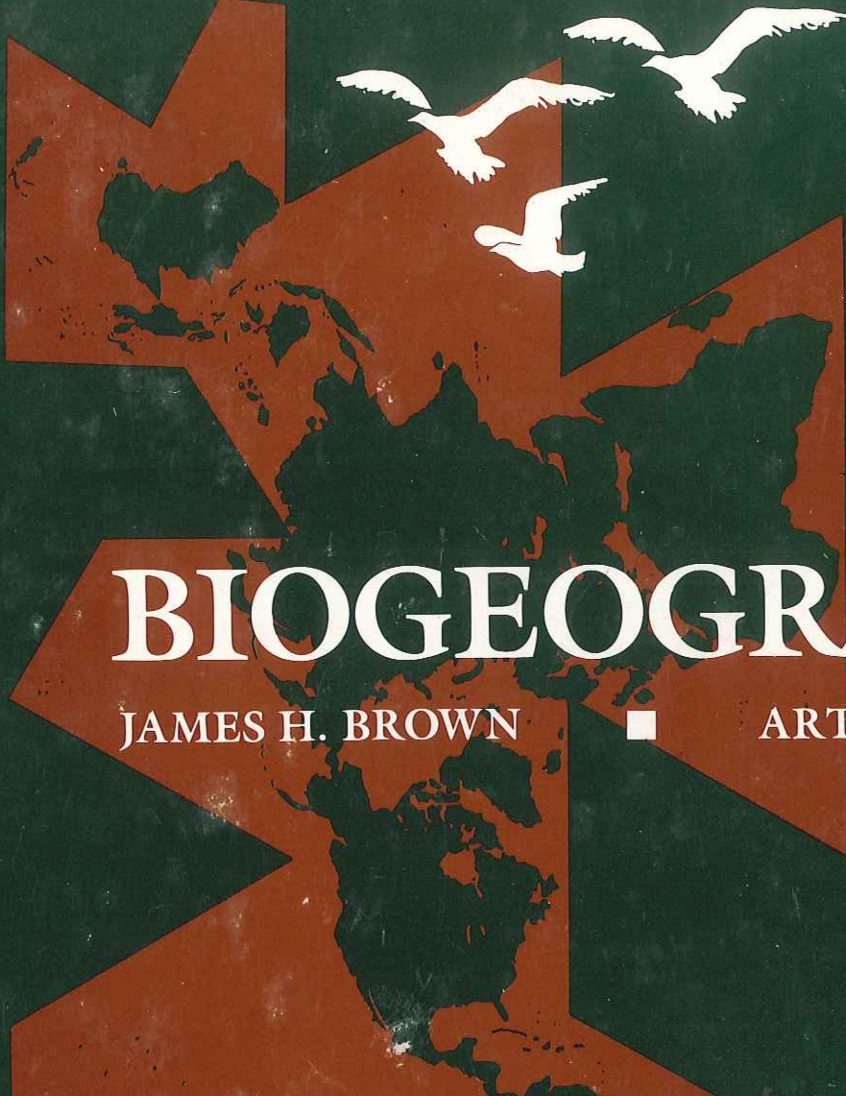

BIOGEOGRAPHY

JAMES H. BROWN ▪ ARTHUR C. GIBSON

BIOGEOGRAPHY

JAMES H. BROWN, Ph.D.
Department of Ecology and Evolutionary Biology,
The University of Arizona,
Tucson, Arizona

ARTHUR C. GIBSON, Ph.D.
Department of Biology,
University of California at Los Angeles,
Los Angeles, California

With 600 illustrations

The C. V. Mosby Company
ST. LOUIS • TORONTO • LONDON
1983

MOSBY

A TRADITION OF PUBLISHING EXCELLENCE

Editor: Diane Bowen
Assistant editor: Susan Dust Schapper
Manuscript editor: Mark Spann
Design: Kay M. Kramer
Production: Linda R. Stalnaker, Judy Bamert

Printed in the United States of America

The C.V. Mosby Company
11830 Westline Industrial Drive, St. Louis, Missouri 63141

Library of Congress Cataloging in Publication Data
Brown, James H.
Biogeography.

Bibliography: p.
Includes index.
1. Biogeography. I. Gibson, Arthur C. II. Title.
QH84.B76 1983 574.9 82-14121
ISBN 0-8016-0824-4

C/D/D 9 8 02/A/261

Chapter 3 The Limits of Species Distributions

The geographic distributions of organisms are not static, but dynamic. Over time the ranges of species shift, expand, and contract. The distributions of higher taxonomic groups such as genera, families, orders, and classes also change because their geographic ranges simply reflect the cumulative distributions of all the included species. These changes are the net result of two opposing processes: colonization, the expansion of populations into new areas, and extinction, the elimination of populations from all or part of their former range. These are ecological processes because they ultimately depend on how environmental conditions cause local populations to increase or decrease.

Biogeographers, ecologists, and evolutionists are concerned with patterns and processes that occur over a wide variety of temporal and spatial scales. For convenience the temporal scale is often divided into ecological and evolutionary time. By ecological time we usually mean periods from milliseconds to decades, in which populations may interact with their environment and respond to environmental fluctuations without undergoing evolutionary modification. By evolutionary time we normally mean periods of tens to millions of years, during which populations can evolve and become adapted to their environments by means of genetic changes. This dichotomy is artificial, because some evolutionary changes, such as the development of antibiotic resistance in bacteria, can be extremely rapid whereas certain ecological events, such as soil formation, may take a long time. Nevertheless, we have different perceptions about ecological processes, which we can study by direct observation and experimentation, and evolutionary mechanisms, which must be investigated indirectly by comparative studies of fossil and living organisms of varying degrees of relatedness. Ecologists are also more likely than evolutionists to investigate the small end of the spatial scale and to be concerned with the fate and characteristics of local populations rather than geographically widespread species and higher taxonomic groups. Because both ecological and evolutionary processes influence the distributions of organisms, biogeographers must be able to integrate phenomena that occur at all spatial and temporal scales. In the last analysis, the ultimate mechanisms controlling distributions are ecological: the influence of the environment on the birth, death, and movement of individuals.

Biogeography is an interesting and challenging science because the distribution of organisms is neither uniform nor random. Each species has a unique geographic range that reflects both its current ecological niche and its past history. Because related species share common ancestors from which they have usually inherited similar biological constraints and ecological requirements, higher taxonomic groups also tend to be confined to limited geographic areas that reflect their common heritage. But the fundamental problem is why each species inhabits only a small portion of the earth's surface. For many organisms this question can be answered at two levels. On the one hand, limited capacity for dispersal may prevent a population from colonizing distant areas where conditions are otherwise suitable for its esof *Pseudomyrmex* may not be dependent on acacias, for numerous species the relationship is apparently obligate. The trees provide the ants with enlarged thorns in which they build their nests and with specialized foods rich in sugars, oils, and proteins. In return, the ants attack herbivorous insects and vertebrates and clear away surrounding vegetation, reducing competition from other plants. Such coevolved specializations apparently have made these mutualists so dependent on each other that they have virtually identical ranges.

Complex interactions. In addition to those cases in which it is possible to isolate the limiting effect of one species on the distribution of another, there are undoubtedly many situations in which ranges are structured by more diffuse biotic interactions. The limits may be the result of different, interacting effects of several species. MacArthur (1972) noted that the southern limits of the ranges of many North American bird species apparently could be attributed neither to climate (because the climate becomes more equable at lower latitudes) nor to habitat (although it might be important for some species) nor to any particular species of competitor or predator. MacArthur suggested that for many species the limiting factor must be the diffuse competition from an increasing number of tropical species. He noted, for example, that of 202 land bird species that breed in Texas, only 29 also breed in Panama, but Panama has a total of 564 breeding land bird species. One of the few species that breeds in both the United States and Panama is the yellow warbler *(Dendroica petechia)*, a small, insectivorous foliage gleaner. In the United States the yellow warbler is abundant in a wide variety of shrubby and forested habitats, but in Panama it is restricted to mangrove swamps and small offshore islands (Figure 3.21). Because the forests of Panama contain many species of highly specialized foliage-gleaning birds whereas mangroves and islands have few species, MacArthur attributed the distribution of the yellow warbler to diffuse competition, the combined negative effects from many bird species. However, it is difficult to rule out a significant influence of predation, because the number of species of snakes, hawks, and other predators shows the same pattern as the species diversity of potential competitors.

We conclude this section by emphasizing that it may not be productive to search for single limiting factors and simple explanations for the distributions of species. Not only may a single species be limited by different factors in different parts of its range, but even in one local area several factors may interact in complex ways to prevent expansion of populations. In some cases, particularly in gradients of increasing physical stress, climate and other physical factors may combine with biotic interactions to limit distributions. In other cases, especially in gradients of decreasing physical harshness, diverse biotic interactions act in concert to prevent range expansion. It will often be difficult and misleading to try to assess the relative contributions of single factors if there are complex interactions between various niche dimensions.

Adaptation and gene flow

Although the geographic distributions of most species and higher taxa appear relatively stable over short periods of ecological time, they undergo major changes over evolutionary time. Some of these changes are primarily the result of long-distance dispersal or of geologic events that have altered the geography and climate of the earth. These will be discussed in later chapters. However, many historical changes in species ranges must have resulted from gradual expansions or contractions of peripheral populations. Since natural selection is a universal process that tends to increase the capacity of individuals to survive and reproduce, we might expect that, in general, peripheral populations would gradually adapt to their local environments, increase in densities, and expand their ranges to colonize adjacent areas (see Baker and Stebbins, 1965). Lewontin and Birch (1966) de-

Chapter 6 Speciation and Extinction

Species have histories that are somewhat analogous to the lives of individuals. New species originate by the multiplication of old ones (speciation); they survive for varying periods of time, during which they may or may not leave descendents; and they die (extinction). There are, however, important differences between the histories of individuals and of species. Whereas the birth and death of most individuals are discrete, easily recognizable events, it is often difficult to determine when a species is fully formed. Rather than becoming extinct abruptly when its last individual dies, some of a species population may disappear in time by evolving into a new kind of organism that will soon be classifiable as a different species.

Related species possess a particular combination of traits, at both the structural and the molecular levels, that are inherited from a common ancestor. If the group has been diverse and successful, one can usually infer that the traits that made the group distinct were adaptive—that is, they represented an innovative solution to a problem that limited survival and reproduction in other populations. It is not necessarily true, however, that all new traits of an evolutionary line are adaptive and have arisen as a direct result of natural selection. Although a particular lineage may have flourished for a period of time and radiated to produce a diverse group of species, this success is usually ephemeral on a geologic time scale. Eventually the rate of extinction exceeds the rate of speciation, and the group diminishes and finally becomes extinct. These repeated episodes of speciation, radiation, and extinction have occurred many times during the history of the earth to produce the variety of living and extinct organisms.

The importance of speciation to biogeography is that it is an evolutionary branching process. Through speciation, evolutionary lineages split and are freed to adapt to different environments and to colonize new regions. Where and when these evolutionary events took place naturally did much to determine present and past geographic distributions.

Speciation

What is a species? Not all taxonomists and evolutionary biologists agree on how the term *species* should be defined, although the specialists on most taxonomic groups share an idea of how different populations must be in order to be classified as separate species. The classical and conventional definition of a species is the morphological species concept. This concept recognizes that each species usually is morphologically distinguishable from its closest relatives. However, the criteria for determining how much a population must differ and in which particular traits vary from group to group.

In sexually reproducing animals and plants, the biological species concept frequently is employed to define a species as a group of organisms that is reproductively isolated from any other group. When a population is isolated reproductively, it constitutes a separate evolutionary lineage that is prevented by geographic or biological barriers from interbreeding with other populations. In the absence of gene flow

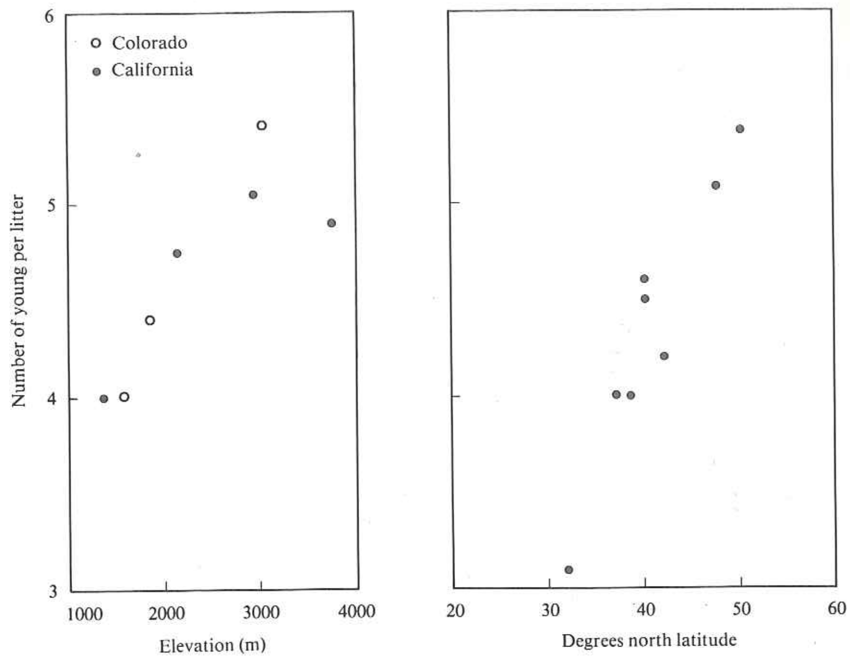

Figure 6.3
Latitudinal and elevational variation in litter size in the deer mouse, *Peromyscus maniculatus,* in North America. Note that litter size increases consistently with both increasing latitude and increasing elevation at the same latitude. Apparently, large litters are adaptive in cold environments with short growing seasons, perhaps because in warmer climates the animals can have more litters per year with fewer young per litter. The lowest latitude point is for the sibling species *Peromyscus polionotus* from Georgia.

to describe the gradual change in one or more features along a single environmental gradient. Many birds and mammals exhibit clinal variation in clutch or litter sizes, respectively, with latitude and elevation (e.g., for *Peromyscus* see Dunmire, 1960; Lord, 1960; Smith and McGinnis, 1968; Spencer and Steinhoff, 1968) (Figure 6.3). Such variation presumably reflects adaptations in life history traits to environments that differ in temperature, seasonality, productivity, and other factors. Similarly, clines in physiological characteristics of plants and insects show that populations at progressively higher latitudes survive and reproduce best under cooler temperature regimes.

Allopatric speciation. The simplest way to model speciation is to assume that genetic differentiation cannot lead to new species unless the populations are geographically isolated, so that gene flow between them is virtually cut off. This is termed allopatric speciation, meaning the divergence occurs in different places. The classic model of allopatric speciation by geographic subdivision (geographic speciation) (Figure 6.4) was championed by Mayr (1942, 1963). If the environment is heterogeneous, a geographically widespread ancestral population will develop regional genetic differences in response to either natural selection or genetic drift. Because of barriers that limit dispersal,

Chapter 7 Dispersal

What is dispersal?

All organisms have some capacity to move from their birthplaces to new sites. Movement of offspring away from their parents is a normal part of the life cycle of virtually all plants and animals. Often dispersal is confined to a particular stage of the life history. Higher plants and some aquatic animals are sessile as adults, but in their earlier developmental stages they are usually capable of traveling small but significant distances from the source (Figure 7.1). Mobile animals may shift their locations at any time during their lives, but many settle down and confine their activities to a limited home range for long periods of time. Dispersal should not be confused with dispersion, an ecological term referring to the spatial distribution of individual organisms within a local population.

Dispersal as an ecological process. Dispersal is basically an ecological process. Natural selection favors individuals that move some distance from their natal site. A more distant location is always likely to be more favorable than the exact birthplace, in part because intraspecific competition between parent and offspring and among siblings is reduced, and in part because the environment, and hence the quality of the natal site, is always changing. Plants and animals have evolved a wide variety of mechanisms of dispersal in response both to the spatial variation in the environment, which determines the probability of survival and reproduction as a function of distance traveled, and to evolutionary constraints on the organism, which influence the kinds and distances of movements that are possible. From an ecological point of view dispersal must be considered simply as an adaptive part of life history of every species. (For an extensive discussion and many examples see Krebs, 1978.)

Dispersal as a historical biogeographic event. The role of dispersal in biogeography is very different. Although dispersal is continually occurring in all organisms, most of it does not result in any significant change in their geographic distributions. As pointed out in Chapter 3, the geographic ranges of most species are limited by environmental factors and remain relatively constant over ecological time. Biogeographers are concerned primarily with the exceptions: those rare instances in which species shift their ranges by moving over large distances. This occurs so infrequently that we seldom see it happening, and even less often are we able to study it. Usually dispersal must be viewed as a historical process, and the nature and timing of past long-distance movements must be inferred from indirect evidence, such as the distributions of living and fossil forms. This is a monumental task. The distribution of every taxon reflects a history of local origin, dispersal, and local extinction extending back to the very origin of life. Patterns of endemism, provincialism, and disjunction of geographic ranges (Chapter 8) indicate that the dispersal of many groups has been so limited that their histories are reflected in the distributions of living and fossil representatives. However, reconstructing this history requires that we deal with a process