

Book Reviews

Population Genetics, Molecular Evolution, and the Neutral Theory. Selected Papers of Motoo Kimura. Edited by NAOYUKI TAKAHATA. University of Chicago Press, Chicago. 1994. 686 pages. Price: Cloth US$80.00 £63.95 Paper US$29.95 £23.95. ISBN 0 226 43562 8.

What would population genetics look like today without Motoo Kimura's contributions? If one viewed the universe of ideas as a panselectionist does mutations, then all ideas are latent and merely waiting an appropriate stimulus to emerge. But Kimura's career explodes that concept. Perhaps no evolutionary biologist in the second half of this century had such impact. It is difficult to imagine that our view of evolution would be very similar if not for the papers collected in this book.

This beautifully edited and produced volume reproduces 57 of Kimura's most important publications in their original formats. They are grouped into 18 thematic sections which are introduced with brief but thoughtful essays by Takahata that put the papers into historical and intellectual context. The volume is a delight for two reasons. The first is scientific. The papers are a shower of stimulating ideas, and the insights they hold are far from being fully mined. Kimura left both technical and conceptual legacies. Almost every paper contains an innovation in theory that solves the problem at hand and suggests new attacks on others. The conceptual legacy is equally profound. The job of a theoretician is to identify interesting problems as well as to solve them, and Kimura was spectacularly successful at both tasks. A second feature that makes this book so welcome is the historical perspective it gives. It includes the papers that laid the foundations for several key topics in modern population genetics. Most important, of course, are the contributions on molecular evolution.

It was simply good fortune for the field that molecular biology came of age at a time when someone with Kimura's abilities was able to seize on the flood of new data it produced. His work on the neutral theory alone is enough to earn Kimura the rank of one of the great thinkers in evolutionary biology. The central idea – that most nucleotide substitutions are caused by random genetic drift rather than positive selection – was proposed in his celebrated 1968 paper. Later papers, also included here, worked to explain levels of heterozygosity, variation in rates of substitution, and other observed patterns within this framework. The proposal ignited a debate that dominated population genetics for ten years. When DNA sequence data became available, the basic hypothesis was largely corroborated for synonymous changes and some types of noncoding DNA. But several patterns, particularly those involving changes in amino acid sequences, were (and still are) more intransigent for the neutral theory. The ten papers included in the section on the neutral theory give a fascinating view of Kimura's efforts to bring the burgeoning data of the last two decades into his world view. These attempts were largely but not completely successful. Kimura was not always receptive to criticisms of the neutral theory, for example the point emphasized by John Gillespie that the variance in substitution rates exceeds the theory's expectation. But perhaps the neutral theory and even the field of molecular evolution as a whole would not have advanced so far and so fast without Kimura's strong advocacy.

The most striking feature of this collection is the diversity of ideas it contains. Kimura is best known for the neutral theory of molecular evolution, of course, and his classic papers on that subject are included here. Many geneticists are familiar with Kimura's research in two or three other areas. But many readers will be as astonished as I was with the number and depth of the contributions entirely outside of molecular evolution. In fact, somewhat more than half of the papers reprinted here are unrelated to molecular evolution. There are entire sections on (for example) population structure, quantitative characters, group selection, inbreeding, meiotic drive, the evolution of sex, and genetic load. Many of the papers in these 'other' areas are seminal and at the foundation of research areas that are active today. Picking some examples stochastically: Maruyama and Kimura (1980) pioneered work on the genetics of what is now fashionably called a metapopulation; Kimura (1965) developed the Gaussian model for quantitative traits later studied intensively by Lande, Turelli, and others; Kimura and Maruyama (1966) introduced the approach at the heart of models for genome-wide deleterious mutation now investigated by Kondrashov, Charlesworth, and others; Kimura (1965) introduced the concept of quasi-linkage equilibrium central to the evolution of genetic modifiers in the current work of Barton and others; Kimura (1962) and later papers studied the fixation of advantageous alleles, with results that are fundamental to current work by Hill and colleagues on the theory of artificial selection. Reading these papers gives a valuable perspective to current research and reminds one of ideas that have not yet been fully explored.

Kimura's overarching technical contribution was to introduce powerful methods based on the diffusion approximation. This achievement marked the start of a second golden age of theoretical population genetics (Ewens, 1979, p. 140), an age that continues to the present. Kimura used this approach most extensively and most famously in studies of drift. The figures from his landmark 1955 paper, showing the probability density for the frequency of a neutral allele through time, may be the most widely reproduced figures in theoretical population genetics. (In fact, they have risen to the status of a scientific totem: I once saw the figures presented to a large undergraduate class with only the explanation that they 'show how genetic drift works'!) The coalescent approach developed over the last 10 years has largely displaced diffusion methods as the preferred way to calculate many quantities important to the neutral theory. Kimura realized, however, that the diffusion machinery has many other applications. He used it to study such problems as evolution under randomly-varying selection. The method is still the only tractable approach available in these areas; it will be interesting to see if alternative methods will eventually be developed there as well.

Reading through these papers, three things struck me time and again. The first was how strongly Kimura was motivated by data. Many experimentalists must think the Gegenbauer polynomials featured in Kimura's early papers to be the apotheosis of inscrutable (and probably useless) theory. But many papers, particularly those on molecular evolution, are motivated by empirical observations. Indeed, several develop new statistical methods to study evolutionary patterns emerging from recently collected data. The second was that there seemed to be no limits to Kimura's ingenuity and creativity. Most of us stop when existing scientific methods prove inadequate. Kimura time and again invented clever new analyses and new concepts. Third was Kimura's tenacity. Important ideas such as the neutral theory do not always carry themselves to wide audiences. This book highlights how critical Kimura's articulate and forceful development of his ideas was to the evolution of modern population genetics.

References

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Arabidopsis. Edited by ELLIOT M. MEYEROWITZ and CHRIS R. SOMERVILLE. Monograph 27, published by Cold Spring Harbor Laboratory Press 1994. 1300 pages. Cloth cover, price $175. ISBN 087969 428 9.

This book is a perfect example of Christ's forecast 'The meek shall inherit the earth'. The Meek are not, of course, the editors and authors of the 40 chapters and two appendices, but the small, insignificant weed *Arabidopsis thaliana*, which has captured rapidly increasing attention over the last couple of decades. The argument runs that all angiosperms (flowering plants) share similar life-styles, environmental challenges, modes of reproduction and body plans, and the roughly 250000 species of angiosperms are thought to have evolved from a common ancestor within the last 150 million years. They will therefore show a good deal of genetic and biochemical homology. Thus a small, rapidly growing flowering plant which can be easily maintained and manipulated in the laboratory should form a good model for intensive study of a variety of aspects of angiosperm biology, whose results can be applied to larger and more cumbersome plants of economic importance.

Friedrich Laibach proposed *Arabidopsis thaliana* as a suitable organism for genetic and developmental study in 1943 and followed with an article on 60 years of *Arabidopsis* research (1905–65), so this little wild mustard was ready to become the role model for research on angiosperms when molecular genetic techniques began to spread to plants. It appears to have all the most suitable characteristics for a laboratory plant: a small genome of 5 chromosome pairs containing roughly 80 Mb of DNA of which only some 10% is highly repetitive or foldback sequences, in one of the smallest of nuclei so far found in a flowering plant; it is very small and fast growing, produces numerous very small seeds (a single plant under optimum conditions can yield over 20000 seeds within a few weeks), and it reproduces almost entirely by self fertilization, so that pure lines of new mutants are easily obtained. It is amenable to the modern techniques of molecular genetics.

Nearly all the 40 chapters in this book manage to sing the praises of its subject while presenting us with much interesting new information, and pointing out the many problems that still need solution. Their enthusiasm will doubtless lead to a further increase in what is clearly a very large Arabidopsis community (for example, we are told that hundreds of laboratories are selecting new mutations). Following nine chapters on genetics, the chapters on development cover seed