578'.09—dc22

2005014443

Printed in U.S.A.

5 4 3 2

*To our families for their love and patience,  
to our colleagues for their insights and inspiration, and  
to our students for challenging our ideas and redefining the frontiers of science.*

# Preface

Simply defined, biogeography is the geography of life. Biogeographers study an impressive and sometimes overwhelming diversity of patterns in spatial variation of Earth's life forms, from molecular variation among populations of the same species, to geographic variation in productivity and diversity of ecosystems, and distinctiveness of entire biotas among the continents and ocean basins. Today, the field is enjoying a modern renaissance, although its roots extend back to the earliest efforts of humans to understand the geography of nature.

Indeed, biogeography must be one of the most ancient human endeavors. A knowledge of spatial variation in numbers and types of organisms across areas inhabited by our aboriginal ancestors was vital to their survival as they searched for particular kinds of animals and plants to use for food and shelter, and, more generally, as they adapted to a heterogeneous but geographically predictable environment. Explorers and naturalists of the seventeenth and eighteenth centuries greatly expanded our understanding of the geographic variation of the natural world, as their interests and experiences expanded from local and regional scales to a global one. They discovered that organisms and biological communities varied in a highly regular fashion along geographic gradients of latitude, elevation, isolation, and habitat area, and they learned that different regions of the globe—even those with similar climates and environments—were inhabited by different assemblages of species and higher taxa. These very general biogeographic patterns challenged the prevailing views which held that the Earth's diversity was relatively limited and that its continents, oceans, climates, and species were immutable—having changed little since the origin of the planet. Thus, the fascinating geographic signatures of nature would ultimately lead to paradigmatic shifts in our understanding of the origins, spread, diversification, and extinction of life. From these scientific revolutions would emerge entire new disciplines focusing on the dynamics of the Earth (geol-

ogy and, in particular, plate tectonics theory), interactions among organisms and their environment (ecology and environmental biology), and heritable changes in the characteristics of populations and species (evolutionary biology).

Ironically, despite its long and distinguished history and its central role in development of other disciplines, biogeography was not widely recognized as a major discipline in its own right until the latter decades of the twentieth century. The very reasons responsible for its great insights and promise—its holistic and integrative nature—also posed great challenges. Few scientists could master the many fields relevant to the diversity of patterns and processes biogeographers study. Indeed, up until the 1980s, the most comprehensive works in biogeography were those written many decades earlier by the “fathers” of the field, including those by Alfred Russel Wallace, Charles Darwin, and Joseph Dalton Hooker. Few universities offered a course in biogeography and many of us, including two authors of this textbook, never had the opportunity to take a course in the subject.

In order to address the need for a modern, comprehensive textbook in *Biogeography*, James H. Brown and Arthur Gibson published the First Edition of *Biogeography* in 1983. For many of us, Brown and Gibson's text was our first comprehensive introduction to the field, and it fundamentally transformed our careers. Soon other authors followed suit, new biogeography journals were launched, more and more universities and colleges began offering courses in the subject, and a growing number of scientists began referring to themselves as “biogeographers.”

Recognition of the heuristic interest and applied relevance of the field of biogeography continued to grow at an accelerating rate. By the 1990s it was clear that this textbook required a complete revision. The Second Edition of *Biogeography* emulated the original text in its balanced coverage of the entire breadth of the discipline, its integration of ecological and evolu-

tionary approaches, and its emphasis on general concepts richly illustrated with empirical examples drawn from a wide variety of organisms, ecosystems and geographic regions. We were pleased to see that, in addition to continuing as a popular textbook, the Second Edition became a general reference and frequently cited source in the primary literature.

Although 15 years passed between the publication of the First and Second Edition of *Biogeography*, after only five years it was clear to us that another revision was required. With the addition of Brett Riddle to our team, we again set out to provide a comprehensive and integrative account of the entire field, restructuring the text and updating it with over 1000 new publications from the most exciting frontiers of biogeography. We hope that the Third Edition of *Biogeography* will contribute to this modern scientific renaissance, and that it will soon be necessary once again to update and revise our text with emerging advances in our understanding of the geography of life. That will be a sign that the field is still healthy, relevant, and advancing.

In addition to those who contributed to the previous editions, many additional people—far too many to rec-

ognize individually—have helped to revise, update, and improve this book. We are especially indebted to Douglas Kelt for his careful reading and insightful comments on the chapters in this book, and to other colleagues including Rob Channell, Paul Giller, Larry Heaney, David Perault, Christopher Scotese, and Robert J. Whitaker for their comments on topics discussed in particular sections of the book. Many readers of the previous editions provided suggestions and corrections that we have incorporated here, and we thank them for their assistance. We also thank Andy Sinauer, Kathaleen Emerson, Christopher Small, Janice Holabird, David McIntyre, Suzanne Lain, and the other editors and staff at Sinauer Associates for their unfailing professionalism and Herculean efforts to produce a high-quality book on a tight schedule. Finally, we are indebted to all biogeographers and other scientists, from the earliest workers to our contemporaries, for their contributions to the discipline. It is their individual, collaborative, and cumulative contributions that make biogeography so exciting to teach and study.

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# UNIT ONE

## *Introduction to the Discipline*





## CHAPTER

# 1

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**L**IFE VARIES FROM PLACE TO PLACE in a highly non-random and predictable manner. This seemingly simplistic observation is none-the-less one of the most fundamental and most important patterns in nature. Even the earliest human societies were aware that as they expanded their search area they would encounter a greater number and greater diversity of plants and animals. Those societies living in mountainous regions could see that vegetation changed in an orderly manner as they moved from the lowlands to the summit. The earliest fishing and seafaring societies learned that their catch varied from place to place and from the shallows to deeper waters of the ocean. These same societies (or their descendants) eventually learned that the numbers and diversity of terrestrial organisms increased as their journeys took them from the tiniest to the largest islands, and from environments of temperate regions to those of the tropics.

Knowledge of geographic variation of life on this planet was thus unavoidable and likely essential to survival of these ancient societies. Thousands of years later, scientists would rediscover these patterns and add many additional insights into the geography of nature during the Age of European Exploration. In order to explain such patterns, these early biogeographers would eventually realize that the Earth, its climate, and its species were dynamic over both space and time. Soon, their explanations for the development and distribution of life would include references to past environments, extinct life forms, and competition and predation among species. Thus the geography of nature became the foundation to entirely new fields of science including geology, meteorology, paleontology, evolution, and ecology.

The early ecologist and evolutionary biologist Ernst Haeckel (1876) once wrote that "the actual value and invincible strength of the Theory of Descent ... [is] ... that it explains *all* biological phenomena, that it makes *all* botanical and zoological series of phenomena intelligible in their relations to one another." Later, Theodosius Dobzansky put it much more succinctly—"Nothing in biology makes sense except in the

light of evolution.” We do not take issue with either of these visionaries but offer an assertion that is just as bold and important; indeed, it is the fundamental theme of this book and modern biogeography in general. Few patterns in ecology, evolution, conservation biology—and for that matter, most studies of biological diversity—make sense unless viewed in an explicit geographic context.

We know that living things are incredibly diverse. There are probably somewhere between 5 million and 50 million kinds of animals, plants, and microbes living on Earth today. Of these, fewer than 2 million have been formally recognized as species and described in the scientific literature. The remainder are represented by specimens awaiting description in museums, or by individuals awaiting discovery in nature. Additional untold millions, probably billions, of species that lived at some time in the past are now extinct; only a small fraction of them have been preserved as fossils.

Nearly everywhere on Earth from the frozen wastelands of Antarctica to the warm, humid rainforests of the tropics; from the cold, dark abyssal depths of the oceans to the near-boiling waters of hot springs—even in rocks several kilometers beneath the Earth’s surface—at least some kinds of organisms can be found. But no single species is able to live in all of these places. In fact, most species are restricted to a small geographic area and a narrow range of environmental conditions. The spatial patterns of global biodiversity are a consequence of the ways in which the limited geographic ranges of the millions of species overlap and replace each other over the Earth’s vast surface.

## What Is Biogeography?

### *Definition*

Biogeography is the science that attempts to document and understand spatial patterns of biological diversity. Traditionally, it has been defined as the study of distributions of organisms, both past and present. Modern biogeography, however, now includes studies of all patterns of geographic variation in nature—from genes to entire communities and ecosystems—elements of biological diversity that vary across geographic gradients including those of area, isolation, latitude, depth, and elevation.

As with any science, biogeography can be characterized by the kinds of questions its practitioners ask. Some of the questions posed by biogeographers include the following:

1. Why is a species or higher taxonomic group (genus, family, order, and so on) confined to its present range?
2. What enables a species to live where it does, and what prevents it from colonizing other areas?
3. What role does geographic variation in climate, topography, and interactions with other organisms play in limiting the distribution of a species?
4. How do different kinds of organisms replace each other as we go up a mountain or move from a rocky shore to a sandy beach nearby?
5. How does a species come to be confined to its present range?
6. What are a species’ closest relatives, and where can they be found? Where did its ancestors live?
7. How have historical events—such as continental drift, Pleistocene glaciation, and recent climatic change—shaped a species’ distribution?



8. Why are animals and plants of large, isolated regions—such as Australia, New Caledonia, and Madagascar—so distinctive?
9. Why are some groups of closely related species confined to the same region, while others are found on opposite sides of the world?
10. Why are there so many more species in the tropics than at temperate or arctic latitudes?
11. How are isolated oceanic islands colonized, and why are there nearly always fewer species on islands than in the same kinds of habitats on continents?

The list of possible questions is nearly endless, but in essence we are asking: *How does biological diversity vary over the surface of the Earth?* This is the fundamental question of biogeography. It has always intrigued scientists and laypersons who were curious about nature. Only within the last few decades, however, have scientists begun to call themselves biogeographers and to focus their research primarily on the distributions of living things. Not surprisingly, biogeographers have not yet answered all the questions listed above. They have, however, learned a great deal about where different kinds of organisms are found and why they occur where they do. Much of this progress has been made in just the last few decades, stimulated in large part by exciting new developments in the related fields of ecology, genetics, systematics, paleontology, and geology, as well as by technological developments.

Biogeography is a broad field. To be a complete biogeographer, one must acquire and synthesize a tremendous amount of information. But not all aspects of the discipline are equally interesting to everyone, including biogeographers. Given different biases in their training, their biogeography courses and writings tend to be uneven in coverage. A common specialization is taxonomic—for example, phytogeographers study plants and zoogeographers study animals, and within these categories one finds specialists in groups at all taxonomic levels. Although viruses and bacteria play crucial roles in ecological communities and in human welfare, microbial biogeography is poorly known and rarely discussed. Some biogeographers specialize in **historical biogeography** and attempt to reconstruct the origin, dispersal, and extinction of taxa and biotas. This approach contrasts with **ecological biogeography**, which attempts to account for present distributions and geographic variation in diversity in terms of interactions between organisms and their physical and biotic environments. Paleoecology bridges the gap between these two fields by investigating the relationships between organisms and past environments and using data on both the biotic composition of communities (abundance, distribution, and diversity of species) and abiotic conditions (climate, soils, water quality, etc.) derived from fossilized remains preserved in ancient sediments, ice cores, tree rings, and other places. Different biogeographers have emphasized different methods for understanding distributions: some approaches are primarily descriptive, designed to document the ranges of particular living or extinct organisms, whereas others are mainly conceptual, devoted to building and testing theoretical models to account for distribution patterns. All of these approaches to the subject are valid and valuable, and discounting or overemphasizing any division or specialization is counterproductive and unnecessary. Whereas no researcher or student can become an expert in all areas of biogeography, exposure to a broad spectrum of organisms, methods, and concepts leads to a deeper understanding of the science itself. As we hope to show, the various subdisciplines contribute to, and complement each other, unifying the science.