

Book Review

Principles of Population Genetics, 4th edition

Daniel L. Hartl and Andrew G. Clark.

Sinauer and Associates, Sunderland, MA, 2007. xv + 652 pp,
ISBN-10: 0-87893-308-5.

In the first 3 editions of their text, Hartl and Clark were able to establish their book as not only a useful introduction to a complex and challenging field but also a highly useful reference that deserves a place on the shelf of any biologist. The fourth edition of the book continues this tradition.

The book provides an excellent summary of the basics of population genetics. As usually taught, this can be pretty boring stuff. But the authors have read widely and are able to enliven the discussion where it is needed. For example, in discussing coalescent theory, which allows us to trace a polymorphic population back to the time when it was monomorphic, they quote Joseph Felsenstein's memorable "bugs in a box" analogy. Felsenstein imagines voracious bugs running around in a box that has $2N$ places, one eating the other whenever 2 of them occupy the same place, until only one bug (allele) is left. In their discussion of the central limit theorem, which predicts that randomly chosen samples from any population of observations will tend to be normally distributed if the sum of the observations has a finite variance, they quote Francis Galton: "The [Central Limit Theorem] would have been personified by the Greeks if they had known of it. It reigns with serenity and complete self-effacement amidst the wildest confusion. The larger the mob and the greater the apparent anarchy, the more perfect is its sway. It is the supreme law of unreason."

One thing I found especially pleasing about the book is the way in which new molecular information is integrated into discussions of phenomena that have been known for decades. One of these is the phenomenon of phenotypic plasticity, in which organisms with identical genotypes can have a range (known as the "norm of reaction") of different responses to different environmental pressures. If characters show phenotypic plasticity, this makes their heritability difficult to measure. Population geneticists have known about this discomfiting fact for decades, though the genetic basis for it is poorly understood. Richard Lewontin and others, including myself, measured how the competitive ability of *Drosophila* flies carrying the same chromosome inversion changed when the environment was altered by the experimenter. Often, the competitive rankings of the flies changed

completely even when the environmental changes seemed small to the observer. (In my data, the rank of fitness values associated with the chromosomes differed dramatically depending on whether the adult flies were allowed to lay eggs in their culture bottles for 2 or for 3 days.) The actual genes that were involved, of course, lay beyond the reach of the investigators.

Now it is possible to examine norms of reaction at the molecular level. The authors discuss new work by Landry et al. (*Gene* 366:343), in which changes in the transcriptional activity of individual genes in *Saccharomyces cerevisiae* can be followed as the environment changes. It is now possible to see, using molecular techniques, that the background genotype can have a strong influence on the expression of individual genes and that this influence can be extremely environment dependent. Although the text does not discuss it, the cited paper also showed that there are a large number of genes that are not affected by the environment and/or the background genotype, so phenotypic plasticity is just one of the things that may or may not influence development and survival on the way from genotype to phenotype.

The text also does not discuss the new and exciting approaches to the process of speciation that are now being made possible by coalescent theory and the availability of entire genomes. The split between humans and chimpanzees, for example, may be far more complex and lengthy than simple speciation models would predict. But the book does introduce students to the tools that they can use to probe how speciation takes place. It is a good place for students to gain an understanding of this fast-moving field.

Population genetics is undergoing a revolution, thanks to the availability of vast amounts of comparative sequence data and the invention of new methods by which to examine it. Each chapter in this revision includes some of this new information. The topic is a vast one, and I am most impressed with how well organized the book is and how much new material has been included in the 10 years since the last revision.

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