

MONOGRAPHS IN POPULATION  
BIOLOGY

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1. The Theory of Island Biogeography, by Robert H. MacArthur and Edward O. Wilson
2. Evolution in Changing Environments: Some Theoretical Explorations, by Richard Levins

EVOLUTION IN  
Changing  
Environments

SOME THEORETICAL EXPLORATIONS

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## Preface

This book, except for Chapter 1, is based on a series of lectures, *Frontiers of Population Biology*, given in January 1965 to the Institute of Biology of the Cuban Academy of Science and in February of that year to the Biology Department at Yale University.

No attempt has been made at completeness. There is obviously an inordinate emphasis on my own work and that of my friends, since that is what I know best and what was most easily written up in isolation from good library facilities. As my contribution to the fight against the information explosion I have completely excluded those topics about which I have nothing to say regardless of their importance.

What remains is a series of explorations in fields where ecology, genetics, and evolutionary studies meet around the common theme of the consequences of environmental heterogeneity.

Many of the ideas presented here were developed in the course of collaboration or association with Robert MacArthur and Richard C. Lewontin, to both of whom I am greatly indebted.

I also give many thanks to Mrs. Lilian Altschul and to Miss Rita Luczynski, who typed the manuscript.

## Preface to the Second Printing

Since the appearance of the first printing I have corresponded with a number of people who have pointed out errors or ambiguities, raised criticisms of some theoretical formulations, or have attempted to apply parts of the theory to particular systems. Meanwhile my own views have changed on some questions. I can only indicate briefly the directions in which a drastic rewrite would change the book:

1. *The metapopulation.* Any real species is a population of local populations which are established by colonists, survive for a while, send out migrants, and eventually disappear. The persistence of the species in a region depends on the rate of colonization successfully balancing the local extinction rate. But if every population has a finite life expectancy, the absolute distinction between stable and unstable communities breaks down into a continuum of extinction probabilities. These extinction probabilities increase as the smallest latent root of the community matrix of Chapter 3 decreases with increasing numbers of species. Therefore, the community matrix still can be used to predict the numbers of species, but in a slightly different way. Aspects of the metapopulation concept are under investigation in relation to group selection, biological control, and geographic distributions.

2. The measurement of competition presented in equations 3.9 and 3.10, although adequate for the *Drosophila* community, which provided most of the examples in Chapter 3, has hidden assumptions which are invalid for other situations. Competition is treated as if it is only the joint occurrence of individuals in the same microhabitat or food. Thus the  $P_{ih}$  sum to 1 for each species and intensities of interaction are ignored.

A new treatment begins with resources  $R_h$  entering the community at rate  $A_h$  and being harvested by the  $i^{\text{th}}$  species at the rate  $R_h P_{ih} X_i$ . Then it can be shown that  $\alpha_{ij}$  is found by the same equation as in Chapter 3 but with each  $P_{ih} P_{jh}$

and each  $P_{ih}^2$  weighted by the factor  $\frac{R_h}{A_h} R_h$ , the abundance of the resource multiplied by the ratio of standing crop to turnover rate. Further,  $P_{ih}$  is now an intensity measure as well as a preference and need not sum to 1.

3. Some ecologists are unhappy about the whole notion of the ecological niche because it is easily reified into a fixed property of a species. In much of Chapter 3 the niche is taken as given. However, since working with ants I have been impressed with the great plasticity of the niche, depending on which other species are present. The theory of coexistence should examine the realized niche in more detail, especially in relation to multidimensional environments.

4. Although I recognized abstractly that the competition coefficients need not be constants, the consequences of variable  $\alpha$ 's were not considered. One major class of variable  $\alpha$ 's can no longer be ignored: much of the real competition in nature occurs between the established populations of one species and the dispersal phase or immature forms of another. The newcomer has a decided disadvantage, and the outcome of competition often depends on priority. This results in alternative equal stable communities and patterns that must be studied at the metapopulation level.

5. The niche parameters are estimated in Chapter 3 and presented without confidence limits. I was hoping that a better statistician than I am would respond to the provocation and develop a sampling theory for the niche parameters and community matrix. This is still pending.

6. Despite my claim that optima are not necessarily achieved but merely indicate the direction of difference, the whole tenor of the book is strongly selectionist. But among students of biochemical evolution and polymorphism at the protein level there is a growing conviction that much of evolution is "non-Dominian" or random. These conflicting approaches may be resolved along lines barely hinted at in the last chapter: a large number of genes interact in various ways to produce a smaller number of phenotypic traits which are the direct objects of selection. Suppose that

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for the  $i^{\text{th}}$  trait there is some optimum function of the gene frequencies  $X_j$ :

$$f_i(x_1, x_2 \cdots x_n) = C_i.$$

For instance, if three genes interact additively in  $f_1$  selection for  $f_1$  puts gene frequencies on the plane

$$x_1 + x_2 + x_3 = C_1$$

the same genes may be recessives with regard to trait  $f_2$ , so that the optimum here is on the sphere

$$x_1^2 + x_2^2 + x_3^2 = C_2.$$

The joint action of selection for both aspects of fitness places the gene frequencies along the circle which is the intersection of the plane and the sphere where this lies in the interval  $0 \leq x_j \leq 1$ . Selection moves the population toward this locus, but movement along it is random. (The discussion in Chapter 3 considers what happens when the  $f_i$  have no simultaneous solution in the unit cube.)

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## CHAPTER ONE

# On Theories and Models

Contemporary population biology has emerged in the last few years as a result of the convergence of the previously distinct disciplines of population genetics, population ecology, biogeography, and evolutionary studies in the context of a new holism and interest in theory.

The prevailing philosophy of American science has usually been reductionist and empiricist. And for a time the spectacular successes of molecular biology reinforced these attitudes. However, in the early sixties evolutionists and systematists began to defend the legitimacy of study at a population level. At the same time, questions of practical importance arose at the level of populations and environments—questions of pollution, conservation, biological control, environmental manipulation which involved the complexities of nature as essential ingredients.

Meanwhile, areas that were less amenable to reductionist analysis, such as developmental biology, also produced holistic currents. At a time when practical questions made the study of complex systems necessary, the independently arisen interest in systems research, cybernetics, and mathematical and theoretical biology created a favorable intellectual mood.

The relation of theory to experiment in biology has been an uneasy one. The word "theoretical" has generally had perjorative connotations, and the right to theorize was the reward for years of laboratory and field work. In fields where progress depends mostly on the refinement of technique in order to facilitate more accurate description, this perhaps did not matter too much, but other areas suffered from an indigestion of facts, while data was collected without reference to problems. In these circumstances, theoretical work often diverged too far from life and became exercises in

mathematics inspired by biology rather than an analysis of living systems. This was accentuated also by the effort of theoreticians to model their work on physical systems.

Theoretical biology appeared on the stage as a correction to these biases. As against the prevailing empiricism it insisted on the right and need to theorize; as against growing specialization it insisted on an interdisciplinary approach; as against the dominant reductionism it emphasized the importance of complexity and holistic properties; as against the almost random lines of research in some fields it was biology self-conscious of its strategy. Therefore, theoretical biology as a distinct discipline is a transient phenomenon; once it has made its points part of the thinking of biology in general, it will lose its identity as a distinct field.

While practical interests created the necessity for an integrated population biology and a revived holism created a favorable climate, the internal logic of the component disciplines also forced this development. Increasing evidence has been accumulated to show that evolutionary, population genetic, biogeographic, and demographic events are not on entirely incommensurate time scales. The rate of evolution of say the size of the horse's foot may be 300,000 times slower than increase in bristle numbers in laboratory selection experiments. But Kurtén and others have shown that the slow rates of change on the scale of 50 million years may be the result of spurts of rapid change on the scale of tens of thousands of years, but with reversals of direction. Field observations have shown the remarkably rapid evolution of introduced species, or of species responding to changed environments over the last century. Experiments have shown that in the time it takes for species to interact demographically in simple competition, genetic changes can alter their competitive ability. Insular biogeography has made us aware of the extraordinarily rapid turnover of species, the rapidity of colonization, the high frequency of extinction. Natural selection has been observed in many cases to be strong enough to maintain differences between adjacent populations only meters apart in the face of high migration

rates. Thus even the apparent stability of many biological situations can be regarded not as indicative of absence or weakness of evolutionary pressures, but rather as the dynamic balancing of strong forces, amenable to observation and measurement.

But the attempt to integrate fields that have developed independently leads to many difficulties. Some are difficulties in the translation of concepts from one area to another. Darwinian fitness (Wright's  $\bar{W}$ ) has to be interpreted in terms of its ecological components, such as the intrinsic capacity for increase (Andrewartha and Birch's  $r_0$ ) and the carrying capacity of the environment for a given genotype ( $K$ ). Short-term fitnesses of this kind have to be related to the probability of long-term survival on a geological time scale. The ecologist's niche must be translatable to interpret the systematist's degree of specialization.

The analytical difficulties are also formidable. While the population geneticist's models generally assume stable age distributions, fixed population sizes, and constant environments in order to study the patterns of genetic heterogeneity in single species, the population ecologist considers genetically uniform populations in multispecies systems in a heterogeneous environment.

The attempt to consider genetic, demographic, environmental, and interspecific differences simultaneously immediately runs into technical difficulties. A precise mathematical description may involve hundreds of parameters, many of which are difficult to measure, and the solution of many simultaneous non-linear partial differential equations, which are usually insoluble, to get answers that are complicated expressions of the parameters which are uninterpretable.

We are clearly in need of a different methodology for coping with systems that are intrinsically complex. The following propositions define our strategy in approaching population biology; Numbers 1, 2, and 9 refer to our goals, while the others refer to methods. Thus they are propositions about science rather than about the objects of study. However, it is obvious where the methodological precept follows from a property of nature.

1. Given the essential heterogeneity within and among complex biological systems, our objective is not so much the discovery of universals as the accounting for differences. For example, instead of seeking a proposition of the form "there is a secular evolutionary tendency toward increasing complexity despite some exceptions," we would begin with the fact of different degrees of complexity and different directions of change, and ask what kinds of situations would give positive selective value to increased or decreased complexity. It may, of course, be argued that the result of such an inquiry would be a universal at a higher level. However, we would guess that such a law would also have a limited domain of relevance.

2. We are concerned more with the process of evolutionary and population dynamics than with their results, and are more interested in qualitative than in quantitative results. Except in applied problems which lie outside the scope of our present concern, numbers are of interest only insofar as they help in the testing of theory.

3. The basic unit of theoretical investigation is the model, which is a reconstruction of nature for the purpose of study. The legitimacy or illegitimacy of a particular reconstruction depends on the purpose of the study, and the detailed analysis of a model for purposes other than those for which it was constructed may be as meaningless as studying a map with a microscope.

4. A model is built by a process of abstraction which defines a set of sufficient parameters on the level of study, a process of simplification which is intended to leave intact the essential aspects of reality while removing distracting elements, and by the addition of patently unreal assumptions which are needed to facilitate study.

5. A sufficient parameter is an entity defined on a high level such as a population or a community which contains the combined relevant information of many parameters at a lower level. Thus genes act in many ways, affecting many physiological and morphological characteristics which are relevant to survival. All of these come together into the

sufficient parameter "fitness" or selective value. The way a gene contributes to fitness does not appear at all in the equations for genetic change. Similarly environmental fluctuation, patchiness, and productivity can be combined for some purposes in an over-all measure of environmental uncertainty, an important sufficient parameter. Since a sufficient parameter is a many-to-one transformation of lower-level phenomena, there is always a loss of information in going from one level to another.

6. There is no single, best all-purpose model. In particular, it is not possible to maximize simultaneously generality, realism, and precision. The models which are in current use among applied ecologists usually sacrifice generality for realism and precision; models proposed by those who enter biology by way of physics often sacrifice realism to generality and precision. The strategy which is followed in this book is the sacrifice of precision for generality and realism. This precision is sacrificed in several ways: we ignore supposedly unimportant factors each resulting in a small modification of the results; we ignore factors which will be important but only rarely; this means that there will necessarily be exceptions to all conclusions. Instead of specifying the exact form of a mathematical function we merely assume convexity or concavity, unimodality or bimodality, increasing or decreasing values. Therefore, the results come out as inequalities, and the hypotheses which are generated can only be tested by comparing whole groups of organisms.

7. The effects of the unrealistic "carrier" assumptions can be removed by replacing them with other sets of "carriers." A theorem which can be proved by means of different models having in common the aspects of reality under study but differing in the other details is called a robust theorem. Therefore the presentation of alternative proofs for the same result is not merely a mathematical exercise—it is a method of validation. Alternative models are also used as samplings from a space of possible models.

8. A theory is a cluster of models and their robust consequences. The constituent models fit together in several ways:



- (a) as alternative schemes for testing robustness;
- (b) as partially overlapping models which test the robustness of their common conclusions but also can give independent results;
- (c) in a nested hierarchy, in which lower-level models account for the sufficient parameter taken as given on a higher level;
- (d) as models differing in generality, realism, and precision (unlike the situation in formal mathematics, in science the general does not fully contain the particular as a special case. The loss of information in the process of ascending levels requires that auxiliary models be developed to return to the particular. Therefore, the "application" of a general model is not intellectually trivial, and the terms "higher" and "lower" refer not to the ranking of difficulties or of the scientists working at these levels but only levels of generality);
- (e) as samples spanning the universe of possible models.

9. The role of general theoretical work is the following:

- (a) The identification of the relevant sufficient parameters as new objects of study.
- (b) The fairly direct generation of testable hypothesis.
- (c) The posing of problems heading to lower-level theories which generate testable hypothesis. In this context, the general theory on adaptive strategy (Ch. 2) leads to the metahypothesis "strategic analysis of particular adaptive mechanisms will lead to verifiable hypotheses." The refutation of any particular one refutes only the lower-level theory, but if the bulk of the generated hypotheses are not confirmed the theory itself is invalidated.
- (d) Besides prediction, a theory should offer plausible explanation for what we know. It is not necessary to derive the chemical properties of all macromolecules from quantum mechanical considerations, provided we can do so in a few cases and show that in principle it can be done for the rest. Similarly, it is no refutation

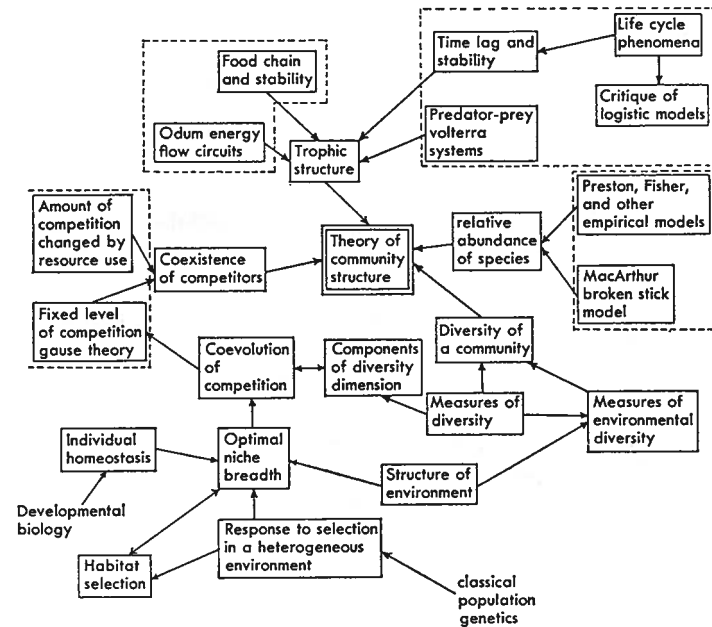


FIGURE 1.1. Relations among some of the components in evolutionary population biology theory. (From Levins, 1966.)

of evolutionary theory that we cannot at present account for the peculiar life cycle of migratory eels. The general theory argues that there is nothing unique to this trait which makes it impossible for it to arise by selection, and it could suggest several more specific models of the adaptive value of this trait.

Figure 1.1 shows schematically the cluster of models which defines the area of interest of these essays.