Sewall Wright on Evolution in Mendelian Populations and the "Shifting Balance"

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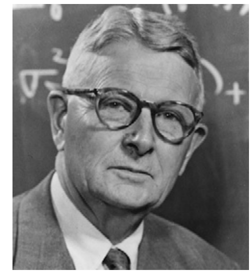

ORIGINAL CITATION
Evolution in Mendelian Populations
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After the rediscovery of Mendel's work in 1900, bitter disputes erupted between the first geneticists and the biometricians who studied quantitative traits. How could the discrete genes of the geneticists explain the continuous variation observed by biometricians? And could natural selection shape variation in these genes? Eventually, the two camps came to understand that quantitative variation is due to multiple Mendelian genes of small effect, and selection on this variation is highly effective. Yet in 1931, very few attempts had been made to formally describe the genetics of evolving populations. By explicitly reconciling Mendel's and Darwin's theories, Sewall Wright and the other pioneers of population genetics laid an enduring mathematical foundation for understanding evolution.

Wright's (1931) *Evolution in Mendelian Populations* is a remarkable synthesis of population genetics and its application, presenting, in essentially its modern form, the population genetics of allele frequency evolution. Wright provides mathematical analyses of selection, mutation, migration, and random genetic drift, synthesizing these processes into a single formula for the stationary distribution of allele frequencies. This laid the groundwork for Kimura's elaboration of the diffusion approximation and its widespread application to understanding molecular variation (Kimura 1954).

Wright uses these mathematics to argue that selection on a large population would not lead to continued evolutionary progress. Instead, the population would be trapped with an allele combination that is favored only locally. Steady progress would be most likely in species subdivided into smaller groups with similar rates of selection, migration, and random drift. This would allow more efficient exploration of the "adaptive landscape."

Wright's theory was highly influential, stimulating many studies of natural population structure. Nevertheless, it is not clear that his "shifting balance" mechanism actually operates in nature (Coyne *et al.* 1997). As Fisher argued, a changing environment allows continual evolution across the vast space of possible genotypes (see Provine 1986 for the correspondence between Fisher and Wright on these issues). The roles of local fitness peaks and gene flow in adaptive evolution remain major open questions in evolutionary biology, nearly a century after Wright first raised the issue.

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