Introduction

RASMUS GRØNFELDT WINTHER

The 1960s and 1970s were a heady time for theoretical biology. Theoretical ecology and population genetics were undergoing fundamental conceptual and methodological changes. Sophisticated mathematical techniques were introduced, computers increased in power and became readily available, and the 'molecularisation' of biology was underway. A. W. F. Edwards at the University of Cambridge was an influential researcher in this early interweaving of mathematics, computation, and molecular data. Edwards contributed to three key areas of inquiry. First, trained under noted statistician and biologist R. A. Fisher, and working alongside L. L. Cavalli-Sforza, another close associate of Fisher's, Edwards developed key methods and models for the reconstruction of the evolutionary history of organisms. This was indeed the birth of modern statistical *phylogenetic inference*. Second, Edwards contributed to theory on sex-ratio evolution and the Fundamental Theorem of Natural Selection. This helped advance our understanding of the operation of natural selection, i.e., *selection theory*. Third, Edwards authored numerous papers on many important researchers in the *history of science*, particularly in the histories of mathematics and genetics. Edwards's subjects included Pierre de Fermat, Blaise Pascal, Thomas Bayes, Francis Galton, John Venn, and, especially, R. A. Fisher.[1] In all of this, Edwards also contributed, indirectly at least, to probability theory and statistics. For instance, he articulated key insights on maximum likelihood and clustering, and helped clarify the Fisher–Neyman controversy.

Given the importance of Edwards's work, it is unfortunate that much of it is difficult to locate, requiring hours of effort from dedicated researchers and expert librarians. The purpose of this book is to make a representative subset of Edwards's papers available and to place Edwards's contribution into its philosophical, historical, and sociological context. To provide this context, commentaries by distinguished

[1] For a small sample of Edwards's contributions to the history of science, see [96] and [235].

experts are provided, as is an in-depth set of interviews of Edwards carried out by the editor, Rasmus Grønfeldt Winther, over three days at the University of Cambridge. Given that Edwards has published over 200 papers, only the most interesting and influential papers could be selected for this volume. Many of the selected papers are on phylogenetic inference, with the remainder distributed among selection theory, the history of science, and probability theory and statistics.

This introduction situates Edwards's impact with respect to three key themes: (1) statistics as a methodology for phylogenetic inference, (2) Fisherian population genetics as a 'gene's-eye view' of selection theory, and (3) human genetic diversity and population structure. It then provides descriptions of each commentary, and concludes by situating and explaining the editor's role in this book, as a philosopher of science, and by briefly discussing future research possibilities.

As in many other episodes of scientific discovery, historical details matter. In the interviews, Edwards recounts some of the variegated early history of statistical phylogenetic inference. Both Edwards and Cavalli-Sforza were inspired by Fisher's suggestion to represent gene frequency data (abstracted from many blood-group polymorphisms) in Cartesian spaces, or state spaces, in which populations occupy distinct but potentially overlapping regions.[2] Reconstructing historical connections could then be seen as a statistical inference problem, which results in producing branching trees via averaging or minimising pairwise distances between population clouds in these state spaces ([25], [27], [28], [29], [53]; Figure 1 of [28], p. 29, this volume; Fig. 1 of [29], p. 43, this volume; Day 2 of the interviews.[3] Cavalli-Sforza had the original idea of trying to 'extract a tree structure from the [blood group] information and see how it related to the geography of the continents.'[4] But Edwards added much theoretical nuance, including the principle of minimum evolution. Edwards and Cavalli-Sforza's subsequent innovation of building an evolutionary model with a Brownian-motion approximation of random genetic drift, upon which maximum likelihood could then be applied as the estimation procedure for inferring the most likely evolutionary trees, can be partly attributed to Motoo Kimura as well as to Fisher's earlier influence ([27], [28], [37], [46], [141]; cf. [35], [56], [60], [225]; Interviews, pp. 432–433, 443, this volume). Edwards also implemented statistical phylogenetic models in computational code, e.g. his program EVOTREE ([32], [197]; Interviews, pp. 435–439, this volume).

In the chapter 'A digression on history and philosophy', Felsenstein comments on 'the remarkably creative work' of Edwards and Cavalli-Sforza, noting that

[2] Interviews, pp. 429–431, this volume.
[3] Numbers in brackets refer to the numerical system for Edwards's articles that is used in this volume, indicating the articles reprinted, as listed in the table of contents; see A. W. F. Edwards: Scientific Publications (pp. 465–482, this volume) for a full list of Edwards's work.
[4] Interviews, p. 429, this volume.

'Edwards and Cavalli-Sforza's paper of 1964 ([27]) is remarkable in that it introduces the parsimony method, the likelihood method, and the statistical inference approach to inferring phylogenies, all in one paper.'[5] Interestingly, [27] contains another first: hypothesised genealogical relationships among modern human populations were computed from blood group allelic gene frequency data and subsequently superimposed on a world map (Figure 1, p. 26, this volume; see volume back cover).[6] The authors' intent was to cartographically represent the history and geography of modern humans (p. 319 (Bodmer); p. 344 (Pagel); interviews, pp. 441–442, 450–451, this volume). In their commentaries, Felsenstein, Pagel, Thompson, and Yang place these advances in phylogenetics in the context of the logic of statistical inference ([42], [146], [227]).[7] Nielsen writes that 'cladistic ideology' has been replaced by more 'pragmatic' statistical methods of phylogenetic tree inference (p. 340; cf. [146], pp. 236–238, [197], p. 259, this volume). It would make for fascinating history of science to track and explore the rise of statistical phylogenetics in the context of the fall – or, at minimum, the retransformation – of cladistics.[8] Which causal connections, if any, exist between the rise of one and the fall of the other? Is the emergence of statistical theory the single most significant historical factor here, or might the flood of genetic data and the shifting patterns of funding at universities, museums, field stations, and other research institutions play a role? Finally, is a pluralistic future possible, one in which we take seriously morphological characters and the concept of homology, as well as certain taxonomic, nomenclature, and documenting practices from cladistic systematics?[9] In cases such as this, historians, philosophers, and sociologists of

[5] Felsenstein, J. 2004, *Phylogenetic Inference*. Sunderland, MA: Sinauer Associates, pp. 125, 128.

[6] This map also appears in [28], together with the actual computed tree of descent (Figures 2 and 3, p. 31, this volume). A topologically distinct tree was published a year later ([29], Figure 5, p. 48, this volume). For further discussion, see Bodmer and Pagel commentaries; Sommer, M. 2015. Population-genetic trees, maps, and narratives of the great human diasporas. *History of the Human Sciences* 28, 108–145; Sommer, M. 2016. *History Within: The Science, Culture, and Politics of Bones, Organisms, and Molecules*. Chicago, IL: University of Chicago Press.

[7] For a synoptic, longer historical view of statistics and probability theory, see Hacking, I. 1990. *The Taming of Chance*. Cambridge: Cambridge University Press.

[8] Elliott Sober covers many of the philosophical points: e.g. Sober, E. 1988. *Reconstructing the Past: Parsimony, Evolution, and Inference*. Cambridge, MA: MIT Press; 2008. *Evidence and Evolution: The Logic Behind the Science*. Cambridge: Cambridge University Press. Sober 1988 explicitly addresses Edwards's phylogenetic work, both alone and with Cavalli-Sforza. On the history of cladistics, see Hull, D. 1988. *Science as a Process: An Evolutionary Account of the Social and Conceptual Development of Science*. Chicago, IL: University of Chicago Press; Williams, D. M. and Forey, P. L. (eds.). 2004. *Milestones in Systematics*. Boca Raton, FL: CRC Press. Note that Williams and Forey contains [197].

[9] Some philosophers of science provide conceptual frameworks for analysing the assumptions and worldviews of a plurality or diversity of research programs (e.g. Longino, H. 2002. *The Fate of Knowledge*. Princeton, NJ: Princeton University Press; Hacking, I. 2004. *Historical Ontology*. Cambridge, MA: Harvard University Press; and Winther, R. G., The structure of scientific theories, In *The Stanford Encyclopedia of Philosophy* (Winter 2016 edition), ed. E. N. Zalta (https://plato.stanford.edu/archives/win2016/entries/structure-scientific-theories/); Winther, R. G. (in press). *When Maps Become the World*. Chicago, IL: University of Chicago Press.

science could engage in recovery, critical awareness, and repurposing of old and even currently marginalised scientific theories and methods.[10]

Turning to mathematical population genetics, according to Edwards, the 'gene's-eye' or 'gene-centred' view 'is implicit in any genetical model of the analytical kind favoured by Haldane and Wright', although 'in Fisher's ["inductive and statistical"] work it was explicit' ([238], p. 297, this volume). Edwards has helped explore and clarify Fisher's Fundamental Theorem of Natural Selection ([36], [140], [238], [248]). Edwards favours a Fisherian gene's-eye selection theory. Fisher stressed adaptive evolutionary change as driven by mutation and natural selection among individuals in large panmictic (random-mating) populations. Gene frequencies are here understood as the one single inductively measurable feature 'capable of rigorous analysis' ([238], p. 297, this volume). Edwards warns, however, that we must be wary of attributing an 'oversimplified "gene-centred" view' to Fisher ([227], p. 281, this volume; Esposito commentary). Despite relying on the power of averaging, Fisher acknowledged gene interactions and genotype-by-environment interactions. Thus, Edwards argues, we should not read Fisher as either a genetic determinist or an arch-reductionist.

As explored in the Ewens, Okasha, and Grodwohl commentaries, the gene's-eye view connects intimately to the assumptions and mathematics of the fundamental theorem, especially in light of George Price's reinterpretation.[11] Historically, the 'shifting balance theory' of Sewall Wright contrasted with Fisher's explanations and predictions of the evolutionary process. Wright's model was more complex, with three phases: (I) random genetic drift within local populations (demes), moving them across rugged adaptive landscapes; (II) mass Fisherian selection within demes, moving each population up to the closest adaptive peak; and (III) interdemic (group) selection, wherein demes at higher peaks send out relatively more migrants than demes at lower peaks, thereby shifting other populations to the gene frequencies and gene combinations of the higher peaks ([49], [173]; Grodwohl commentary).[12] Furthermore, ongoing debates surrounding inclusive fitness theory, levels of selection, group selection, epistasis, indirect genetic effects, and other phenomena nuance or challenge the gene-centred view.[13] Whatever our

[10] Hasok Chang's notion of *complementary science* is useful here (Chapter 6 of Chang, H. 2004. *Inventing Temperature: Measurement and Scientific Progress*. Oxford: Oxford University Press, 235–250).

[11] Price, G. R. 1972. Fisher's 'fundamental theorem' made clear. *Annals of Human Genetics* 36, 129–40.

[12] Provine, W. 1986. *Sewall Wright and Evolutionary Biology*. Chicago, IL: University of Chicago Press; Hodge, M. J. S. 1992. Biology and philosophy (including ideology): a study of Fisher and Wright. In *The Founders of Evolutionary Genetics*. ed. S. Sarkar, Kluwer, Dordrecht, 231–293; Winther, R. G. 2006. Fisherian and Wrightian perspectives in evolutionary genetics and model-mediated imposition of theoretical assumptions. *Journal of Theoretical Biology* 240, 218–232; Winther, R. G., Wade, M. J. and Dimond, C. C. 2013. Pluralism in evolutionary controversies: styles and averaging strategies in hierarchical selection theories. *Biology and Philosophy* 28, 957–979.

[13] Because inclusive fitness is often seen as a part of a gene's-eye perspective, theoretical controversies vis-à-vis inclusive fitness also involve disagreements about the centrality and scope of application of the gene's-eye

theoretical and philosophical perspectives, let us revisit Edwards's work for a learned and influential theoretical characterisation of the gene-centred view.

Inferences about the history and population structure of our species are associated with rampant conceptual confusions. With 'Human genetic diversity: Lewontin's fallacy' ([192]), Edwards helped eliminate confusions regarding population clustering and individual classification. Consider a thought experiment. Imagine pulling miscellaneous metallic objects out of two immense and otherwise indistinguishable bags labelled 'Bag A' and 'Bag B'. Every object you pull out has physical properties such as weight, sound when struck, melting point, and colour. These features can be measured for each object, and you know the averages and variances for each property, for each bag. For instance, you know that the average weight of objects in the two bags is almost identical, as are the weight distributions. You also know that sounds emitted by Bag A objects when hit are almost always very tinny, though a few objects emit the same deep rumbling sound as *all* the objects of Bag B. Moreover, you are told that these properties vary independently of one another.[14] This might be because each feature is controlled by a different set of chemical elements or distinct object substructures, for example, and hence the different characteristics are not causally related, even within the same bag. Now, a friend hands you an object she has drawn from one of the bags, and she asks you to guess which one. She also hands you a scale and a metallic rod. Do you think you would be able to guess correctly using just the scale? No. What if you hit the object with the rod? Better, but this is still a very error-prone classification strategy. What if you simultaneously evaluated the mysterious object's weight, sound when struck, melting point, and colour? The basic argument of [192] is that by assessing increasingly many genetic loci of a human (or, analogously, by examining sufficiently many distinct and independent physical features of an object drawn from one of our bags), we can, with decreasing error, correctly classify from which original biological population(s) or bag a human or metallic object was sampled. As [192] concludes, citing Rosenberg *et al*. 2002: '[I]t was only in the accumulation of small allele-frequency differences across many loci that population structure was identified' ([192], p. 253, this volume).[15]

view. Consider debates about models for the evolution of eusociality (Nowak, M. A., Tarnita, C. E., Wilson, E. O. 2010. The evolution of eusociality. *Nature* 466, 1057–1062; Abbot, P., Abe, J., Alcock, J., *et al*. 2011. Inclusive fitness theory and eusociality. *Nature* 471, doi: 10.1038/nature09831) or for the evolution of reduced virulence (Wild, G., Gardner, A., West, S. A. 2009. Adaptation and the evolution of parasite virulence in a connected world. *Nature* 459, 983–986; Wade, M. J., Wilson, D. S., Goodnight, C., *et al*. 2010. Multilevel and kin selection in a connected world. *Nature* 463, doi: 10.1038/nature08809). For the possibly most influential public statement of inclusive fitness as an essential feature of the gene-centred view, see Dawkins, R. 1976. *The Selfish Gene*. Oxford: Oxford University Press. Contrasting perspectives, such as multilevel selection, look beyond single additive and averaged genes (e.g. Winther, Wade, and Dimond 2013).

[14] Strictly speaking, the features are independent, *conditional on the bag*.

[15] This is the penultimate sentence (p. 2384) of Rosenberg, N. A., Pritchard, J. K, Weber, J. L., *et al*. 2002. Genetic structure of human populations. *Science* 298, 2381–2385.

As Lewontin pointed out, there is indeed very little classificatory information in a locus with similar allelic frequencies across populations: 'based on randomly chosen genetic differences, human races and populations are remarkably similar to each other' (Lewontin 1972, p. 397).[16] But as we increase the number of loci measured for allele frequencies across different populations, our probability of misclassifying individuals diminishes ([192], Figure 1, p. 251, this volume; Rosenberg commentary; Appendix 1).[17] Edwards's earlier work on clustering analysis and classification resonates with his more recent arguments ([30]).[18] In short, the robust result that (approximately, and averaging the variances across loci) 85% of all genetic variance is found within human subpopulations (e.g. Han Chinese or Sami), 10% across subpopulations within a continental region, and only 5% across the three Old World continents[19] is *not* inconsistent with the increase of classificatory accuracy as we examine gene frequencies of more and more (roughly) independent loci. Some commentators point out that Lewontin and Edwards were asking different questions; others observe that their approaches correspond to distinct research programs or paradigms.[20] Despite the fraught ethical concerns involved in this

[16] Lewontin, R. C. (1972) The apportionment of human diversity. *Evolutionary Biology* 6, 381–398.

[17] See also Fig. 1, p. 34 of Edge, M. E. and Rosenberg, N. A. 2015. Implications of the apportionment of human genetic diversity for the apportionment of human phenotypic diversity. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 52, 32–45.

[18] The two are distinguished because inferring or postulating the populations from which multiple samples are drawn (i.e. clustering) is logically distinct from having a sample and inferring the population(s) from which that sample was drawn, as in our bag example (i.e. classification). Computer programs such as *structure* are intended to infer population structure, though they can also be used for classification. Lewontin 1972 used populations postulated by linguistic and anthropological data, and he investigated the degree of overlap among these populations with respect to their genetic structure. Lewontin relied on previously specified clusters and was not interested in the statistical procedures of either clustering or classification. See Rosenberg commentary; Winther, R. G. 2011. ¿La cosificación genética de la 'raza? Un análisis crítico. In *Genes (&) mestizos: Genómica y raza en la biomedicina Mexicana*, ed. C. López Beltrán, UNAM: Mexico City (in Spanish), 237–258; Winther, R. G. 2014. The genetic reification of "race"? A story of two mathematical methods. *Critical Philosophy of Race* 2, 204–223, reprinted in Appendix 2; Kaplan, J. M. and Winther, R. G. 2013. Prisoners of abstraction? The theory and measure of genetic variation, and the very concept of "race," *Biological Theory* 7, 401–412.

[19] As pointed out in Bodmer's commentary, almost certainly the earliest published data for this statistical result is found in Table 12 'World Variation of Gene Frequencies' of Cavalli-Sforza 1966, p. 367 (Cavalli-Sforza, L. L. 1966. Population structure and human evolution. *Proceedings of the Royal Society of London B* 164, 362–379). Averaging the standard variances (Table 12, penultimate column) for the 15 loci investigated gives the ~15% across-population variance Lewontin also found. For studies verifying the robustness of these statistics of human genetic diversity, which also include populations from Oceania and the Americas, see also: Barbujani, G. A., Magagni, A., Minch, E. and Cavalli-Sforza, L. L. 1997. An apportionment of human DNA diversity. *Proceedings of the National Academy of Sciences of the USA* 94, 4516–4519; Rosenberg, N. A. 2011. A population-genetic perspective on the similarities and differences among worldwide human populations. *Human Biology* 83, 659–684.

[20] Regarding the first: Feldman, M. W. and Lewontin, R. C. 2008. Race, ancestry, and medicine. In *Revisiting Race in a Genomic Age*, eds. B. A. Koenig, S. S.-J. Lee, and S. S. Richardson, New Brunswick, NJ: Rutgers University Press, 89–101; regarding the second: Winther 2011, 2014; Winther, R. G. 2018. Race and biology. In *The Routledge Companion to the Philosophy of Race*, eds. P. C. Taylor, L. Martin Alcoff, and L. Anderson, Abingdon: Taylor and Francis, 305–320. For practical appraisals of basic patterns, and methods of measuring, human genetic diversity, see, e.g., Barbujani, G., Ghirotto, S., and Tassi, F. 2013. Nine things to remember about human genome diversity. *Tissue Antigens* 82: 155–164; Bodmer, W. F. 2015. Genetic characterization of human populations: from ABO to a genetic map of the British people. *Genetics* 199, 267–279; Cavalli-Sforza, L. L. and Feldman, M. 2003. The application of molecular genetic approaches to the study of human evolution. *Nature Genetics* 33, 266–275.

topic, Edwards's controversially titled paper, [192], acted as a wake-up call to embrace the logical and statistical consistency of variance-partitioning and clustering-classification approaches to human genetic diversity.[21] Regardless of our political and moral stance on human populations, clusters, or races, we scientists and philosophers must directly address all known evolutionary and genetic information. Our arguments will be stronger for it.

Let us now turn to a description of each commentary, in the following rough order: general background, phylogenetic inference, selection theory, history of science, and human genetic diversity.

Walter Bodmer provides a bird's-eye perspective of Edwards's career and contributions. Bodmer takes Edwards's major scientific contribution to be the construction of phylogenetic trees of human populations using gene-frequency data. After discussing 'Evolutionary trees from human blood 17 group frequency data', he analyses Edwards's diverse body of work in the following three sections: 'Likelihood', 'Historical papers', and 'Human genetic diversity: Lewontin's fallacy – comments based on Bodmer (2015)'. Throughout his commentary, Bodmer supplies relevant details about his interactions with Edwards, Fisher, and Cavalli-Sforza.

Joe Felsenstein describes how he came to work on the statistical approach to inferring phylogenies after meeting Edwards and Cavalli-Sforza, both of whom had wanted to use trees to describe the differentiation of gene frequencies among local populations. Edwards invented a parsimony method and Cavalli-Sforza a distance matrix method; they then sought to discover whether maximum likelihood recommended either approach. Using a Brownian-motion approximation, they encountered technical difficulties, but could see that it was a third distinct method. Felsenstein argues that with Edwards's 1970 paper ([46]) discussing Bayesian inference approaches, the four major approaches to inferring phylogenies had effectively been invented in one body of work.

Rasmus Nielsen traces how insights from population genetics informed methods for estimating trees in the early seminal work of Edwards and Cavalli-Sforza. Nielsen argues that partly as a casualty of the dominance of cladistic ideology, phylogenetics and population genetics subsequently diverged and became separate fields of scientific inquiry. The advent of genomic data from multiple loci has

[21] See the penultimate paragraph of [192], including this sentence: '[I]t is a dangerous mistake to premise the moral equality of human beings on biological similarity because dissimilarity, once revealed, then becomes an argument for moral inequality'; see also [117]. On normative concerns, including Lewontin's tireless critique of 'hereditarianism' and its linking of race and IQ, see Kaplan and Winther 2014, pp. 1043–1046. Kaplan, J. M. and Winther, R. G. 2014. Realism, antirealism, and conventionalism about race. *Philosophy of Science* 81, 1039–1052; and Winther, R. G. and Kaplan, J. M. 2013. Ontologies and politics of bio-genomic 'race'. *Theoria. A Journal of Social and Political Theory (South Africa)* 60, 54–80. It might be worth noting that while Edwards's work on clustering and classification is only a small part of his total opus, his contribution has been particularly striking to philosophers of science.

renewed the interest within the field of phylogenetics for understanding population-level processes, and some state-of-the-art modern methods for estimating the historical relationship between evolutionary units are essentially simple extensions of the methods developed by Edwards and Cavalli-Sforza half a century ago. Nielsen's commentary discusses this historical development and the relationship between phylogenetics and population genetics in general.

Mark Pagel describes how the foundations Edwards and Cavalli-Sforza had laid down influenced Paul Harvey and him to write their book *The Comparative Method in Evolutionary Biology*.[22] Modern comparative statistical methods for analysing evolutionary trends among species owe an intellectual debt to the methods of maximum likelihood that Edwards and Cavalli-Sforza were pioneering in the mid 1960s to infer phylogenetic trees. The connection was inevitable: where phylogenetic inference makes use of a suite of characters to infer patterns of relatedness among species, comparative methods typically study just one or two traits to develop inferences about how those traits evolved or co-evolved along the branches of a phylogeny.

Elizabeth Thompson describes her experience from 1970 to 1974 as a graduate student under Edwards's mentorship, and the deep influence he had on her scientific and statistical thinking. In terms of population genetics, Edwards's earlier work with Cavalli-Sforza and his broad and deep knowledge of topics such as descent at the individual level led to Thompson's abiding fascination with genetic and genealogical structure among individuals and between populations. In statistical thinking, Edwards's clear views on model-based inference and more specifically on likelihood have influenced not only Thompson's own work but also broad areas of statistical genetics.

Ziheng Yang recaps [46] for the biologist reader. He traces the efforts made by Edwards and Cavalli-Sforza in the 1960s to apply Fisher's maximum likelihood method to estimate the relationships among human populations. When the confusion between parameters and random variables is cleared up, the procedure described in [46] is recognised as a Bayesian approach to phylogenetics, using the Yule branching process to specify the prior for trees. Yang discusses the impact of Edwards's paper on the introduction of the Bayesian approach to molecular phylogenetic reconstruction in the 1990s.

Warren Ewens's commentary takes the form of a conversation in which he encourages Edwards to write a population genetics-based biography of Fisher. Fisher is highly admired by both Ewens and Edwards, and Ewens considers the first four chapters of Fisher's classic *The Genetical Theory of Natural Selection*,

[22] Harvey, P. H. and Pagel, M. D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

discussing how, in such a biography, Edwards would change and improve the chapter contents. Ewens formulates some criticisms of the book. His commentary describes aspects of Fisher's work (in particular his Fundamental Theorem of Natural Selection) that appear to be opaque or even wrong. He also discusses how Fisher's treatment of the stochastic theory can be simplified and brought up to date.

Samir Okasha examines one of Edwards's lifelong interests, Fisher's Fundamental Theorem of Natural Selection. Owing to the opacity of Fisher's presentation, there has been considerable confusion over the years about the true meaning, scope, and validity of the fundamental theorem. Happily, this confusion has been largely resolved, thanks in no small part to Edwards's work. Okasha traces the development of Edwards's ideas on this topic from the 1960s to the present day.

Maurizio Esposito focuses on two of Edwards's hermeneutical suggestions related to Fisher's 1930 magnum opus: first, that Fisher's gene-centric view was more sophisticated than many interpreters have maintained; and second, that Fisher's eugenics should not be taken as the driving motive of Fisher's science. In taking seriously these two suggestions, the chapter complements Edwards's interpretive effort with an analysis of Fisher's use of the human sciences. In so doing, it shows how Fisher's ideas on human evolution were unexpectedly anti-reductionist and his epistemic approach interestingly pluralistic.

Jean-Baptiste Grodwohl revisits Edwards's contributions to the history of population genetics, by relating them to his lifelong reading of Fisher. Grodwohl's chapter reads as an intellectual biography of Edwards, from his first steps in Fisher's Department of Genetics up to his most recent historical work on the Fundamental Theorem of Natural Selection.

Noah Rosenberg discusses Edwards's article on multivariate classification and human genetic diversity ([192]), distinguishing Edwards's classification question from the variance-partitioning problem posed by Lewontin. Rosenberg comments on earlier iterations from the 1970s and 1980s of the conversation between Lewontin and others with views similar to Edwards's. In doing so, he confirms the importance of both perspectives, remarking on contexts in which one or the other appears to be more salient. The chapter ends with a description of the influence of Edwards's model of multivariate classification on a new extension in which classification proceeds from phenotypes rather than genotypes.

On being provided with an opportunity to respond to the commentaries, Professor Edwards preferred to add a previously unpublished autobiographical talk, which can be found in Appendix 3.

As for the editor, how did this book about Edwards come to be edited by a philosopher of science rather than a bona fide biologist? Ian Hacking (Stanford; University of Toronto; Collège de France), one of my mentors and a distinguished philosopher of science, author of the inspiring book *Representing and Intervening*, brought [192] to my attention, and we discussed it at length.[23] Hacking, furthermore, was once Edwards's peer at the University of Cambridge, which provided me easy introduction and a strong recommendation to Edwards. I quickly became fascinated with Edwards and Cavalli-Sforza's early technical work in statistical phylogenetics. The probability theorist and data analyst Amir Najmi added immeasurably to my understanding of the quantitative methodologies of this book (his geometric interpretation of Edwards's 'Lewontin's fallacy' argument is included in Appendix 1), as did biologist Michael 'Doc' Edge (Stanford University; University of California, Davis). Historian and philosopher of science Carlos López Beltrán (Universidad Nacional Autónoma de Mexico, Mexico City) helped me to frame relevant ethical and political concerns. Conversations with Richard Lewontin (Harvard) and Noah Rosenberg helped clarify further subtleties, technical and conceptual alike. In a number of publications, some of them co-authored with philosopher Jonathan Kaplan (Oregon State University), I have explored the philosophical implications of the simultaneous truth of variance-partitioning (Lewontin) and clustering and classification (Edwards) approaches to human genetic diversity. (One of these is reprinted in Appendix 2.) Another of my immediate concerns was how various social and common conceptions of race in modern humans seemed to turn on details of the theoretical and experimental methodologies explored in this volume.

It has been an honour and a significant education to work with and learn so much from Professor Edwards. Corresponding with Edwards, reading his work, and interviewing him proved to be deeply enlightening. Katrina Halliday's expert judgment at Cambridge University Press also added immensely to this book, and Natasha Whelan, Zoë Lewin, Claire Heidi Hafner, Lucas McGranahan, and Oliver Baker have provided significant editorial assistance of various kinds.

In addition to the education I received during the editing of this book, I already had considerable interest and foundation in the pertinent science. Furthermore, as *Phylogenetic Inference, Selection Theory, and History of Science* analyses controversies and intellectual lineages, it seems important to declare by whom and in what I received my scientific tutelage. I was taught evolutionary biology in the American tradition of Sewall Wright. My teachers included Marcus Feldman, Michael J. Wade, Peter Godfrey-Smith, and Elisabeth A. Lloyd, at Stanford

[23] Hacking, I. 1983. *Representing and Intervening: Introductory Topics in the Philosophy of Natural Science*. Cambridge: Cambridge University Press.