

# **Ecological Genetics**

**David J. Merrell**

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In writing this book on ecological genetics, I have not attempted an exhaustive review of the literature, but have instead tried to cite pertinent references to illustrate particular points. One problem is that the literature in ecological genetics is widely scattered and often does not travel under that label. In the process I have undoubtedly omitted some significant work and have probably cited my own work more than necessary simply because it was familiar and came quickly to mind.

The background assumed in the book is some knowledge of plants and animals, and some understanding of elementary mathematics and statistics. Perhaps it should be added that we do not deal with what is usually referred to as "the evidence for evolution," but this is hardly necessary, for ecological genetics is the study of evolution in progress.

## Preface

Recently a new approach to the study of populations has appeared under a variety of labels, among them ecological genetics, evolutionary biology, Darwinian ecology, evolutionary genetics, and population biology. This approach is an effort to merge the previously separate fields of population genetics and population ecology into a common discipline. Thus far, the union between population genetics and population ecology has been an uneasy one, but it seems inevitable that studies of populations must move in this direction, and this book is an attempt to further the process.

My preference for "ecological genetics" as the term to characterize the emergent discipline undoubtedly reflects my own background in genetics. Each of the labels cited above has somewhat different connotations, and the diversity of names used reflects to some extent the differences in background and interests of the authors, most of whom were trained either as ecologists or as geneticists. Another dichotomy among students of populations is that between the mathematical theorists on the one hand and the experimental naturalists on the other. Although some of the underlying theory is indicated, the book is focused primarily on the results of studies of actual populations.

In one sense ecological genetics is a methodology. The combination of laboratory and field research provides insights into the way populations adapt to their environments that can be gained in no other way. In another sense ecological genetics is a state of mind,

for it provides a different perspective on the biological world and makes possible the study of problems of both theoretical and practical interest, ranging from the origin of pesticide resistance to the origin of species.

In writing this book on ecological genetics, I have not attempted an exhaustive review of the literature, but have instead tried to cite pertinent references to illustrate particular points. One problem is that the literature in ecological genetics is widely scattered and often does not travel under that label. In the process I have undoubtedly omitted some significant work, and have probably cited my own work more than necessary simply because it was familiar and came quickly to mind.

The background assumed for readers of the book is some knowledge of plants and animals, a familiarity with the principles of genetics, and some understanding of elementary mathematics and statistics. Perhaps it should be added that we do not deal with what is usually referred to as "the evidence for evolution," but this is hardly necessary, for ecological genetics is the study of evolution in progress.

D. J. M.

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## CHAPTER 1

# The Nature of Ecological Genetics

Ecological genetics represents a union between population genetics and population ecology, combining certain aspects of each discipline, but also differing in certain respects from both. Even though both population ecology and population genetics are concerned with populations, the two fields developed independently until quite recently. Population genetic theory, developed initially by R. A. Fisher, J. B. S. Haldane, and S. Wright, is based on the principles of heredity established by Mendel, Morgan, and their successors. Population ecology developed in the absence of a comparable set of general ecological principles. The union of population genetics and population ecology has been an uneasy one and, according to Levin (1978) and Lewontin (1979), has yet to be consummated. As Lewontin wrote:

Despite the pious hopes and intellectual convictions of evolutionary geneticists and ecologists, evolutionary genetics and ecology remain essentially separate disciplines, traveling separate paths while politely nodding to each other as they pass. The functional separation of population genetics and ecology is immediately obvious in books on "population biology," as, for example, the superb introductory text by Wilson and Bossert (1971), in which the sections on population genetics, ecology and biogeography are totally independent entities, each standing on its own feet, each quite self-contained in its analysis.

The difficulty was identified by Lerner (1965) with a delightful analogy drawn from Dickens, which he called Pott's synthesis. Mr. Pickwick, when informed by Mr. Pott of the *Eatanswill Gazette* of

an extensive review of a work on Chinese metaphysics in the *Gazette*, was interested to learn the source of the author's information about such an abstruse subject. He was quite amazed to learn that it had come from the *Encyclopedia Britannica*, for he was not aware that the encyclopedia contained any information whatever on Chinese metaphysics. However, Mr. Pott explained that the author "read for metaphysics under the letter M, and for China under the letter C, and combined his information." Thus it has often seemed with ecological genetics.

In 1968 Waddington wrote, "The two major, long-standing problems of evolution are speciation and adaptation." The origin of species and the origin of adaptations have occupied this central position ever since 1859 when Darwin proposed, in *The Origin of Species*, that natural selection is the mechanism of evolution. Darwin's thesis was that the adaptation of populations to their environments resulted from natural selection and that if this process continued long enough, it could ultimately lead to the origin of new species. In short, those individuals with traits most favorable under the existing environmental conditions would survive to reproduce and, to the extent that these favorable characteristics were hereditary, would pass on their favorable genes to their offspring. These offspring would then, on the average, be somewhat better adapted to the environmental conditions than the previous generation. If the environmental conditions changed, the favored traits might change, and the adaptations in the population would tend to track the changes in the environment. This process, continued without limit in time or space, eventually could lead to the origin of distinct new species.

Darwin's theory of evolution is obviously a genetic theory, but only after 1900, when understanding of the principles of genetics began to emerge, did it become possible to frame evolutionary theory in quantitative terms according to known principles of heredity. The influence of Fisher, Haldane, and Wright, the three scientists primarily responsible for developing the mathematical theory of population genetics and evolution, was so pervasive that Lewontin (1965) wrote:

In many ways the lot of the theoretical population geneticist of 1963 is a most unhappy one. For he is employed, and has been employed for the last thirty years, in polishing with finer and finer grades of jeweller's rouge those three colossal monuments of mathematical biology *The Causes of Evolution*, *The Genetical Theory of Natural Selection* and *Evolution in Mendelian Populations*. By the end of 1932 Haldane, Fisher and Wright had said everything of truly fundamental importance about the theory of genetic change in populations and it is due mainly to man's infinite capacity

to make more and more out of less and less, that the rest of us are not currently among the unemployed.

Somewhat earlier, however, Waddington (1953a) had written of the mathematical theory:

Examined after this lapse of time it has the peculiar character of not having achieved either of the two results which one normally expects from a mathematical theory. It has not, in the first place, led to any noteworthy quantitative statements about evolution. The formulae involve parameters of selective advantage, effective population size, migration and mutation rates, etc., most of which are still too inaccurately known to enable quantitative predictions to be made or verified. But even when this is not possible, a mathematical treatment may reveal new types of relation and of process, and thus provide a more flexible theory, capable of explaining phenomena which were previously obscure. It is doubtful how far the mathematical theory of evolution can be said to have done this. Very few qualitatively new ideas have emerged from it. Wright's theory of drift has, perhaps, the most convincing claim to be something quite fresh and novel, but several other authorities express grave doubts whether it plays any important role in nature.

Perhaps the sentiment expressed by Waddington can be better understood in the light of a comment by Lewontin (1968):

There is . . . a wide misunderstanding of the function of theoretical studies in population biology. It is *not* the function of theory to describe what has happened in a particular instance. Only observation can do that. The purpose of theoretical studies in population biology is *to set limits*. . . . Theoretical population biology is the science of the *possible*; only direct observation can yield a knowledge of the actual. But theoretical studies can then put limits on the experimental and observational procedures of observers and can also "explain" the results of experiments and observations.

However, the words of Crow (1955) are worth recalling:

A full quantitative theory of evolution would be impossibly complex. For example, it would have to consider adaptability as well as adaptedness, for in the long view the former must also be important. Such a complete description is far beyond the capacity of workable mathematical models, and in so far as evolution depends on essentially unique events it is even in principle incapable of mathematical analysis.

In other words, the mathematical theory may aid in the interpretation and understanding of the evolutionary process, but it should not be mistaken for the evolutionary process itself.

A difficulty with the mathematical theory is that simplifying assumptions are usually made in order to keep the mathematics more

tractable. For example, population geneticists often assume a constant environment while population ecologists usually assume that all members of a population have identical genotypes. Seldom is either assumption true. Thus, the validity of the theory and of the limits set by the theory depend on the validity of the assumptions made. As it is easier to make assumptions than it is to collect the data needed to verify them, the theory has often seemed to develop in its own merry way, unconstrained by the limitations imposed by the real world. A theory is most useful when it approximates reality; otherwise it may be irrelevant. The great need at present is for more and better estimates of the parameters involved in population biology. This call for more empirical evidence is hardly new; it was sounded by Timoféeff-Ressovsky (1940a, p. 104) more than a generation ago, but the need still exists.

In contrast to the approach to the study of populations taken by the mathematical theorists is that of the "experimental naturalists" (Waddington, 1953a). In recent years this area of research has come to be identified as ecological genetics. The first symposium on ecological genetics at an International Genetics Congress was held at the Hague in 1963, and the first edition of E. B. Ford's book entitled *Ecological Genetics* appeared in 1964. Ford stated that he had employed the term "ecological genetics" for many years in lectures and scientific discussions and indeed it appeared in his introductory remarks (1960) to his paper at the Darwin Centennial. His colleague, R. M. Sheppard, had a brief chapter entitled Ecological Genetics in his book *Natural Selection and Heredity* (1958), but used the term in a matter-of-course way without definition. Lerner (1965), in his synthesis at the conclusion of the symposium on Ecological Genetics at the Hague, attempted to trace the origins and meaning of the term, and found that it had been used by various workers with somewhat different shades of meaning and that priority in the use of the term was somewhat difficult to establish. One reason is that research in ecological genetics had been carried on for some time before the 1960s when "ecological genetics" began to come into general use.

Certainly one of the first, if not the first, to carry out research in ecological genetics and to set forth in some detail the nature and objectives of such research was Turesson (1922a, 1922b, 1923, 1925, 1930). He coined a number of terms related to this work, most of which have fallen into disuse, among them the word *genecology*. In doing so, he wrote (1922a), "The species problem is thus seen to be in large measure an ecological problem," and in 1923, "It seems appro-



priate for several reasons to denote this study of species-ecology by the term *genecology* (from the Greek 'genos,' race, and 'ecology') as distinct from the ecology of the individual organism, for which study the old term autecology seems to be the adequate expression." Thus he reserved autecology for the ecology of individuals, genecology for the ecology of species, and synecology for the ecology of communities. He also wrote (1923), "The Linnaean species represents as such a much (*sic*) important ecological unit, to which unit the name *ecospecies* has been given by the present writer." Furthermore, he wrote (1922a), "The term *ecotype* is proposed here as (an) ecological unit to cover the product arising as the result of the genotypical response of an *ecospecies* to a particular habitat. The *ecotypes* are then the ecological sub-units of the *ecospecies*." Of these terms, and others, proposed by Turesson, only *ecotype* remains in widespread use. However, not only his writing but the nature of his research with plants make clear that his conceptual approach to his research incorporated both genetics and ecology in a manner we now recognize as typical of studies in ecological genetics.

Population ecology is concerned with the kinds of organisms in an area and with their distribution and numbers, and may deal in statics, the description of a population at a single point in time, or in dynamics, the assessment of the physical and biological factors that produce changes in species composition, distribution, or numbers. In population genetics, the unit of study is the breeding population, which may be as small as a local breeding population (or deme) or as large as an entire species. Statics in population genetics usually involves the description of some form of gene-frequency equilibrium; dynamics involves the study of gene-frequency change due to mutation, selection, migration, and random genetic drift. The major requirement for research in population genetics is the presence of detectable genetic variation.

Ecological genetics is the study of the adaptation of natural populations to their physical and biological environments, and the mechanisms by which they respond to environmental change. It requires an awareness that populations are dynamic units very precisely adapted physiologically and genetically to their environments and sensitive to, and within limits responsive to, any change in their environmental conditions. The interplay between a genetically variable population and its ever-changing environment is the focus of attention in ecological genetics. Thus, the ecological geneticist must be concerned not just with the kinds of organisms present and their distribution and