Book Reviews

Biogeography and Ecology in a New Setting

The Theory of Island Biogeography. ROBERT H. MACARTHUR and EDWARD O. WILSON. Princeton University Press, Princeton, N.J., 1967. 215 pp., illus. Cloth, $8; paper, $3.95. Monographs in Population Biology, No. 1.

Robert H. MacArthur and Edward O. Wilson have now presented us with a book which may revitalize ecology. This joint endeavor is entitled *The Theory of Island Biogeography,* but I contend that the book also has strong implications for the future development of ecology as a predictive science. It represents an effort to take biogeography out of its present natural-history setting and place it in a new one, more conducive to experimentation and more amenable to theoretical analysis. In this new setting, the first principles of population genetics and ecology are used to provide mathematical models which help to explain the patterns of biotic diversity and distribution in archipelagos. In the future, presumably, a more complete theory of biogeography will be developed, treating islands and continents together.

The first and major problem to which the authors address themselves is that of the control of the number of species found on islands of various sizes and distances from their sources of colonizers. Their analysis of this problem involves the application of the equilibrium theory, which they first advanced in 1963 (*Evolution* **17**, 373–87). By this theory, it is assumed that the number of breeding species of (say) birds on a given island is a resultant of the rate of immigration of new species to the island and the rate of extinction of species on that island. According to the theory the number of species for a given island will be increased by any factor of the insular environment—such as increased insular area or environmental diversity—which decreases the extinction rate. The number of species will be decreased by any environmental factor or situation which decreases the rate of immigration of species to the island. Increased isolation from other land areas and opposing wind or water currents are among the factors which reduce the dispersal of propagules to islands. A propagule is defined as the minimum number of individuals required for the colonization of a habitable island by a species.

As first proposed by the authors, the equilibrium theory predicts that the number of species increases more rapidly on far than on near islands. That is, the slope of the species-area curve (estimated by z, the regression coefficient for the logarithm of species regressed on the logarithm of area) increases more rapidly the greater the distance between islands. They have evidence (see fig. 10 in chapter 2) that this may in fact be the case for the insular avifauna of the east central Pacific. The subsequent testing of this particular prediction ("the distance effect") of their model is a critical one for determination of the general validity of their equilibrium theory for insular biotas. They are careful, however, not to lean too heavily on the one set of data that supports their prediction. Indeed, they call attention to T. W. Schoener's yet unpublished finding that for analyses of sets of islands *within* archipelagos the z values of species-area slopes for near archipelagos are larger than those for far archipelagos. In dealing with Schoener's finding they argue that in certain situations their model predicts that such z values decrease with the increase in the isolation of islands. One wonders with sympathy as well as some amusement if the model has been rapidly altered to subsume Schoener's observation! However, MacArthur and Wilson have available data from multiple-regression analyses which support nicely their model's prediction of increased species-area slope for far islands. Listed in order of increased distance from continental or other sources of colonizers, the "corrected" z values for species-area slopes for the avifaunas of the West Indies, the East Indies, and the east central Pacific vary as follows: $0.24 \rightarrow 0.28 \rightarrow 0.30$. The authors also have the benefit of the data assembled by Ernst Mayr for variation in avian endemism as a function of island size. Mayr demonstrated [*Science* **150**, 1587 (1965)] a direct relation between island size and the percentage of endemic bird species. Presumably, the smaller the island, the greater the turnover of species as a result of extinction. Thus, on small islands many species become extinct before they can diverge to the level of the endemic. I am convinced of the general validity of the MacArthur-Wilson equilibrium theory for biogeography, and even if their theory is subsequently replaced or excluded by a larger, more comprehensive theory of biogeography, that new theory will in all probability also be of an equilibrium type, emphasizing stochastic elements in the control of insular species numbers.

Ecologists and evolutionists familiar with the recent papers of the two authors should not bypass the last chapters (4–8) of their work as being merely old wine in new bottles. Chapter 4 deals, to put it briefly, with the "strategy of colonization" and the use of the values of r (intrinsic rate of population increase) and K (equilibrial population size) in defining a superior colonist. It is concluded that the most effective propagules are those at the age of maximum reproduction value. In chapters 5 and 6, problems concerning the limitations of numbers of species on islands, the variations in the size or expression of ecological niches, and the exchange of species between different biotic areas are considered. The interactions between invading species and the resident ones are discussed, and some examples of expansion and contraction of niches are described. Of particular interest is the existence of some evidence, at least for birds, that niche compression is induced more frequently by the habitat selected than by variation in the diet preferred. The case of the mixed biota of New Guinea is discussed, and the tentative suggestion is made that this is a result of slight but significant differences in the dispersal curves and distances of the separated biotas which contribute jointly to the biota of New Guinea.

Consequences of Colonization

Although I have considered the equilibrium model at some length above, in my opinion MacArthur and Wilson's seventh chapter is the keystone of the book. Here are considered the populational and genetic changes that follow as consequences of insular colonization. In addition, the nature of such changes on continents and on islands is compared. This is postcolonization evolution, and two kinds of selection are delimited: *K* selection, whereby a more efficient utilization of available resources is favored, and *r* selection, which results in a higher population growth rate and productivity. Selection for *r* is dominant in new and growing populations in the early stages of colonization, and in unstable habitats where species may be repeatedly colonizing because their numbers are being regularly and dramatically diminished by environmental vicissitudes. Old and stable populations exhibit the results of *K* selection, as it were, a closer fit to the environment. M. L. Cody's analysis [*Evolution* **20**, 174 (1966)] of the variation in clutch size among birds of different biologies and environments is discussed as a good example of the interplay of *K* and *r* selection in different environmental situations. The average clutch size in birds is known to be large in the higher latitudes or elevations of continents, and smaller in the lower latitudes and elevations of continents and on islands. This suggests that natural selection in density-dependent species operates for quantity of offspring produced in the unstable environments, but more for quality of the (fewer) offspring produced in the more stable environments. Since changes in *r* and *K* indicate changes in life-history parameters, MacArthur and Wilson's discussion of the possible evolutionary significance of selection by the two methods raises important problems for all ecologists. This discussion, derived logically from the previous discussions by L. Cole and R. Lewontin of life-history phenomena and the role of *r* in population adaptation, is a useful one. It may well be that the recent arguments over density-dependent and density-independent regulation of population size and over individual versus group selection can now be reexamined in a more realistic manner. Presumably this revaluation would be made not in "either-or" terms, but in equilibrial terms according to which one process may override the other in certain circumstances, with environmental variation or certain historical factors regulating which process predominates.

In addition to advancing new ideas and updating old ones, the book directs attention to many problems in biogeography, the accounts of which have previously been scattered in various journals or books. One would hope that all ecologists and evolutionists will take the time to read it in its entirety. The authors are clearly attempting to stake out a new area in the biological sciences. In order to do this, they are deliberately bypassing many conventional and standard problems in ecology. They are calling for a new approach utilizing the principles of population genetics and ecology in a more precise approach to evolutionary ecology. Undoubtedly some biologists will say that the authors, and MacArthur in particular, are simply posing untestable models or setting up straw men against the only model that is valid in the context of the data advanced. This is not true, and indeed if it were true it would be an unimportant criticism. The authors are practicing a hypothetico-deductive approach to their scientific interests, not unlike L. Slobodkin's effort for community ecology some years ago. They appear to be very successful in this practice.

Hopes and Prospects

There is in science a natural selection of new ideas. The success of an idea expressed in a paper or in a book is tested by the frequency with which it, as compared to other, related ideas advanced previously or at the same time, appears in future years or generations. As the recent increase in numbers of papers concerned with species diversity, species-area phenomena, and character displacement that have been appearing in journals of ecology and evolution testifies, the research of MacArthur and Wilson during the past five to ten years has generated a marked enthusiasm and response on the part of many contemporary biologists. This response in itself can be considered a sign of selection for their ideas. It is to be hoped that, in the future, experimental studies of single species as well as of the biotas of small islands or of special environmental situations on continents will result in major advances in our knowledge of "the biogeography of the species." And, in their concluding chapter 8, the authors call for specific and detailed studies of this type. They emphasize that investigators can create "miniature Krakatus" on small islands by removing, by poisoning or by manual means, certain or all elements of the biota. Thereafter the immigration, colonization, and turnover rates can be measured for the propagules reaching an island. For certain insects and other organisms having short life cycles, investigators may well simulate biogeographic phenomena.

If MacArthur and Wilson's hopes are realized, we may see a new day for the science of ecology. My only reservation about this is whether or not such experimental studies can provide precise information on the composition of the gene pool and the genetic changes that are manifested during the "biogeography of a species." Population geneticists are presently having a field day describing isozymic variation in natural populations, however, and are finding a wide array of allelic diversity at many if not most loci of the genome. If these geneticists or others can discover the adaptive significance of such isozymic variation and its contribution to the fitness of the individual whose phenotype is the unit of natural selection, and if these techniques of genetic analysis can be successfully applied to populations of "manipulated biotas," we may see a development of population biology or community ecology without a parallel in the biological sciences since the rise of molecular biology a decade or so ago. Finally, at the minimum, it is clear that this book by MacArthur and Wilson is the most significant and original contribution to biogeography since P. J. Darlington's book *Zoogeography: The Geographical Distribution of Animals* of 1957.

TERRELL H. HAMILTON
Department of Zoology,
University of Texas, Austin

Beginnings of Hydrology

On the Origin of Springs. PIERRE PERRAULT. Translated from the Paris, 1674, edition by Aurele LaRoque. Hafner, New York, 1967. 213 pp. $15.

As far as is known, this is the first translation into English of the full text of the work that O. E. Meinzer said established Perrault as one of the principal founders of the science of hydrology. That distinction stems from Perrault's measurements of rainfall over the upper basin of the Seine, his estimates of discharge from that part of the basin, and his calculation that yearly precipitation was about six times the runoff. The study was the first quantitative demonstration —albeit crude—that precipitation is adequate to account for the flow of springs and rivers. About a decade later Marriotte confirmed Perrault's results. Between the two, the ancient idea that