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This Week's Citation Classic

Wright S. Evolution in Mendelian populations. *Genetics* **16**:97-159, 1931.
[University of Chicago, Chicago, IL]

An evaluation is made of the evolutionary roles of mutation (recurrent or novel), of population structure (homogeneous or with randomly differentiating demes), and of natural selection at two levels (among individuals and among demes, the latter by selective diffusion from the better adapted ones). [The *SCI*® indicates that this paper has been cited over 350 times since 1961.]

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"Darwin's synthesis in 1859 of the available data soon convinced scientists of the truth of evolution. His theory of the mechanism, natural selection, was less successful. There was still a bewildering array of alternative theories when I became a graduate student in 1911. As Darwin was well aware, the principal gap in his theory was in knowledge of heredity.

"One difficulty was resolved soon after the rediscovery in 1900 of Mendelian heredity. It was soon recognized that gene frequencies tend to remain unchanged in the absence of disturbing factors. Even the weakest selection suffices for ultimate fixation. Most early Mendelians accepted the theory of evolution by the fixation of rare favorable mutations.

"It was generally thought that Mendelian heredity does not apply to quantitative variability and that, contrary to Darwin's views, selection of such variability has no permanent effect. My mentor at Harvard University, Professor Castle, was, however, wholly Darwinian. He conducted successful selection experiments with hooded rats (in which I was his assistant). Meanwhile, Professor East, in the same laboratory, was obtaining massive support for the multiple locus theory of quantitative variability.

"My own experiments with guinea pigs impressed me with the complexity of the interactions relating genes to characters. Moreover, a given phenotype could usually be simulated fairly closely in different ways, but ones not in general equally advantageous. I had started with a purely Darwinian view, but such considerations pointed to serious shortcomings of individual selection. Selection would be much more adequate if among interaction systems, but this is impossible in random-breeding populations under biparental reproduction, because of rapid breaking up of all combinations.

"It is possible, however, in a finely subdivided population. Assume that there are thousands of loci in which slightly different alleles are maintained by recurrent mutation in balance with weak selection, and that in each locality there is a balance be tween the differentiating effect of inbreeding (random drift) and incursion from neighboring localities. There would be a never-repeated sequence of sets of gene frequencies within each locality, never reaching fixation, and occasional shifts from rough selective control by one interaction system to control by a superior one, with reversal of signs of two or more selection coefficients. The new systems would spread throughout the species (at least whenever actually superior) by selective dispersion. This shifting balance process is as truly a form of natural selection as is individual selection.

"My 1931 paper was largely devoted .to mathematical formulations of these states of balance. It has probably been frequently cited as one of the first attempts at filling the main gap in transformation theory. It supplemented Haldane's systematic study of courses of fixation of single favorable mutations,[1] and Fisher's mathematical formulation of pure Darwinian selection under random mating.[2] I have recently published work in this field."[3,4]

1. **Haldane J B S.** *The causes of evolution.* New York: Harper, 1932. 234 p.
2. **Fisher R A.** *The genetical theory of natural selection.* Oxford: Clarendon Press, 1930. 272 p.
3. **Wright S.** Genic and organismic selection. *Evolution* **14**:825-43, 1980.
4. ..... *Evolution and the genetics of populations.* Chicago: University of Chicago Press, 1978. 4 vols.