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BOOK REVIEW

Population Genetics, Molecular Evolution, and the Neutral Theory: Selected Papers of Motoo Kimura

Edited by NAOYUKI TAKAHATA
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Thanks primarily to the work of R. A. Fisher, J. B. S. Haldane and S. Wright, the edifice of classical population genetics theory was essentially completed in the 1920s and 1930s. To a good approximation, it may be said that subsequent developments have involved an elaboration of the themes set out by these three founders. The researches of Motoo Kimura stand out as one of the exceptions to this general rule. Arguably, few others have stood out as more original or more path-breaking than Kimura.

Kimura, who died in 1994, is known mainly for his sustained advocacy of the idea that a large fraction of newly occurring genetic variation has very little, or no, consequence from the viewpoint of natural selection. Specifically, the suggestion is that most changes in DNA are either selectively neutral or are deleterious; and if the latter, with such a low coefficient of adverse selection that for all practical purposes (i.e. given realistic population sizes) they are neutral. His name is so closely linked to the Neutral Theory of molecular evolution that at times one tends to lose sight of major contributions to other areas of evolutionary theory. By bringing together a selection of his papers in a single volume, Naoyuki Takahata and the University of Chicago Press have performed a major service to the community.

Fiftyseven publications have been reprinted here. The oldest is a brief report of 1953 in which Kimura introduced the 'Stepping-Stone' model of population structure, in which genes are exchanged within groups and between adjacent groups. The last of his papers to find a place is a discussion in the *Journal of Molecular Evolution* (1987) regarding a central but still unresolved question. Namely, is the observed regularity—in real time—with which the molecular evolutionary clock ticks just as it should be according to the theory, or does the theory predict constancy per generation (typical generation lengths differing a great deal between groups)? Thus not only do the papers span the major portion of his working life, but, thanks to the manner in which Takahata has chosen them, cover just about every major problem that Kimura dealt with in his lifetime.

The publications have been grouped into 18 chapters by area. The main ones are headed Random gene frequency drift, Linkage and recombination, Genetic load, Evolution of quantitative characters, Probability and time of fixation or extinction, Age of alleles and reversibility, Molecular evolution, Molecular clock, and Neutral theory. As this partial listing makes evident, *the* issue that Kimura thought about over his entire career, and kept reformulating and returning to, was the possible importance of chance in evolution. Among his lasting contributions to the field was one of methodology, the introduction of the so-called diffusion method. I am of the opinion that his 1964 review in the *Journal of Applied Probability* (included here) continues to provide the most satisfying approach to the subject (having just attempted to discuss the topic in a course, I say this with some confidence). One piece of writing that would have enriched the book but does not find a place is the charming autobiographical note 'Genes, populations and molecules: a memoir' (in *Population Genetics and Evolution*, T. Ohta and K. Aoki, editors, Japan Scientific Societies Press, Tokyo, 1985).

A brief review is not the place for an assessment of Kimura's place in population genetics and evolutionary biology, nor am I competent to undertake such a task. I restrict myself therefore to a few subjective comments. In going through this collection, the first thing that struck me (anew) was Kimura's clarity. This comes through both in his mathematics and in his prose. Anyone who has tried to wrestle with Wright's monograph-length pioneering paper of 1931, 'Evolution in Mendelian populations', will agree that it was Kimura who first made Wright's mathematics understandable (gratifyingly, Kimura has said that even he found Wright too difficult to follow in the beginning). Thus it is startling to realize that his training was in cytogenetics and botany; the mathematics was self-taught. Interestingly, an important role appears to have been played in his initiation into modern biology—and undoubtedly this must have included population genetics—by the journals *Genetics* and *Journal of Genetics*.

As for the quality of writing, anyone who wants a standard to emulate would do well to study *The Neutral Theory of Molecular Evolution* (Cambridge University Press, 1983). The same style is visible in these papers, particularly in the later ones. The introductions to the articles, especially reviews, are models of lucidity. I do not know of any crisper history of population genetics and evolutionary theory than can be found scattered through Kimura's publications. A striking feature (and J.F. Crow draws attention to it in his Foreword) is that elegant and sophisticated as the mathematical treatment is, it is always important to Kimura to relate his results to what is observable, if not experimentally testable. This is most evident in his efforts to link the neutral theory to observational data. It is worth drawing attention to an irony here. Many distinguished workers have wondered whether population genetics theory has had any worthwhile contribution to make to our understanding of evolution. The skeptics have ranged from naturalists of the standing of Ernst Mayr to mathematically minded scholars such as Richard Lewontin. The neutral theory constitutes the preeminent example of mathematical analysis informing—indeed, motivating—experimental evolutionary studies; the irony is, of course, that in a sense the neutral theory can be thought of as a theory of non-evolution.

Kimura's interests encompassed a diverse range of problems and one may ask whether there are areas of contemporary interest in evolutionary biology not touched by him. To my mind only three come close. With the exception of a single paper on a diffusion model of intergroup selection, the question of the appropriate unit or units on which natural selection acts—and the ramifications of the choice of unit for issues that range from intragenomic conflict to the evolution of cooperation and social behaviour—appears not to have engaged Kimura deeply. Another is sexual selection. The third is evolutionary ecology and the stability of ecosystems, an area around which an impressive body of mathematical theory has developed. These gaps serve to point out that, while practically everything else was grist to his mill—linkage, sex, fitness, genetic load, inbreeding, quantitative traits—, Kimura was not a universalist in the sense that (say) Haldane was. But the depth and quality of his contributions, to which this volume bears excellent testimony, mean that in the years to come he will surely be counted as one of the fathers of modern evolutionary theory.

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