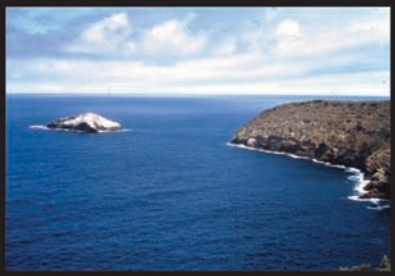
PRINCETON
LANDMARKS
IN BIOLOGY

THE THEORY OF ISLAND BIOGEOGRAPHY



WITH A NEW PREFACE BY EDWARD O. WILSON

ROBERT H.
MACARTHUR

EDWARD O.
WILSON

THE THEORY OF

Island Biogeography

PRINCETON LANDMARKS IN BIOLOGY

The Theory of Island Biogeography
by Robert H. MacArthur and Edward O. Wilson
With a new preface by Edward O. Wilson

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ROBERT H. MACARTHUR AND

EDWARD O. WILSON

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Preface to the Princeton Landmarks in Biology Edition

Robert Helmer MacArthur's death from cancer in 1972, at the very early age of 42, deprived ecology of a creative genius who, with less than two decades of research, had already left a permanent impression on his discipline. He was a gifted mathematician, which in the notably nonanalytical milieu of the time was a key to his success. But even more importantly, he was a dedicated naturalist with a deep love and understanding of birds, his favorite group of organisms. He combined the logic and imaginative process of mathematics with the fingertip feel of ornithology to create simplifying models of complex phenomena in evolutionary and community ecology, and thereby set the tone for an entire generation's effort in theoretical studies.

It was my privilege to collaborate with Robert (he preferred not to be called Bob) on island biogeography, arguably the piece of work for which he is best and most favorably remembered today. The success of our effort was due to *The Theory of Island Biogeography*, published in 1967. In this summary work, we spelled out the likely parameters of the assembly of discrete biotic communities, and then, not satisfied, struck out from this base to explore other, related phenomena, such as demography and competition.

When our friendship began in 1960, I brought to our discussions two of the main elements of island biogeography. The first was a detailed knowledge of animal distribution and ecology and especially of the ants of Melanesia, on which I had recently conducted field and museum studies. The second was the theory, developed

earlier by William Diller Matthew, Philip J. Darlington, and George G. Simpson, of faunistic replacement and balance in the major groups of Cenozoic land vertebrates. These authors had conceived of a rough equilibrium in continental faunas at the taxonomic level of families. Matthew and Darlington, in particular, envisaged a cyclical pattern of newly dominant groups replacing older ones, only to retreat themselves before fresh competitors across evolutionary time. Subsequently, I worked out similar patterns at the finer, species level in the ants of New Guinea and neighboring archipelagoes. In the process, I documented the logarithmic relation of species to island area in ants and a few other animal and plant groups. All this I brought to MacArthur's attention and suggested that we might create a more rigorous theory of biogeography than had hitherto been possible. He responded by devising the famous crossing curve of species immigration and extinction. We were then off and running in broader exchanges of ideas and data on the implications of biotic equilibrium for ecology. In 1963 we published a bare-bones article, "An Equilibrium Theory of Insular Zoogeography" (*Evolution* 17:363–387), and followed it in 1967 with *The Theory of Island Biogeography*. The article was scarcely noticed, but the book was an instant critical and—at least by university press standards—commercial success.

The Theory of Island Biogeography has exerted an important influence on both biogeography and ecology. True, after more than three decades, it has been largely replaced by a generation of far more detailed and sophisticated studies. Yet I believe that its basic structure remains sound, and the content still serves as a good introduction to the subject. Furthermore, in a way that MacArthur and I failed to appreciate, the book has had a major impact on conservation biology. This young discipline grew significantly in the 1970s and came into flower in the 1980s and 1990s. Because *The Theory of Island Biogeography* deals centrally with habitat fragmentation, hence insularization, the creation of biotic

communities, and species extinction, its relevance to conservation biology was immediately clear.

The flaws of the book lie in its oversimplification and incompleteness, which are endemic to most early efforts at theory and synthesis. Large numbers of experiments and field data on many biotas supported the hypothesis of species equilibrium, but many others did not. In some cases the variance was explained—for example, by frequent environmental disturbance and chronic disequilibria—but often no clear cause was adduced, and in the latter circumstance the basic theory found little use except perhaps to stimulate further study. Also, MacArthur and I had been satisfied to account for the effect of area on equilibrial species numbers as an outcome of varying population size and fluctuation. Thus, small islands, supporting small populations, are more prone to lose species than large ones, and the effect is exacerbated when the amplitude of population fluctuation is increased. Later, others were quick to point out that population size is far from the whole story. The area effect owes a lot to the happenstance of physical geography. In particular, large islands have more variable topography, soil types, and other determining features of vegetation and microclimate, which in turn affect colonization and extinction rates.

Thus, island biogeography has evolved into a subject far more enmeshed in the particularities of natural history. Departing from the early models of species equilibrium, it has also engaged most other disciplines of biology, including population genetics, life-cycle studies, ethology, and ecosystems studies. To a considerable degree, it has been dissipated into them. I call that progress and would have it no other way, and I am certain Robert MacArthur, if he were here, would agree.

Edward O. Wilson
Harvard University
November 1999

Preface

This book had its origin when, about five years ago, an ecologist (MacArthur) and a taxonomist and zoogeographer (Wilson) began a dialogue about common interests in biogeography. The ideas and the language of the two specialties seemed initially so different as to cast doubt on the usefulness of the endeavor. But we had faith in the ultimate unity of population biology, and this book is the result. Now we both call ourselves biogeographers and are unable to see any real distinction between biogeography and ecology.

A great deal of faith in the feasibility of a general theory is still required. We do not seriously believe that the particular formulations advanced in the chapters to follow will fit for very long the exacting results of future empirical investigation. We hope instead that they will contribute to the stimulation of new forms of theoretical and empirical studies, which will lead in turn to a stronger general theory and, as R. A. Fisher once put it, "a tradition of mathematical work devoted to biological problems, comparable to the researches upon which a mathematical physicist can draw in the resolution of special difficulties." Already some strains have appeared in the structure. These have been discussed frankly, if not always satisfactorily, in the text.

We owe the strains, as well as many improvements, to colleagues who read the entire first draft. We are very grateful to John T. Bonner, William L. Brown, Jr., Walter Elsasser, Carl Gans, Henry Horn, Robert F. Inger, E. G. Leigh, Richard Levins, Daniel A. Livingstone, Monte Lloyd, Thomas Schoener, and Daniel Simberloff for this favor. We are also indebted to William H. Bossert, Philip J. Darlington, Bassett Maguire, Ernst Mayr, and Lawrence B. Slobodkin for critically reading selected portions of the manuscript; and to J. Bruce Falls, Kenneth Crowell,

Bassett Maguire, Ruth Patrick, and Bernice G. Schubert for adding new materials. A preliminary draft of the book was used as a text in graduate seminars at Harvard University and Princeton University in the fall of 1966 and has thus benefited from a testing in the classroom.

The illustrations were prepared by John Kyrk. The typescript and much of the bibliography and index were prepared by Kathleen Horton with the assistance of Muriel Randall. Our personal research projects have been generously supported from the beginning by grants from the National Science Foundation and our respective home institutions.

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December 15, 1966

Symbols Used

A	Area of an island
B	The age of an organism at which first offspring are produced (see the fecundity model of Chapter 4).
b_x, b_τ	The number of offspring born to an individual at age x or at age τ.
D (and d).	The distance between two islands.
E	The extinction rate, in species per unit time. The particular value of E found when the biota is in equilibrium is labelled X (q.v.).
F_i	The density of individuals in prey populations above which the predator species specializing on them can increase (Chapter 5).
G	In the turnover model for single islands (Chapter 3), G is used to designate $d\mu/dS - d\lambda/dS$, in other words, the difference in the slopes of the extinction curve and the immigration curve.
I	The immigration rate, in species per unit time.
J	The total number of individuals in a taxon at a given time.
K	The "carrying capacity of the environment," i.e., the number of individuals in a population of a given species at the population equilibrium. A population with more than K individuals will decrease.
Λ	The mean overseas dispersal distance of propagules of a given species.
λ	Used without subscript, this letter symbolizes the per capita birth rate, measured in individuals per individual per unit time.
λ_S	The rate of immigration of new species when S species are present.

λ_x	The rate of birth of organisms when x organisms are present, measured in individuals per unit time.
l_x, l_τ	The probability of an organism's surviving to age x or to age τ.
μ	Used without subscript, this letter symbolizes the per capita death rate, measured in individuals dying per individual per unit time.
μ_S	The rate of extinction of species when S species are present.
μ_x	The rate of death of organisms when x organisms are present, measured in individuals per unit time.
$n_0(t)$	The number of newborn individuals in a population between time t and time $t + 1$.
P (and p).	Used to designate the number of species in the "species pool," that is, the number capable of immigrating to the island whether they all survive or not.
P_i	The density of individuals in a population of predator species i (Chapter 5).
P_S	The probability of occurrence of a certain number (S) of species.
ρ	Density of organisms, i.e., number of organisms per unit area.
R	Number of propagules (as opposed to species) arriving on an island in a given unit of time.
r	The "intrinsic rate of increase," the per capita rate of net increase in a given environment. (Mathematical explanation in Chapter 4.)
R_i	The density of individuals in a population of prey species i (Chapter 5).
R_0	The replacement rate: the average number of female offspring left during her life by each female.
S	Number of species.
$\hat{S}$	Number of species at equilibrium.
T	In the fecundity model of Chapter 4, the age of greatest fecundity.

T_x	The average length of time before a population containing x individuals goes to extinction.
$T_{0.90}$	The time required for a given taxon to reach 90% of the equilibrial number of species on an island.
$U(x)$	The reproductive function of individual organisms: the probability of survival to age x times the number of offspring produced at age x.
v_x	The reproductive value: a measure of the expected number of offspring yet to be produced by an individual of a given age. In biogeographic terms, it may be defined as the expected number of individuals in a colony (at some remote future time) founded by a propagule of x-year-olds.
W	In the fecundity model of Chapter 4, the last age at which offspring are produced.
X	The extinction rate at species equilibrium.
x, y	Used generally to designate discrete numbers, with different meanings given in various equations.
z	The slope of the log-log plot of the area-species curve. The z value varies with the kind of area unit employed, e.g., square miles as opposed to hectares.

THE THEORY OF Island Biogeography

CHAPTER ONE

The Importance of Islands

"The Zoology of Archipelagoes," Charles Darwin wrote at an early moment in his career, "will be well worth examination."[1] And so it has proved. The study of insular biogeography has contributed a major part of evolutionary theory and much of its clearest documentation. An island is certainly an intrinsically appealing study object. It is simpler than a continent or an ocean, a visibly discrete object that can be labelled with a name and its resident populations identified thereby. In the science of biogeography, the island is the first unit that the mind can pick out and begin to comprehend. By studying clusters of islands, biologists view a simpler microcosm of the seemingly infinite complexity of continental and oceanic biogeography. Islands offer an additional advantage in being more numerous than continents and oceans. By their very multiplicity, and variation in shape, size, degree of isolation, and ecology, islands provide the necessary replications in natural "experiments" by which evolutionary hypotheses can be tested.

Insularity is moreover a universal feature of biogeography. Many of the principles graphically displayed in the Galápagos Islands and other remote archipelagos apply in lesser or greater degree to all natural habitats. Consider, for example, the insular nature of streams, caves, gallery forest, tide pools, taiga as it breaks up in tundra, and tundra

[1] As he left the Galápagos in 1835, Darwin was struck by the variation among the skins of mockingbirds he had just collected from the different islands. He then wrote in his notebook what is considered to be the first reference to an awakening interest in evolution, as well as the first glimpse of modern island biogeography: "When I see these Islands in sight of each other, & possessed of but a scanty stock of animals, tenanted by these birds, but slightly differing in structure & filling the same place in Nature, I must suspect they are only varieties . . . . If there is the slightest foundation for these remarks the Zoology of Archipelagoes will be well worth examination; for such facts would undermine the stability of species."

as it breaks up in taiga. The same principles apply, and will apply to an accelerating extent in the future, to formerly continuous natural habitats now being broken up by the encroachment of civilization, a process graphically illustrated by Curtis's maps of the changing woodland of Wisconsin seen in Figure 1.

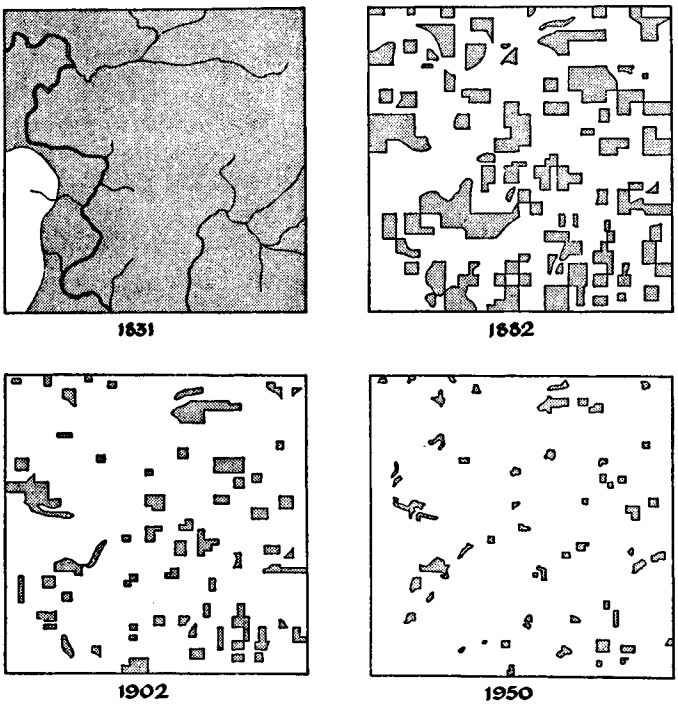


FIGURE 1. Reduction and fragmentation of the woodland in Cadiz Township, Wisconsin, 1831–1950. (After Curtis, 1956.)

Biogeography is a subject hitherto little touched by quantitative theory. The main reason is that the fundamental processes, namely dispersal, invasion, competition, adaptation, and extinction, are among the most difficult in biology to study and to understand. Stating postulates for even the simplest models is a risky business, because we are unsure of the complex biological phenomena underlying

them. Another reason is that most research has been taxonomic in origin, and dominated by the historical viewpoint. The conventional issues relate to special places and special groups of plants and animals. The major questions are *ad hoc* and historically oriented; for example:

What was the ultimate origin of the Antillean vertebrate fauna?

Did Central America develop a discrete insular fauna during the Tertiary?

How can we account for the phylogenetic similarities of the biotas of southern South America and New Zealand?

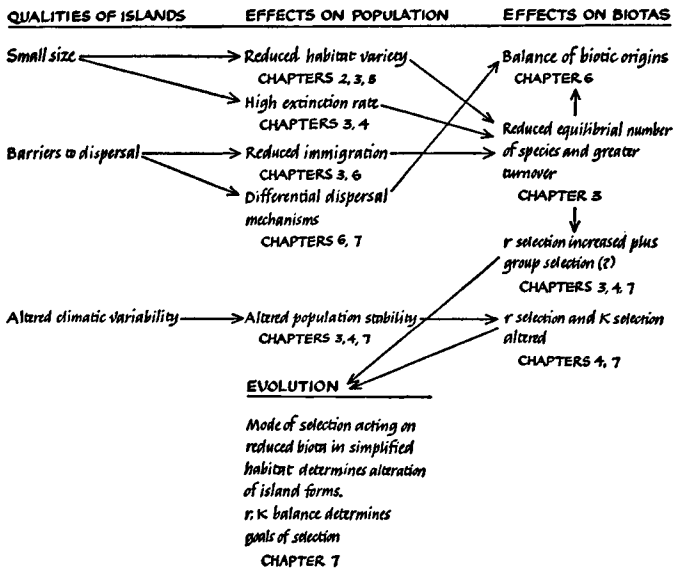
Why is Hawaii rich in species of *Nesoprosopis* but lacking in other native bee genera?

Partly because such questions are concerned with a limited number of higher taxa, and partly because of the considerable intrinsic interest in these taxa in the first place, the historical solutions have tended to be satisfying in themselves and have not encouraged generalizations.

The purpose of this book is to examine the possibility of a theory of biogeography at the species level. We believe that such a development can take place by looking at species distributions and relating them to population ecological concepts, both known and still to be invented. Although such formulations will be crude at first and perhaps often fall short of the intended goals in particular cases, the effort deserves to be made, for the following reason. A theory attempts to identify the factors that determine a class of phenomena and to state the permissible relationships among the factors as a set of verifiable propositions. A purpose is to simplify our education by substituting one theory for many facts. A good theory points to possible factors and relationships in the real world that would otherwise remain hidden and thus stimulates new forms of empirical research. Even a first, crude theory can have these virtues. If it can also account for, say, 85% of the variation in some phenomenon of interest, it will have served its purpose well. We need to ask next whether biogeography has a solid enough empirical basis at the present time to make such an

attempt. Certainly the amount of information on distribution is vast; it has been created by two hundred years of accumulated descriptive taxonomy. But data of use to a population theory of distribution are quite scarce. A main goal of this book is to identify those kinds of data needed for a further development of a population theory and, ultimately, the full explanation of distribution itself.

TABLE 1. Interrelations of chapters



In the chapters to follow we begin with a consideration of one of the more strikingly orderly relations encountered in biogeography: the area-diversity curve. Starting with the known facts concerning this relation, a rather extensive theory of the equilibrium of species is developed. The theory leads first to a consideration of the influence of life-table parameters of individual organisms on the immigration and extinction rates of populations and then to generalizations about the evolutionary strategies species must adopt in order to be good colonizers. The role of stepping stones in