alleles from populations is similarly mentioned only briefly. Correspondingly, quite a few important recent developments are not described, including John Wakeley's very helpful description of the coalescent process in a subdivided population in terms of successive 'scattering' and 'collecting' phases, the latter being reducible to a standard coalescent process.

The book thus needs to be read as an account of one particular approach to the study of subdivided populations, not as a comprehensive overview of the current state of play. It is also not a book for the mathematically faint-hearted, because extensive use is made of matrix algebra. Few applications to biological data are described. Within these limitations, it is an exceptionally thorough treatment of this difficult area, and provides an excellent source of information for those who wish to delve into it.

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Church records advancing evolutionary biology

Consanguinity, Inbreeding, and Genetic Drift in Italy by Luigi Luca Cavalli-Sforza, Antonio Moroni and Gianna Zei.
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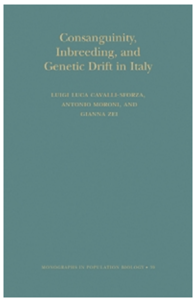

Consanguinity,
Inbreeding, and
Genetic Drift in Italy

LUIGI LUCA CAVALLI-SFORZA,
ANTONIO MORONI, AND
GIANNA ZEI

MONOGRAPHS IN POPULATION BIOLOGY • 39

In 1951, Luigi Luca Cavalli-Sforza was lecturing in genetics in Parma, Italy, when Antonio Moroni, a student and priest, informed him of Italian Church records that were rich in patterns of matrimony and demography. The day that the Church was persuaded to disclose its records marked the beginning of an epic examination by Cavalli-Sforza, Moroni, and Gianna Zei of consanguinity, inbreeding and drift that would comprise 300 years of data, fill half a century and eventually encompass all of Italy. This book represents an exclusive unification of the team's research over those 50 years.

The primary aim of *Consanguinity* is to investigate the demographic, ecological and social correlates of marriages between relatives and to determine the effects of such marriages on inbreeding depression, genetic disease prevalence and drift. To this end, the authors use an impressive and unique blend of data and approaches, including the extensive church records documenting demography and marriage relations, knowledge of local ecology, blood group data, hospital records, nationwide statistics about frequencies of different surnames (used here as a surrogate for genetic markers), as well as mathematical modelling and computer simulation techniques.

The coverage of *Consanguinity* is undoubtedly impressive and the consequences of the findings far reaching. However, as Bob Dylan would put it [1], you can keep half of the people part-right all of the time and you can keep some of the people alright part of the time, but you can't keep all of the people alright all of the time. Personally speaking, I would like to have seen a couple more chapters. First, in spite of the data about consanguineous marriages being individual based, the approach throughout the book is purely demographic. In addition to the more conventional method of historical demography, which base analyses on census data or non-nominative evaluation of Church register entries, I was missing a chapter examining the causes and consequences of consanguineous breeding in the context of the individual or family.

Second, the title of this book places the study in Italy, and there, with few exceptions, the reader remains through to the very last page. Given the pioneering nature of this project, an attractive addition to the book could have included a commentary by the authors on some of the following questions, all of which, to my mind, were conspicuous by their absence. Did the novel research methods introduced by Cavalli-Sforza and his colleagues stimulate researchers in other countries to follow suite and, if so, how do the results compare? Do other researchers have the same opinions and have they reached similar conclusions? How do the conclusions of this book compare to similar research on animal populations, wild and laboratory?

The short reference list at the end of the book is testament to the lack of curiosity that the authors have for the studies or findings of others. However, Cavalli-Sforza and his colleagues do highlight several interesting studies conducted in the first two-thirds of the last century, which newcomers in the field, who restrict their searches to the 'Web of Science' might otherwise miss or ignore. Nevertheless, the authors have passed on an opportunity to place their results (many published during the 1960s) in the context of current understanding and evaluate the overall impact of their project on subsequent studies elsewhere. Without this addition, it is difficult to perceive, among other things, the value of computer simulations carried out with IBM 7040s with their restricted iterative power in the 1960s.

Consanguinity is therefore a case study, but if a case study is what you are looking for, you will be hard-pushed to find one that is more detailed and extensive than this. In terms of both methods used and findings discovered, the accomplishments of this project over the past 50 years will be immensely influential on our understanding of human social structure in the light of historical demography and genetics, as well as on the genetic effects of drift and inbreeding. One should not

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forget that the use of Church register data such as theirs documenting the demography of the whole country and providing pedigrees comprising several generations for each consanguineous marriage in alliance with data on ecology and health is the stuff of dreams for most of us.

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What determines the direction of evolutionary change?

Biased Embryos and Evolution By Wallace Arthur. Cambridge University Press, 2004. £50.00/£18.95 hbk/pbk (252 pages)
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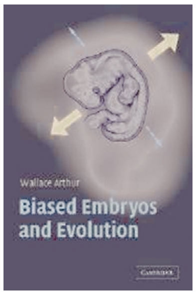

Modern evolutionary biology began with the ‘modern synthesis’ and the story is well known in evolutionary circles. Several researchers from different disciplines (e.g. Dobzhansky in genetics, Simpson in paleontology and Mayr in systematics) reviewed evidence from their scientific fields to demonstrate its compatibility with Darwin’s theory of evolution by means of natural selection and Mendel’s laws of inheritance. In *Biased Embryos and Evolution*, Wallace Arthur develops the argument that the modern synthesis and its present-day descendant are naive in some respects (the nature of mutations) and not all-inclusive in others (absence of a developmental perspective), highlighting the need for a substantial revision.

But lets start from the beginning. The central claim developed by Arthur is that natural selection should be considered in conjunction with developmental bias as the agents of evolutionary change. In a nutshell, developmental bias states that mutations, although occurring at random in respect to the trait under selection, are not random in their direction, with changes in certain directions being more likely to occur than in others. According to Arthur, three are the major factors influencing the direction of evolutionary change; natural selection, developmental bias as well as the occasional historical accidents (contingency).

The traditional model for the genetics of adaptation goes back to Fisher’s geometrical model [1]: the larger the phenotypic effect of a given mutation, the smaller its probability of being advantageous. Accordingly, evolutionary change is being driven by natural selection acting on a large number of mutations, each of which has a small phenotypic effect. Arthur contests two aspects of Fisher’s model: the relative phenotypic magnitude of mutations and their direction (developmental bias). For example, evidence that many phenotypic changes between taxa are governed by relatively few allelic changes, some of which are of small and some of which are of large effect [2]. As for developmental bias, the raw material for change is more readily available for some directions than others. Arthur claims that we need to develop an ‘inclusive theory’ to take into account both developmental bias and the magnitude of mutations. However, the phenotypic magnitude of mutations explaining differences among taxa is still compatible with modified versions of Fisher’s model [2] and developmental bias, at least in its basic form, would hardly be contested by anyone. But here lies a more general issue; throughout the book, Arthur is mainly concerned with presenting the larger theoretical framework and says little about which theories are supported by actual data, and to what extent. But, without knowing the relative importance of the various evolutionary agents (e.g. developmental bias), it difficult to assess their potential influences, if any, in driving evolutionary change.

Arthur makes several simplifications that somewhat bias his conclusions. For example, modern synthesis had little to do with the British school of ecological genetics (E.B. Ford and colleagues) so attacking the modern synthesis for the ideas espoused by the British school (and especially for their pan-selectionism) is misguided. Furthermore, Fisher’s magnum opus [1] was different in scope than Darwin’s *Origin* and hence accusing Fisher for a more restricted evolutionary worldview is unfair in this context.

Arthur also makes the case for the addition of a developmental perspective in the study of evolutionary biology and I couldn’t agree with him more. To be fair, the omission was readily understood and acknowledged by the architects of the synthesis, and happened for a good reason; there was no data to weigh on the issue. However, it is surprising that, in spite of Arthur’s stress on the importance of a developmental perspective, his treatment of comparative developmental genetics (also known as ‘evo–devo’) is rather brief.

So, do we really need to revise the modern synthesis? I think that regarding modern evolutionary research as strictly adhering to all the principles championed by the modern synthesis is misleading. Similar to organisms, scientific theories undergo their own development. Granted, a great many inferences from the time of the modern

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