
Book Reviews

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The Origins of Genome Architecture. M. Lynch.
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The astonishing ability to obtain sequences of organisms' complete genomes, and the amazing number of them now available, are well known to all biologists. For biologists working in the fields of molecular evolution, these genome sequences have offered new opportunities to work in an integrated way with other kinds of biologists, which has been rare since the development of molecular biology led to a focus on gene functions, and understanding their evolution became a minority activity within biology. Genome sequences have been a wonderful gift to evolutionary biologists, giving them new data sets large enough or detailed enough to test old-established evolutionary questions, such as the importance of selection on different kinds of sequences, or to estimate things like the rates of different kinds of chromosome rearrangements. But many biologists have viewed such topics as peripheral, and could continue to do so until analyses of genome sequences turned out to need molecular evolutionary expertise. These sequences were obtained largely in order to catalogue the genes of different organisms, and their functions, but it quickly became clear that we cannot see genes in a genome sequence, and so we cannot count them or list them. Comparative genomic analyses, using evolutionary approaches to find conserved sequences, soon became an integral part of gene finding, opening a period of rapprochement between the fields of molecular biology and molecular evolution. Lynch's book spans these two fields, and fills a major gap in providing a coverage of this developing area. Perhaps his main aim is to demonstrate to molecular biologists the value and importance of molecular evolutionary thinking and of population genetics, eloquently and interestingly summarised in the final chapter (which many readers might like to read first). However, evolutionary biologists will certainly also find the book valuable, both for its summaries of many interesting aspects of molecular biology (including the details of DNA synthesis and

base composition, introns of eukaryote genes and their splicing mechanisms, transposable elements, centromere functions, and regulatory DNA sequences) and for Lynch's use of data to estimate important quantities and use them to illuminate evolutionary questions.

Apart from the chapter on the human genome, which is described in chapter 3, and introduces many topics that are later discussed in detail, most chapters have an evolutionary focus, and many contain useful 'boxes' with the relevant theory laid out briefly. The first two chapters review the main taxonomic groups of organisms, and the vast range of genome sizes, stressing the idea that small organisms have much larger population sizes than large organisms. A main theme throughout the book is the well-established idea that small effective population sizes of large organisms leads to low efficacy of selection. The idea is that, for a mutation or variant with a given effect on organismal survival or reproduction, selection is less likely to be effective in a population with a small effective size, so that deleterious changes may not be prevented by selection, and advantageous mutations may fail to be incorporated. In his other, more evolutionary, chapters Lynch argues that for this idea as an explanation for a wide range of otherwise puzzling features of genomes.

In reviewing genome architecture, Lynch deals mostly with differences between the genomes of different kinds of organisms, for instance the small, compact genomes of prokaryotes, compared with eukaryotes, and the presence of introns only in eukaryotes. Differences between different genome regions of the same species are mentioned here and there, but are not his main focus (for instance, heterochromatin is hardly mentioned; the reasons for different recombination rates in different genome regions are also not discussed, though this is a question where there are good arguments for the involvement of selection). The emphasis on differences between distantly related taxa makes it difficult to test the arguments Lynch puts forward, because the taxa differ in so many ways. For example, breeding system differences affect the frequency with which

recombination occurs, and this affects many aspects of genome evolution. It is thus dangerous to ignore such differences when comparing taxa with many asexual species (such as prokaryotes) with eukaryotic taxa that are mostly sexual. The main value of the book is thus not that it answers the many questions discussed (Lynch would probably not claim to do this), but to highlight interesting questions, and show that it is not scientifically productive to assume that one should always invoke natural selection to explain the observed differences between genomes. In trying to understand these differences, it is also important to consider whether a process not involving selective differences could be consistent with the observations (e.g. a bias in mutations that could account for some aspects of base composition); we can conclude that selection has shaped a genome feature only when this is clearly indicated. Lynch is certainly right in saying that this rule is not always followed. There are many examples of both molecular biologists and evolutionary biologists proposing selective explanations for genome features which have later turned out to be incorrect, generally because alternatives were not considered. This book shows the kinds of factors that ought to be considered when thinking about the evolution of sequences, and should help biologists do better in the future. On the other hand, we should not to dismiss a reasonable hypothesis such as natural selection, merely for want of enough currently available evidence. For example, some duplicated genes have been shown to have evolved adaptively, and now have distinctive functions in organisms, but this is known for only a few cases of duplications. Genome sequences have been available for only a few years, and the skills needed to think about the evolution of genomes are in short supply, so absence of current evidence for selection may often merely reflect the fact that we have not yet thought of a good test, or not yet analysed enough data. For example, it is only very recently that data on divergence between sequences from related species has revealed that selection affects more non-coding sequences, including parts of introns, than was previously suspected.

Given the importance of hypothesis testing, the main weakness of the book is its rather rough and ready explanations of the how the evidence is obtained for some of the conclusions, so that it is sometimes difficult to evaluate them. For example, Paland and Lynch's study concluding that asexual lineages of *Daphnia* accumulate more deleterious mutations than sexual relatives is mentioned on p. 187, but readers are not told how deleterious substitutions are recognised, nor how substitutions are counted. Many of the tables presenting easily digested estimates of various quantities do not make clear how much data were used in the calculations, making it difficult to assess the reliability of the conclusions from the

numbers. An example is table 4.1, giving ratios of mutation to recombination rates, using data on nucleotide sequence diversity, often from small samples of the species included. However, many of these estimates need only be rough, and of course, these examples can serve to show what is needed, so that the estimates can be improved in the future. Nevertheless, some caution would be advisable, if the book will be used by students and others not expert in diversity studies. The Dobzhansky-Muller model of reproductive isolation between species is dismissed and mischaracterised as invoking 'the evolution of coadapted complexes of epistatically interacting factors', whereas it requires only a detrimental interaction between advantageous alleles that have evolved at different loci in two species, which is plausible, and for which some good evidence for selection exists (which Lynch does not mention, see Presgraves, 2006; Brideau, 2006). The chapter on sex chromosomes is too vague in places, and parts will probably mystify readers (the last sentence mentions sexual antagonism, but this has not been explained, although Rice's experiments are mentioned); the mention of sex-determining regions of fungi may also cause confusion, as there are no sex differences in these species. If this book is used for teaching, the students will therefore need considerable guidance.

Another difficulty for students will be Lynch's use of his own terminology for some important concepts, rather than the standard terms. His terms for effective population sizes are clearly explained, so this may not be a serious problem (although the term 'genes at a locus' seems unfortunate), but his use of R and S for the per site rates of substitution for non-synonymous and synonymous sites (which are generally called K_a and K_s); the fact that this is not the usual notation is not mentioned.

The recent literature on genomes is huge, even considering just papers analysing their evolution, so one cannot criticise Lynch for omissions and inaccuracies, but some omissions of recent work are unfortunate. For instance, it is a pity that the recent conclusion was not mentioned that non-coding sequences in *Drosophila* may be evolving under positive selection (Andolfatto, 2005). Indeed the use of the McDonald-Kreitman test (McDonald, 1991) is not mentioned at all, which is a large gap if there is to be a fair discussion of the evidence for selection (although Malik and Henikoff's study of centromere protein arms races is mentioned in chapter 5); this test is also one of the most useful for molecular biologists, as it is simple to perform. This omission is part of a rather general scarcity in the book of evidence using data from within species, rather than from comparisons between different species. Despite Lynch's appeals for more population genetics, the book uses only a small range of approaches – of course, this may be a plus

for molecular biologists, but readers should be aware of what is left out.

This is mainly an ideas book, and Lynch openly makes clear that the main idea he is advocating is a lesser role for selection than is often found in the literature on genome evolution, and greater importance of fixation in species of deleterious changes that selection is unable to prevent. Many of the ideas are controversial, and many are currently under debate in the evolutionary community, and it is a valuable contribution to present them in an accessible manner, and set them in the context of the relevant population genetics theory. Lynch's evident bias in favour of his view is plain enough that it is not likely to impede progress in testing other ideas. Rather, the book is likely to create fruitful debates, and be valuable in getting assumptions clear, and helping create a focus on the most important issues, and thus contribute to beginning to understand many aspects of genome evolution.

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Plant Breeding and Biotechnology. D. Murphy. Cambridge University Press. 2007. 410 pages. ISBN 9780521530880. Price £29.99 (paperback). ISBN 9780521823890. Price £70.00 (hardback).

The success of plant breeders in improving the productivity of the major crop species has been an important factor in enabling the large increases in world population and food availability over recent decades. Accompanied by changes in farming practice, including fertiliser and pest and disease control, average yields have been increased many times over during the past century. Classical cases include the development of hybrid maize in the USA, improved wheat varieties by institutes in Europe such as the Plant Breeding Institute at Cambridge (PBI), and the 'green revolution' facilitated by development of new varieties of

wheat and rice by breeders at the International Maize and Wheat Improvement Centre Mexico (CIMMYT) and the International Rice Research Institute (IRRI) in the Philippines.

Most of the genetic improvement has been obtained by classical methods of selection on yield, on straw strength allowing heavier use of fertilisers, and on disease and stress resistance, aided by incorporation of genetic material from diverse sources. Most of the improvement has been undertaken in publicly funded research stations, for example in the USA by USDA and State Experiment Stations, and by PBI, CIMMYT, IRRI and others. The notable exception has been maize improvement where large commercial breeding companies have operated for over half a century, but Denis Murphy points out that their efforts have been greatly enhanced by support in terms of provision of technology and germ plasm by publicly funded researchers. In the UK and, following the British lead, elsewhere there has been substantial privatisation in the last few decades: for example the Agricultural Research Council's PBI was privatised in 1989 and subsequently sold on to a series of international companies.

Commercial breeders need to recoup their investment through continued income from a good variety, but the farmer can save his own seed for new planting. In maize the market was developed by the need for breeders to return for hybrid seed each year. In Europe and elsewhere this has come from legislation giving plant breeders rights to income on marketed seed down the multiplication chain. The strongest route is via patenting, and the opportunity to patent the product has been a major stimulus to the development of GM varieties, with the biggest success so far being in development of herbicide resistance varieties to reduce growing costs. Murphy is critical of the hype attached to the GM developments, which he points out are really only an extension of the introgression techniques long used by breeders to bring in useful genes or gene combinations from other stocks. He also argues that much of the public antipathy has been because the GM crops have been developed by very large companies such as Monsanto, and have, with minor exceptions, been for traits of importance to the producer and not the consumer. (The notable exception was 'Flavr SavrTM' tomatoes but, they were not a commercial success.) Ignorance of the biology by the popular press and limited but publicised experiments contributed. Even so, Murphy is concerned that the benefits of GM technology have been overstated, arguing they are no more than another tool in the breeders' arsenal such as introgression using marker assisted selection. Albeit he is mostly thinking of incorporation of genes rather than gene construction, but that is for the future and his perspective is rather limited.