Models and mergers in mathematical ecology

Oscar Kempthorne

Theory of Population Genetics and Evolutionary Ecology: An Introduction. By J. Roughgarden. Pp.576. (Collier-Macmillan: 1980.) $24.95, £15.95.

THIS large book is an attempt to present the basic ideation behind two fields of biology — population genetics and ecology — and to initiate the merger between the two which has long been overdue. Population genetics had a pre-Mendelian start with Galton, but, of course, it was the discovery of the Mendelian processes that led to the useful application of concepts of mathematical probability to the subject. Over the same period that Fisher, Wright and Haldane were formulating mathematical theories of the genetics of populations, workers such as Kostitzin, Lotka, Volterra and Gause were developing ideas about the dynamics of populations. In writing this book, Roughgarden is following the tradition of Haldane, Fisher and Norton who took the initial steps in combining the two streams of thought.

Roughgarden's purpose is to formulate mathematical models that incorporate aspects of birth, ageing and death, and to establish the consequences of such models. The mathematics involved in doing this become rather complex, but there is no doubt that this is one of the necessary approaches to a greater understanding of many biological processes. The result of this is that it is now common — indeed necessary — for departments of biology to include members of staff who have had a rigorous training in both biology and mathematics. Roughgarden is obviously an exemplar; he has made a fine effort to give an overall picture of a complicated field.

His book consists of five parts. The first is concerned with the basis of the subject, and in it he develops the elementary theory of a simple infinite Mendelian population with a two-stage life. Individuals contribute according to genotype (but not sex) to male and female genetic pools, newborns arising by the random union of gametes. This leads into what Roughgarden calls "Wright's adaptive topography" (an unfortunate term), with the correct (but misleading) result that such a population will move towards maximum mean fitness. The rest of the opening part of the book is taken up with considerations of the fundamental theorem of natural selection for asexual populations — which has no genetic content at all — genetic drift (for a diallelic locus) and the neutrality controversy. This last chapter provides a good introduction to a somewhat obscure area.

I had anticipated that Part 2 would include detailed discussion of complex genetic systems. In fact, Roughgarden considers only models based on variation at a multi-allelic single locus and two biallelic loci. Yet, even in this relatively simple case, what is really going on is far from clear (see Fig. 8.8, for example). This is followed by a rather curious chapter on natural selection and quantitative inheritance; the first half is purely biometrical and not Mendelian, the second does incorporate elements of simple Mendelism. Part 2 concludes with a consideration of Fisher's fundamental theorem — which is not at all as fundamental as Fisher thought — and a chapter on non-random mating, a reasonable introduction to inbreeding and assortative mating.

The next section of the book was, to me at least, the most disappointing. It deals with evolution in general, and in spatially varying and temporally varying environments, and with the development of altruism; few results having general implications have come from recent work in these areas.

Once again, in the first five chapters of Part 4, one soon gets involved in difficult integral equations. Here, Roughgarden considers the dynamics of an asexual population in what is a neat, but perhaps oversimplified, presentation. Finally, in this part of the book, stochastic environments are treated; here, it is a great surprise to find the use of Ito and Stratonovich stochastic calculus.

The final section of the book deals with interacting populations. It starts with a consideration of competition between asexually reproducing populations and leads on to predator–prey models — a useful exposition. Then we are given chapters on coevolution (incorporating a single Mendelian locus and based mostly on Roughgarden's own recent work) and on niche theory and island biogeography.

My overall impression of the book is that it provides a useful but on occasions oversimplified picture of research in the field between 1910 and 1950. Its real value lies in that large portion which deals with more recent work, that undertaken over the past decade, and in this it will undoubtedly be of great value to specialists in mathematical ecology. A deep lacuna in the whole effort is the absence of real quantitative data and then the testing of models by reference to such data. Part of this is due to the immense difficulty of obtaining "hard" data on the dynamics of real ecological systems.

Theoretical ecology incorporating genetics is a young yet complicated area of biological enquiry. We must be grateful to Roughgarden for giving us a base from which to proceed. □

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Thermodynamics and macromolecules

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An Introduction to Physical Properties of Large Molecules in Solution. By E. G. Richards. Pp.298. (Cambridge University Press: 1980.) Hardback £18, $29.50; paperback £5.95, $9.95.

TO MANY teachers of biophysical chemistry it seems strange to note that over the past two decades instruction on the subject of macromolecules has progressed to a position of marked contrasts. On the one hand, structural descriptions of macromolecules are based on accurate methods of X-ray crystallography, so students persevere in understanding details of this technique. On the other, emphasis in the teaching of the properties of macromolecular solutions has moved slowly away from exact thermodynamic interpretations and so student interest in the fundamental understanding of thermodynamics has waned. It is a pity that some recipe cannot be found which convinces students that the three laws of thermodynamics provide a thread for connecting many phenomena associated with macromolecular solutions.

The present book contains little philosophical discussion along these lines but it is particularly good at referring proofs back to the fundamental laws of thermodynamics without stating the laws as a starting point. The contents range over configurational statistics of polymers, helix–coil transitions and hydrodynamic properties of macromolecules, as well as providing sound introductions to molecular interactions of neutral molecules and polyampholytes. The lack of experimental results which direct the students' attention to the phenomena under discussion means that the book must be supplemented through lectures; for example, experimental results from the melting curves of nucleic acids would have formed a useful start to the discussion on helix–coil transitions. Further examples will come to the mind of other readers, but this criticism is minor and only serves to show that this book is mainly concerned