# BIOGEOGRAPHY

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# Preface

For years before we actually began to work on this book, we discussed the challenge of trying to write a basic textbook for college courses in biogeography. We realized it would be extremely difficult to produce a text that would do justice to the broad field of biogeography and satisfy the diverse needs of its teachers and students. Most large universities and many smaller institutions offer courses in biogeography, but these vary enormously in content and emphasis. Few scientists actually call themselves biogeographers. Consequently, biogeography courses tend to be taught by those whose real specialty is another discipline such as systematics, ecology, or paleontology. Although most courses are offered as part of a biology curriculum, sometimes they are offered by departments in related disciplines such as geography or the geosciences. Often zoogeography and phytogeography are taught as separate courses. Perhaps it is too much to expect that a single textbook could meet the needs of the diverse courses in biogeography or of the specialists who teach them.

Our book is intended to introduce advanced undergraduates and beginning graduate students to a very broad but exciting field. We have tried most of all to provide these students with a balanced, conceptual, and synthetic approach. We attempt to bring together specialized subdisciplines and information on both plants and animals in order to explain patterns of geographic distribution of organisms in terms of the historical geologic and contemporary ecological processes that have caused them. To do this we must deal with a time scale extending from near the beginning of life billions of years ago to the present, a spatial scale encompassing everything from local patches of habitat to the entire earth and the scala naturae, or variety of organisms, from the simplest microbes to the highest plants and animals. If biogeography is to be presented as a single, coherent field it is essential that patterns and processes on all of these scales be interrelated and synthesized. We hope that in this way biogeography will come alive, and the student will acquire a truly global perspective on the variation in the distribution of organisms and the different processes that have caused these patterns.

Like many diverse and active disciplines, biogeography is a field filled with competing ideas and clashing personalities. For any field this is a sign of vigor because much of the disagreement will stimulate research that will lead eventually to resolution of the controversial issues and to increased understanding. For authors of a textbook, however, this makes it difficult to achieve a balanced approach that will be acceptable to teachers and serve their students well. We have tried to convey a feeling for the dynamism of the field and to present the controversial issues and yet still retain a balanced coverage of topics. This is not a textbook of plate tectonics, techniques of phylogenetic reconstruction, vicariance biogeography, macroevolution, faunal and floral analysis, geographic ecology, or mathematical theory. All of these are important areas of current research in biogeography or allied fields, but to emphasize any one of them at the expense of the others and of more classical biogeographic subjects would be to present the beginning student with a biased view of what biogeography is all about.

The book is organized in four parts. These are preceded by an introductory chapter on the nature and history of the science of biogeography. The first unit describes the contemporary environmental setting that influences the distribution of living organisms. Individual chapters discuss the physical geography and climatology of the earth, the ecological factors that limit the geographic ranges, and the composition and distribution of ecological communities. The second part of the book discusses the historical events and evolutionary processes that have influenced the distributions of both extinct and living forms. A chapter on the theory of plate tectonics and the geologic history of the earth is followed by chapters on the processes of speciation and extinction, on the mechanisms and consequences of dispersal, on patterns of endemism and disjunction, and on the methods and difficulties of reconstructing the distributional histories of taxa. The third unit describes the distributions of contemporary animal and plant groups and considers the historical explanations that have been proposed to account for these patterns. Separate chapters on aquatic animals, terrestrial animals, flying animals, and plants are followed by a chapter on the role of the dramatic geologic and climatic changes that have occurred within the last 1.7 million years.

The last part of the book treats ecological biogeography. It emphasizes the development and testing of theories to explain general patterns of diversity and distribution that are relatively independent of the evolutionary histories of particular taxa. Two chapters are on islands, which have been a source of inspiration for biogeographers since the earliest beginnings of the field. A chapter on patterns of continental and marine species diversity is followed by a discussion of the ways that historical events and ecological processes interact to influence the present and past distribution of organisms.

The book is intended to be an introduction to the basic facts and concepts of biogeography, rather than an encyclopedia of data or a theoretical treatise. Although we have tried to use specific examples from a variety of organisms and geographic regions to illustrate our points, we have not done justice to the vast literature of relevant information. What we have offered, however, can be used as a starting point. Students can use the selected references at the end of each chapter in conjunction with the bibliography at the end of the book to pursue topics of interest. Instructors should have no difficulty embellishing or criticizing the themes that we present to develop their own distinctive emphasis.

Writing this book has been much more difficult than we anticipated when we began, but it has also been more rewarding. We have both learned a great deal, from the literature, from our colleagues, and from each other, as we have tried to distill the diverse data and ideas into an integrated conceptual framework. The extent to which we fail to convey this synthesis to readers reflects our own shortcomings. The degree to which we succeed depends largely on the contributions of others.

This book could not have been written without the help of many generous and dedicated people. We are particularly grateful to our colleagues and students at the University of Arizona, the University of California at Los Angeles, and elsewhere who have shared their interests and ideas and who have encouraged us to write the book. S. Carlquist, T.J. Case, J. Cracraft, L. Key, P.S. Martin, M.E. Mathias, P.L. Meserve, E.C. Olson, D.M. Porter, C. Robbins, H.J. Thompson, and R.F. Thorne read all or part of the manuscript and made many helpful suggestions that greatly improved the final version. For the shortcomings and errors that remain we alone are responsible. T.J. Case, D. Dunn, J.F. Eisenberg, R.D. Holt, R.B. Huey, D. Jablonski, J. Roughgarden, T.W. Schoener, E.W. Stiles, E.E. Williams, and D.H. Wright provided unpublished information. A.K. Brown, W.A. Dunson, J. Faaborg, J.R. Hastings, V.C. LaMarche, and R.M. Turner allowed us to use their photographs. J. Smith drew nearly all of the maps, and S. Edwards and G. Ige drafted most of the other illustrations. Several people, especially B. Bonanno and R. McKinley, helped type the manuscript. Our editors at The C.V. Mosby Co. were increasingly supportive: S.E. Abrams got us started, and D. Bowen and S.D. Schapper advised us throughout the writing. To all of these people, and to any we may have forgotten to mention, we express our most sincere gratitude.

**James H. Brown**
**Arthur C. Gibson**

# Contents

# Chapter 1 The Science of Biogeography

There are more than 1.6 million known kinds of animals, plants, and microbes living on earth today, and certainly as many more undescribed forms have yet to be discovered. We can add to this list untold millions of species that lived sometime in the past but are now extinct, only a small fraction of which were recorded as fossils. Organisms are found in almost all conceivable environments, yet each extant and extinct species has or had a unique geographic distribution. Each species inhabits only a part of the earth's surface, occurs only in some habitats, and varies in abundance over its geographic range. These ranges change dynamically, usually starting small, experiencing increases and decreases in size, and finally decreasing to extinction. Contemporary forms will eventually become extinct as well, leaving future species in their places.

## What is biogeography?

Biogeography is the study of distributions of organisms, both past and present. It is the science that attempts to describe and understand the innumerable patterns in the distribution of species and larger taxonomic groups. Few biological subjects are enjoyed by amateurs and professionals alike as is biogeography, because we possess an inherent interest in the organisms sharing this world and a desire to speculate about where they came from and why they occur where they do. Biogeography is in part a historical science. From the study of fossils, which provide valuable information on the history of life on earth, we can obtain the answers to some of the interesting questions. How did a species come to be confined to its present range? What are its closest relatives and where are they found? What is the history of the group, and where did their ancestors live? Why are the animals and plants of large, isolated regions, such as Australia, New Caledonia, and Madagascar, so distinctive? When did the distribution of a particular group expand or contract to assume the present boundaries, and how have geologic events, such as continental drift and Pleistocene glaciation, shaped this distribution? Why are some closely related species confined to the same region, and other pairs separated and found on opposite sides of the world?

Other questions that biogeographers ask are primarily ecological, because they concern the relationships between organisms and their environments. Why is a species confined to its present range? What enables it to live where it does, and what prevents it from expanding into other areas? What roles do climate, topography, and interactions with other organisms play in limiting the distribution? How do we account for the replacement of species that we observe as we go up a mountain or move from a rocky shore to the sandy beach nearby? Why are there so many more species in the tropics than in temperate or arctic latitudes? How are islands colonized, and why are there always fewer species on islands than in the same kinds of habitats on nearby continents?

The list of possible questions is nearly endless, but in essence we are asking: How do the number and kinds of species vary, from region to region, over the surface of the earth, and how can we account for this variation? This is the fundamental question of biogeography. It has always intrigued people who are curious about nature, but only within the last century or so have scientists called themselves biogeographers and focused their research on the study of the distribution of living things. They have not yet answered all the questions, but they have learned a great deal about where different kinds of organisms are found and why they occur where they do. Much progress has been made in the last two decades, stimulated in large part by exciting new developments in the related fields of ecology, systematics, paleontology, and geology.

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 biases in their training, their biogeography courses and writings tend to be uneven in coverage. A common specialization is taxonomic, e.g., phytogeographers study plants and zoogeographers study animals, and within these categories one finds specialists for groups at all taxonomic levels. Although viruses and bacteria play crucial roles in ecological communities and in human welfare, microbial geography 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 in terms of interactions between the organisms and their physical and biotic environments. Paleoecology bridges the gap between the two fields. Recently, some workers 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 approaches to the subject are valid and valuable, and ridiculing 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. As we hope to show, the various subdisciplines contribute to and complement each other, unifying the science.

## Relationships to other sciences

Biogeography is a synthetic discipline, relying heavily on ecology, population biology, systematics, evolutionary biology, the geosciences, and natural history. Consequently, we do not want to draw sharp lines between biogeography and its related subjects, as some authors have attempted. For example, various authors have recommended that paleontology (the study of fossils and extinct organisms) and ecology should be divorced from biogeography; this would make biogeography a purely descriptive, mapmaking endeavor. Instead, biogeography is a branch of biology, and not surprisingly, a good knowledge of biology is an important starting point. This is why our treatment devotes considerable space to reviewing and developing ecological and evolutionary concepts that are used throughout the book (Chapters 3, 4, 6, and 7). In addition, we must be acquainted with the major groups of plants and animals and know something about their physiology, anatomy, development, and evolutionary history, so these topics are integrated in Chapters 10 to 13. For example, the distributions of frogs and salamanders begin to make sense once we know that these are amphibians, a group of vertebrates that are usually terrestrial as adults but aquatic as larvae. They thrive in moist places, but most are intolerant of salt water. This helps us to understand why amphibians are common in mesic habitats on continents but are poorly represented in deserts and on oceanic islands.

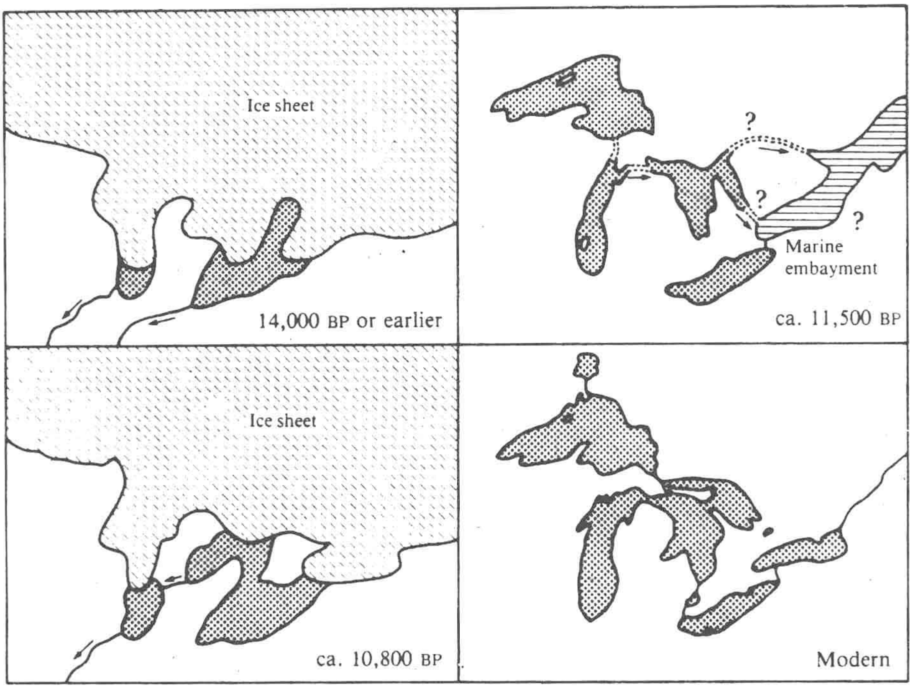


**Figure 1.1**
Changes in the geography of the Great Lakes region within the last 14,000 years, during and after the last episode of Pleistocene glaciation. Note the dramatic changes in the distribution of ice sheet, land, and water, and imagine the effects on the ranges of plants and animals. (Maps redrawn from Hutchinson, 1957.)

Naturally it is important to know some geography. Locations of continents, mountain ranges, deserts, lakes, major islands and island chains, and seas during the past as well as the present are indispensable information, as are past and present climatic regimes, ocean currents, and tides. Even looking back a mere 14,000 years, since the latest Pleistocene, we discover a vastly different topography in the Great Lakes region (Figure 1.1), where three of the present lakes were covered with glacial ice, and the other two, antecedents of Lake Erie and Lake Michigan, had markedly different shapes and were somewhat interconnected. Imagine how this could have influenced migration and speciation of organisms.

Contemporary climatic patterns are equally intriguing. For example, diverse and distinctive plant formations are found throughout the world in isolated regions where mediterranean-type climates prevail. Total annual precipitation is low, over two thirds occurring in the mild winter months, whereas summers are dry and often hot. Places sharing this climatic regime are widely disjunct in warm temperate latitudes: around the Mediterranean Sea, in coastal central Chile, in southwestern Australia and coastal southern and central Australia, in the Cape Region of South Africa, and in coastal and inland southwestern North America, especially California (Figure 1.2). These distinctive semiarid plant communities, named by local people as

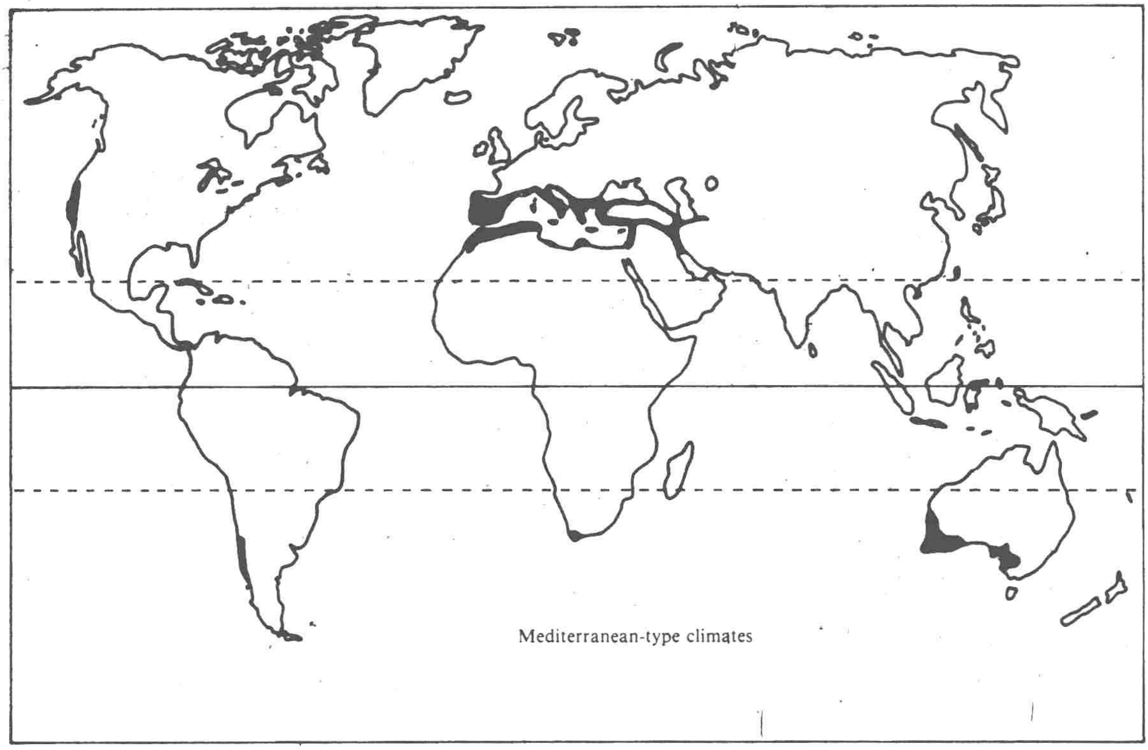


**Figure 1.2**
Worldwide distribution of regions experiencing mediterranean-type climates. These areas tend to occur as small patches on the western or southern coasts of continents between 30° and 40° latitude. Although these regions are isolated on different continents, they contain similar vegetation because distantly related plant species have evolved similar adaptations to the distinctive climate. (Map redrawn from Thrower and Bradbury, 1977.)

chaparral, matorral, macchia, maquis, fynbos, or sclerophyllous scrub, strongly resemble each other in vegetative structure and adaptations to periodic burning of the dense shrub cover. However, in each area the dominant vegetation is taxonomically unique, showing that the plants are derived from different ancestors and that they have converged in many traits in adapting to similar environments. Background knowledge of physical geography and climate presented in Chapter 2 is relevant to elucidating such patterns of evolutionary and ecological convergence.

Trying to understand distributions of organisms without knowing the past positions of continents and oceans means working with the same handicaps that plagued the pioneers of our science, who thought the geography of the earth has remained fixed over time. The modern biogeographer must appreciate not only the evolutionary history of different groups of organisms but also the geologic history of the earth on which they lived, because these processes have interacted to determine present distributions, especially over the last 250 million years. Reflect for a moment on the history of

North America. For most of its history North America has been in close proximity to if not connected with western Europe, and the final break of these two landmasses occurred only 60 million years ago when several northern seas and Iceland were born, resulting in the permanent separation of Europe and Greenland. Also about 60 million years ago western North America achieved a solid land connection with Siberia, which served as an important highway for biotic exchange until 8000 years ago. To the south lies South America, which was separated from North America during most of its late history until about 4 million years ago, when Panama began to emerge as an isthmus to connect Colombia with Central America. This is a different land connection than the one 80 million years earlier that was later displaced into the Caribbean region. Knowledge of such land connections is essential in providing biogeographic explanations for the distribution of some modern groups in terms of historical migrations. Similarities in some living fishes, insects, birds, earthworms, and certain extinct plants and reptiles among South America, Africa, and Australia make sense when we realize that at least until 135 million years ago, while these groups were evolving and expanding their ranges, all three continents were joined as part of a single giant southern landmass called Gondwanaland. For these reasons, considerable attention is given to geologic information, especially to the origin of current ideas and the latest information on plate tectonics (Chapter 5).

## Philosophy and basic principles

Most people have a vague, misleading impression of what science is, how scientists work, and how major advances are made. Scientists try to understand the natural world by reducing its diversity and complexity to general patterns and basic laws. Philosophers and historians of science, viewing its progress with 20/20 hindsight, often suggest that it is possible to give a recipe for the most effective way to conduct an investigation. Unfortunately, most practicing scientists know that scientific inquiry is much more like working on a puzzle or being lost in the woods than baking cookies or following a roadmap. There are numerous mistakes and frustrations; luck, timing, and trial and error play crucial roles even in modest scientific advances. This is not meant to imply that intelligence, creativity, perseverance, and precision are not important. These attributes, plus sound technique, are as valuable to good scientific investigation as they are to solving a puzzle or finding the way when lost.

In essence, science is the investigation of the relationships between pattern and process. Pattern can be defined as nonrandom, repetitive organization. Occurrence of pattern in the natural world implies causation by a general process or processes. Science usually proceeds by the discovery of patterns, then the development of mechanistic explanations for them, and finally the rigorous testing of these theories until the ones that are necessary and sufficient to account for the patterns are accepted as scientific fact.

Traditional treatments of the philosophy of science usually devote considerable space to distinguishing between inductive methods, reasoning from specific observations to general principles, and deductive methods, reasoning from general constructs to specific cases. Several influential modern philosophers, especially Popper (1968a) have strongly advocated the so-called hypothetico-deductive method. Any good scientific theory has logical assumptions and consequences that must be verified before acceptance. The hypothetico-deductive method provides a powerful means of testing a theory by setting up alternative, falsifiable hypotheses. First, an author puts forth a new, tentative idea, stated in clear, simple language, that can be tested and thus falsified by means of experiments or observations. Only after a statement has withstood the severest tests should the statement be considered trustworthy or corroborated, but no theory is ever proven true.

New general theories are the ultimate source of most major scientific advances, and most of them are and have been arrived at by inductive methods. The theory of evolution by natural selection, the proposed double helical structure of DNA, and the equilibrium theory of insular biogeography all were derived largely by assembling factual data, recognizing a pattern, and then proposing a general explanation. Although it might be safe to generalize that theories usually arise by inductive methods and are tested by deductive ones, often the actual conduct of scientific research is much more complex. Empirical observations and conceptual generalizations are played back and forth against each other, theories are devised and modified, and understanding of the natural world is acquired slowly and irregularly. This is particularly true of biogeography. For this reason, some critics accuse the discipline of being metaphysical or pseudoscientific; they claim that some authors shield their ideas from contradictory evidence, dodging complaints and changing theories as they go.

Unlike most of contemporary biology, biogeography usually is not an experimental science. Questions about molecules, cells, and individual organisms typically are most precisely and conveniently answered by artificially manipulating the system. In such experimentation the investigator searches for patterns or tests specific hypotheses by changing the state of the system and comparing the behavior of the altered system with that of an unmanipulated control. It is impractical and often impossible to use these techniques to address many of the important questions in biogeography and the related disciplines of ecology and evolutionary biology. Historical evolution and historical biogeography are, as the names imply, history; they produce no exact predictions for the future.

Recently some biogeographers have used experimental techniques to manipulate small systems, particularly tiny islands, with spectacular success, e.g., Simberloff and Wilson (1969). However, most important questions have huge historical or geographic dimensions that make experimentation impossible. This methodological constraint does not diminish the rigor and value of biogeography, but it does pose major challenges. Other sciences, such as astronomy and geology, face the same problems. Copernicus, Galileo, Kepler, and Newton never moved a planet, but that did not prevent them from making tremendous contributions to our understanding of the motion of celestial bodies. Wallace and Darwin used patterns of animal and plant distributions observed in their world travels to develop important new ideas about evolution and biogeography. Islands had great influence on Wallace, Darwin, and numerous subsequent biogeographers, ecologists, and evolutionists because they represent natural experiments, replicated natural systems in which many factors are held relatively constant while others vary from island to island. Despite the difficulty of performing artificial experiments, it is possible to develop and rigorously evaluate biogeographic theories by the logical procedures used by other scientists: searching for patterns, formulating theories, and then testing the assumptions and predictions independently with new observations.

In dealing with historical aspects of their science, most biogeographers make one critical assumption that is virtually impossible to test: they accept the principle of uniformitarianism or actualism. This inferred concept holds that the physical processes now operating at the earth's surface have remained unchanged and are the result of the same fundamental laws that have acted throughout time. The principle of uniformitarianism is usually attributed to the British geologists Hutton (1795) and Lyell (1830), who realized that the earth was much older than had been previously supposed and that its surface was constantly changing as rocks were formed and weathered away and as mountains were uplifted and eroded down. In this same spirit, one of Darwin's great insights was the recognition that changes in domesticated plants and animals over historical time by selective breeding represent the same process as changes in organisms over evolutionary time through the process of natural selection.

As noted by Simpson (1970a), acceptance of uniformitarianism has never been universal, in part because authors have attached additional meanings to the concept. To many the term implies that the average intensities of processes have remained approximately constant over time and that changes are always gradual. Neither of these amendments is wholly acceptable. We have data to show how certain processes are now more or less intense than in the past; how forces are more active in one part of the globe than in others; where effects of forces have been sudden, not gradual; and where rates of change have not been constant over time. One must expect that intensity of forces varies from time to time and place to place; only the nature of the processes themselves is timeless.

To avoid unfortunate connotations associated with uniformitarianism, Simpson, after others, prefers to adopt the term *actualism,* conceptually similar to methodological uniformitarianism (Gould, 1965). Historical biogeographers in particular use this principle to account for present and past distributions, assuming that the processes of speciation, dispersal, and extinction operated in the past in the same manner that they do today. This premise is hard to falsify, of course, but fortunately most observations support the principle and have made it an accepted tool for understanding the past and predicting the future. The most serious problem in using the principle is that students must, of course, decide which timeless properties apply to a particular situation.

## A brief history

**Developments in the early nineteenth century.** It is hard for us to appreciate that 200 years ago biologists had described and attempted to classify only 1% of all the plant and animal species we know today. Therefore biogeography really was founded and accelerated rapidly by world exploration and the accompanying discovery of new kinds of organisms, which gained great momentum in the 1800s. One of the early explorer-naturalists was Alexander von Humboldt, who usually is honored as the father of phytogeography. His treatises, beginning in 1805, were the first to conceptualize and quantify the primary role of climate in the distributions and forms of plants around the world. The close relationship between vegetation and climate was quickly expanded by Humboldt's contemporaries, such as A.P. de Candolle, J.F. Schouw, W.J. Hooker, and A. Grisebach, thus establishing the study of ecological phytogeography. Schouw (1823) published a remarkable textbook that not only included a classification of floristic regions of the world but also attempted to standardize descriptions of plant communities using Latin suffixes. From these humble beginnings, thousands of later scientists have attempted to quantify these botanical patterns.

Adolphe Brongniart is regarded as the father of paleobotany because he carried the theme of climate and vegetation into interpretations of the fossil record. From his studies, the use of plants as indicators of past climates became the basis of a new discipline, paleoclimatology. Brongniart (from 1827 to 1837) compared present and past floras of Europe; basing his discussions on the nature of fossil forms, he concluded that some of these localities once had tropical climates.

One of the great conceptual achievements of the early period was the law of the minimum, lucidly presented by Justus Liebig in 1840. Simply stated, the distribution of an organism is restricted by one particular basic requirement for life that is critically limiting, e.g., a foodstuff, a mineral, water, light, or temperature. This viewpoint is no longer widely held. We generally do not find that only one substance or factor is limiting; to the contrary, much evidence demonstrates that the interactions of these factors can be the mechanism for limiting distributions. Nevertheless, the investigation of limiting factors, both abiotic and biotic, stimulated interest in the fledgling disciplines of ecology and soil science in the late 1800s.

The study of animal distributions lagged behind phytogeography during its early history. Two factors contributed to this delay. First, because of the much greater number of animal species (about half of the 1.6 million described species are insects!), the task of describing and classifying animal life was several times greater than for plants, offering huge challenges for identifying general patterns. Second, the relationships between animal distributions and climate are mostly indirect; in fact, distributions of animals are more often closely associated with vegetation than with climate per se.

An early synthesis was produced by William Swainson (1835), but the first popular global classification of faunal regions that approaches our present-day classification of realms (Figure 1.3) was made for birds by W.L. Sclater (1858). As the pace of description and classification of animals was accelerated in the latter half of the

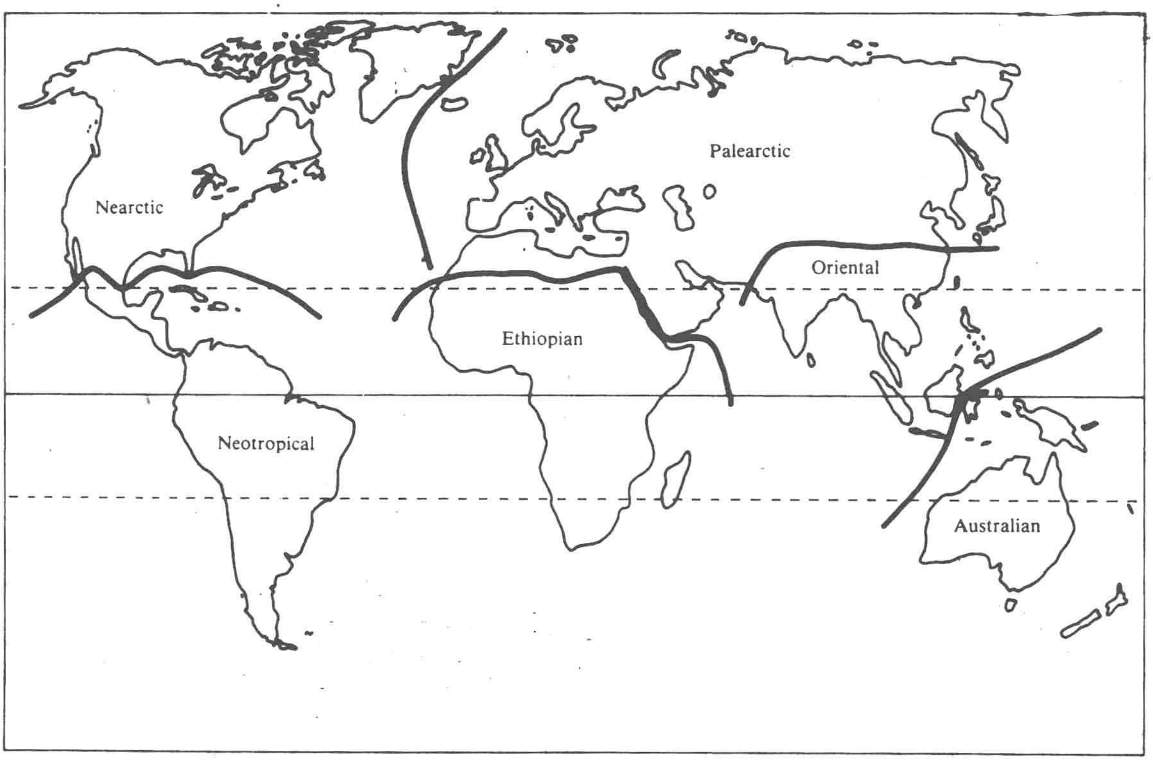


**Figure 1.3**
Major biogeographic regions reflect attempts of biogeographers to divide the landmasses into a classification reflecting the affinities of the terrestrial flora and fauna. The regions shown here are those described by A.R. Wallace in 1876 and are still widely accepted today. This classification is similar to that proposed by Sclater (1858) for birds.