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Edited by Rama S. Singh and Marcy K. Uyenoyama
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Introduction

This series provides a forum for the review and discussion of some facets of the extraordinary intellectual contributions of Richard C. Lewontin. Previous volumes have addressed evolutionary genetics and the philosophy and politics of evolutionary biology. This volume invites consideration of the Lewontin/Levins vision of an integrated population biology.

R. C. Lewontin and Richard Levins outline the conceptual framework of population biology. They provide examples of the methodological developments the establishment of this field demands and of the kinds of insights it would inspire. Both, however, decry that this vision remains largely unfulfilled, nearly half a century after its explicit formulation as a scientific objective.

One advantage of starting with such a dyspeptic assessment is that each subsequent chapter can only contribute positive evidence that the precepts of population biology have become an inextricable part of modern evolutionary thought. In each of the several constituent fields of population biology, it has been the focused study of particular forces in isolation from the global network that has permitted major advances. This approach has entailed reduction of complex processes into more basic component mechanisms within a given level of biological organization and the substitution of simplified surrogates that represent lower levels in their entirety. The Lewontin/Levins vision of population biology challenges workers to transcend this very productive research strategy: to confront the considerable residual complexity that separates a biological system at a given level from its crude effigy assembled from independent building blocks and, even more difficult, to address interactions between levels. While acknowledging that this grand synthesis has not yet been achieved, contributors to this volume offer abundant evidence that the vision of an integrated population biology has enriched and deepened its component fields.

The most significant development since the 1950s in evolutionary genetics and ecology (and indeed in all of biology) has of course been access to molecular genetic information. Trudy F. C. Mackay provides a comprehensive review of the tremendous increase in resolution of the genetic basis of morphological traits, from QTL to gene to particular nucleotides. Daniel L.

Hartl *et al.* illustrate the characterization of the genomic response of an individual organism to its environment. G. Brian Golding describes methods for characterizing entire populations with respect to genomic properties.

However complex is the mapping between genotype and phenotype in the laboratory, it becomes incalculably more complex within the natural context of evolutionary change. Ward B. Watt presents case studies detailing adaptation to strong environmental challenges through the structural modification of key catalytic enzymes. Bryan Clarke calls for the analysis of biotic and abiotic components of the environment that may serve as sources of balancing selection for the maintenance of nonsynonymous polymorphism. Complementing the study of adaptive polymorphism, John H. Gillespie addresses the process of adaptive substitution in response to changing selection pressures.

In addition to greatly increasing resolution of the genetic basis of evolutionary change, the analysis of molecular-level variation now permits detailed reconstruction of the demographic context of evolution. L. Luca Cavalli-Sforza recounts the development of key concepts and methods that have endowed population biology with the historical dimension fundamental to evolutionary analysis. John Wakeley presents new methods for the inference of history from neutral variation. Daniel Lachaise *et al.* describe the various demographic contexts in which closely related species of *Drosophila* have diverged from a common ancestor.

A progressive broadening of perspective has enriched population genetics, with evolving units increasingly characterized as a series of nested, interconnected networks rather than as a set of independent, homogeneous gene pools. Rama Singh and Richard Morton use the framework of Sewall Wright's shifting balance theory to explore how interactions among multiple levels, from ontogeny to population structure, collaborate in the maintenance and origin of adaptation. Edward C. Holmes explores whether the entire gene pool of RNA viruses evolves as a unit, according to its own set of rules for the generation of variation and for selection, or whether processes at the level of individual viruses must also be considered. Daniel J. Howard *et al.* present a historical review of the study of hybrid zones, arguing that hybrid zones themselves constitute an evolutionary force that can act to facilitate, maintain, or limit the process of adaptation.

Recognition that genetic and ecological change may not only evolve towards different ends but actually contravene one another has become integral to evolutionary biology. A fundamental of this view is evolutionary conflict among organisms and among units of selection. Paul W. Ewald and Gregory M. Cochran review some key insights these concepts have permitted into the coevolution of host and pathogen. Marcy K. Uyenoyama and Naoki Takebayashi address the evolution of self-incompatibility, a mechanism that promotes outbreeding in flowering plants but only at the cost of postponing the expression of inbreeding depression and altering the course of evolution of the mating specificities themselves.

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Optimization principles and other key generalizations are fundamental to the analysis of the evolutionary process at any given level of organization. While the importance of such insights is beyond question, the development of an integrated population biology challenges even these scaffolds from which the study of each successive level of organization is built. To what extent do maximization of population size or rate of growth, for example, determine the course of evolutionary change at the population level? Freddy Bugge Christiansen's examination of the extent to which evolutionary ecology can rely on implicit characterizations of evolutionary processes at lower levels serves to define and delimit the sphere of influence of key generalizations. Within the context of conservation biology, for which the consequences of a less than comprehensive understanding of the implications of intervention policies are immediate and global, Philip Hedrick addresses the effect of genetic composition of a species on its evolutionary potential and resistance to extinction. In his review of life-history theory, Brian Charlesworth explores the conditions under which principles developed for models that ignore age structure can serve as guides to the evolution of age-dependent fertility and mortality schedules. Shripad Tuljapurkar documents recent rapid declines in human mortality, explaining the increasing importance of an understanding of the evolution of mortality schedules and the nature of evolutionary constraints on lifespan.

While changes in mortality schedules have been attributed to environmental changes alone, the determinants of cultural or social differences among human populations have historically been regarded as genetic to the virtual exclusion of other factors. William B. Provine richly illustrates how prevailing belief systems have predisposed scientists, no less than other members of society, towards genetic determinism of social traits, in the absence and sometimes even contradiction of direct evidence. Peter Taylor describes analytical methods developed from conceptual frameworks that admit broader perspectives of the ontogeny of cultural phenotypes.

Have the efforts of innumerable scientists who view themselves as population biologists succeeded in realizing the Lewontin/Levins vision of a population biology that integrates interactions at all levels of organization? While the answer is clearly negative, it must be qualified by noting that the development of the field was not so much abandoned as postponed. Genetically based parameters represent keystones of population biology and ecological genetics, fields bridging population genetics and ecology. It is only now, after the pervasion of the molecular revolution throughout evolutionary biology, that the central concerns of population biology, especially interactions among levels of organization, can be explored in depth. This collection of essays offers various perspectives on the profound conceptual and methodological transformations that have brought population biology to the threshold of full realization.

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PART I

HISTORICAL FOUNDATIONS AND PERSPECTIVES

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1

Building a science of population biology

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There has long been a distinction made by biologists between those phenomena and explanations that are at the level of individual organisms and their constituent parts, and those that are at the level of populations. Developments in individual-level biology are almost entirely motivated by prior empirical discoveries, despite efforts, largely unsuccessful, to create a mathematical basis for molecular, cellular, and physiological events. In contrast, the investigation of population level phenomena has been almost entirely theory driven. Models have been created of population-level phenomena which are then represented as mathematical structures, with specific functional forms, variables, and parameters. Empirical work is, at the very least, informed by these models or, more often, is designed to measure the variables and estimate the parameters of a specific model, or to test whether a particular model is an adequate representation of the natural process. That does not mean that the structures of models are not reciprocally informed by empirical findings. In some cases discoveries of new phenomena at the individual level may require the enrichment of the variety of population models, as for example when the discovery of non-Mendelian segregation patterns such as t-alleles in mice (Dunn 1957) and segregation distorters in *Drosophila* (Sandler *et al.* 1959) required the inclusion of the segregation ratio in gamete pools of heterozygotes as a parameter to be empirically determined. In other cases phenomena that appear in population experiments require the enrichment of standard models, as for example the inclusion of density dependence and composition dependence in models of natural selection (Lewontin 1955). But these enrichments of models are not typical and usually become part of the standard corpus only when the need in a specific case seems compelling.

Because the investigation of population-level phenomena is so organized by specific models, a contemplation of the bulk of these models quickly reveals a characteristic of "population biology" as a science – its nonexistence. There are essentially two sets of problems that are represented at the population

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level. One is population and evolutionary genetics, whose problematic is the rate and direction of genetic change within populations and the genetic divergence between populations consequent on the phenomena of genetic segregation, mating pattern, mutation, migration, stochastic events, and natural selection. The second is population ecology, which is concerned with changes in population size and age distribution within a population as a consequence of interactions of organisms with the physical environment, with individuals of their own species, and with organisms of other species. For most of the history of their study population genetics and population ecology have been carried out independently of each other and with a curiously complementary and non-overlapping structure that has minimized the degree to which they have been melded into a coherent science of "population biology." It is important not to confound with a general science of population biology the kind of evolutionary study embodied in "ecological genetics," whose purpose is to describe and measure in a natural population the actual patterns of mating, migration, and reproduction of different genotypes and to provide a physiological, behavioral, and ecological basis for understanding the operation of natural selection in a specific case (e.g., Grant and Grant 2002). Ecological genetics, in this sense, is the attempt to map the abstract quantities of population genetics onto concrete biological processes.

Beginning in the late 1950s and continuing during the 1960s there was a self-conscious movement among population ecologists and evolutionists to create a coherent science of population biology. Among the manifestations of this movement were the appearance of university courses in "population biology," of training programs in population biology, of a few textbooks on population biology that attempted to bring ecology and evolution together (e.g., MacArthur and Connell 1966), of symposia on population biology (e.g., Lewontin 1968), and of the creation of population biology programs in granting agencies. An important outcome of this movement was the creation of a body of theoretical and empirical research that brought together concepts in population ecology and population genetics. These included a theory of the evolution of ecological niches (MacArthur and Levins 1967) and the successful development of a dynamical model of natural selection in continuously breeding species, a problem that even R. A. Fisher had failed to solve correctly (see the chapter by Charlesworth in this volume for a history of this development). Despite its early successes, however, this movement failed to become the general model for work in population biology, and the communities of population ecologists and population geneticists have remained largely independent in their work.

First, the theories operate in different dynamical state spaces. The basic state space in which population genetic changes are modeled is one of the relative frequency of different genetic variants. The laws of transformation in that space are framed entirely in terms of the changes over time in the frequencies of genotypes that are induced by mating, mutation, migration,

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natural selection, and stochastic sampling. Absolute numbers of individuals appear as a formal parameter, N, the effective population size, but this is a statistical abstraction used in evaluating the size of stochastic effects, rather than an actual census number of individuals. In contrast, in population ecology the basic dynamic state space is not that of relative frequency but of absolute numbers of individuals or, more rarely, of biomass or total energy flux. For special purposes such absolute numbers can be reduced to relative proportions of different classes, as for example changes in the age distribution within a population, but the basic dynamic model is one of numbers rather than frequency.

Second, the bases on which the laws of transformation are derived are of a different kind of generality. The rigidity and near-universality of the mechanism of passage of DNA between generations in sexually or asexually reproducing populations provide an unchallenged skeletal framework which is then the basis for further elaboration of simple perturbing “forces” like mutation or migration or differential reproduction of different genotypes. For sexually reproducing populations modeling begins with Mendel’s principle of segregation. The famous Hardy–Weinberg proportions of genotypes (which appear explicitly even in the analysis of nonrandom mating) are nothing but the quantitative expression of the consequences of segregation of alleles at meiosis. Even the law of transformation of allelic frequencies by mutation, which appears to be framed entirely in allele frequency terms, with no reference to the frequencies of diploid genotypes, depends for its validity on the phenomenon of equal segregation of alternative alleles in the gametes produced by heterozygotes. Thus, the laws of transformation in population genetics appear as universals operating in an abstract space of relative frequencies, the contingencies of environment being effective only as determinants of specific parameter values. As we will see, this appearance of universality can be maintained only by a commitment to a form of natural selection that is seldom realized in actual biology and to a form of life history, discrete, nonoverlapping generations, that does not apply to a large fraction of the living world.

Population ecological models are, from their foundation, more contingent in form. In contrast to the case of population genetics, there is no well-established universal mechanism that produces an unchallenged basic model and mathematical formulation. Certainly it is the case that organisms are produced by parent organisms, so that the absolute growth rate in numbers of a population must, all other things being equal, increase linearly as the population size increases. But it is also universal that organisms need external finite resources for their reproduction, so there is a countervailing decrease in the rate of population growth with increasing numbers as the competition for limiting resources grows greater. The usual assumption is that the rate of growth in numbers decreases linearly as the population size increases so an equilibrium size is reached at the “carrying capacity” of the environment in which the population lives. But no universal phenomenon of biology forces us to assume that the decrease of growth rate with the competition from increasing numbers is linear. Moreover, some resources that are ultimately consumed are themselves produced by the very species that is consuming them (worker ants build nests, farm, and forage, increasing the resources for the colony as a whole), further complicating the relationship between population growth rate and numbers. At least one important school of population ecology has denied that populations are generally found at or near the carrying capacity of the environment (Andrewartha and Birch 1954).

A further level of contingency in the laws of population growth arises when the interactions with other species are considered. These may be competitors or predators, decreasing the growth rate of a given species, or they may be resources for the species. The dynamic laws of community ecology must then consider the simultaneous differential equations of population growth for multiple interacting species. The usual models, which make each species growth rate a simple linear function of the abundances of each of the other species with which it interacts, are arbitrary simplifications of what may turn out to be a rather messy multispecies interaction.

From the standpoint of creating a coherent population biology, the most important feature of most models in population ecology is the mirror image of that in population genetics: the failure to include the dynamics of its complementary phenomenology. In their classical form neither demography nor community ecology included a consideration of genetic heterogeneity within populations, treating the species demography typologically. It follows that the dynamical changes that are occurring in the biological properties of the species as a result of changes in genetic composition of the population are not taken into account. In many cases this genetic heterogeneity can be safely ignored because the processes of genetic evolution are slow compared with demographic processes, but they cannot be ignored for species in newly disturbed and disrupted habitats or in species suffering drastic reductions in population numbers.

1.1 Natural selection and demography

A great irony in the separate histories of evolutionary genetics and demography is that Fisher's original development of a genetical theory of natural selection was explicitly demographic. The *Genetical Theory of Natural Selection* (1930) is an attempt to derive the dynamics of natural selection from the theory of population growth. Fisher postulated a species whose reproduction is continuous in time and which is at a stable age distribution and growing at an equilibrium rate m, that is the root of the Euler equation

$$1 = \int e^{-mx} l_x b_x dx,$$