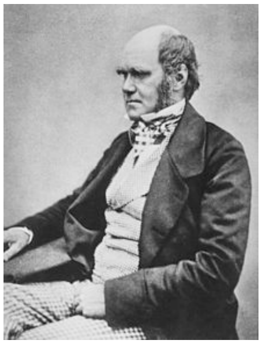
Overview of the Modern Synthesis
Thanks to Frank Smith for many images

I. Pre-synthesis: Darwin and *The Origin of Species*

Darwin and Wallace discover Natural Selection and Darwin writes *The Origin of Species.*

1.) all organisms are related and share a common ancestor.

2.) natural selection is the mechanism underlying adaptation.



Charles Darwin

Alfred Russel Wallace

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I. Pre-synthesis: Darwin after *The Origin*

Problem: In Darwin's day blending inheritance was the accepted mode of inheritance.

Darwin's Mechanism of Inheritance:

The Variation of Animals and Plants under Domestication (1868)

Pangenesis: Atomic sized gemmules formed by cells diffuse and aggregate in the reproductive organs, passing on trait values.

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I. Pre-synthesis: The rediscovery of Mendel’s work


Gregor Mendel

In 1866 Gregor Mendel (1822-1864) published his work on peas and provided a system of inheritance.

The *Laws of Segregation* and *Independent Assortment*

Mendel’s work went largely ignored until the 1890’s, and in 1900, three scientists published ‘rediscoveries’. Hugo de Vries (1848-1935), Carl Correns (1864-1933) and Erich Tschermak (1871-1962) came to similar conclusions and then discovered Mendel’s work.


Hugo de Vries


Carl Correns


Eric Tschermak

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I. Pre-synthesis: Biometricians vs. Mendelians (1st two decades of the 20th century)

Mendelian Genetics:

William Bateson (1861-1926) influenced Hugo de Vries to do crosses in plants which lead to rediscovery of Mendel’s work.

Bateson became on of the most ardent supporters of Mendelian principles.

Claimed to have a better understanding of biology than the biometricians.

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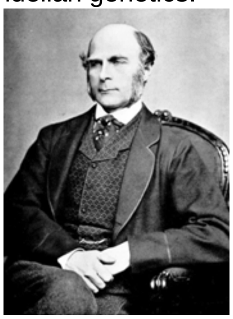
I. Pre-synthesis: Biometricians vs. Mendelians (1st two decades of the 20th century)

Biometricians:

Galton (1822-1911), Pearson (1860-1906) and Weldon (1860-1906) used statistical approaches to study continuously variable characters.

Claimed to be more statistically and mathematically rigorous than Mendelian genetics.



Francis Galton

Karl Pearson

Walter Weldon

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I. Pre-synthesis: Summary

- Darwin had convinced the scientific community of biological evolution, but there was still debate about the importance of natural selection in the process.
- Saltational evolution was seen as a viable alternative to Darwin's gradual evolution.
- Mendelian/biometrician debate arose because of the assumption that different mechanisms must underlie the production of continuous and discrete variation.

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II. The Modern Synthesis: Early Development

Ronald A. Fisher

Fisher (1890-1962) was a founder of both modern parametric statistics and evolutionary biology.

In 1918 he published “The Correlation between Relatives on the Supposition of Mendelian Inheritance”.

This paper showed that a system of many genes, each acting in accordance with Mendelian principles, could produce continuously varying phenotypic distributions.

This largely defused the debate between Biometricians and Mendelians

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II. The Modern Synthesis: The Pioneers

Ronald A. Fisher

In 1930, Fisher published his book *The Genetical Theory of Natural Selection.*

In this work, Fisher showed how Natural Selection could be the primary driving force in evolution.

Fisher believed that only additive components of phenotypic variance in a population were important for natural selection, i.e., the phenotype was the sum of the additive affects of genes.

He envisioned evolution as climbing a hill to an optimum at the peak.

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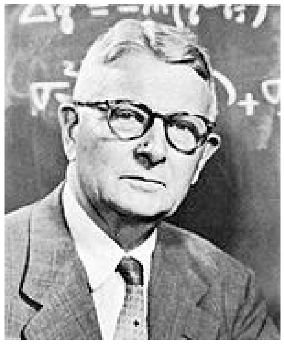
II. The Modern Synthesis: The Pioneers



Sewall Wright

Sewall Wright (1889-1988) was both a theoretician and experimental biologist.

Unlike Fisher, Wright conceived of evolution as occurring on a landscape with multiple peaks and valleys.

He introduced the idea of fitness landscapes in his seminal 1932 paper "The roles of mutation, inbreeding, crossbreeding, and selection in evolution".

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II. The Modern Synthesis: The Pioneers

First depiction of a fitness landscape

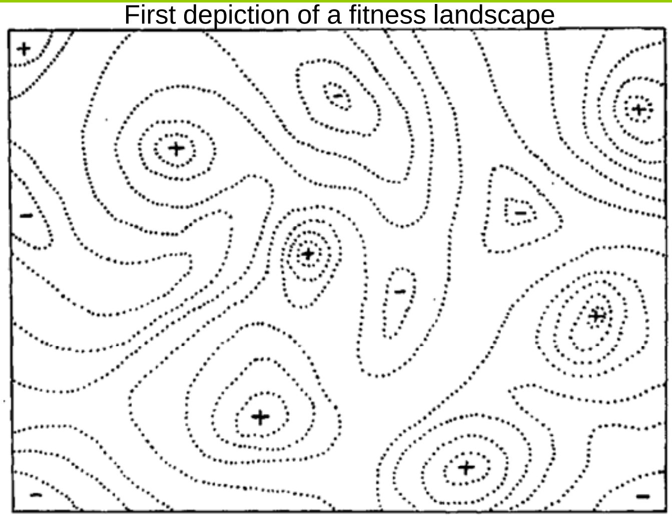

FIGURE 2.—Diagrammatic representation of the field of gene combinations in two dimensions instead of many thousands. Dotted lines represent contours with respect to adaptiveness.

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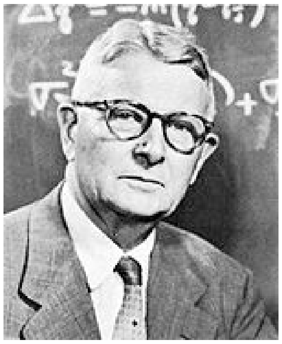
II. The Modern Synthesis: The Pioneers



Sewall Wright

Wright thought that several processes could be important in moving populations across a landscape.

His overall view of the evolutionary process is embodied in his Shifting Balance theory, which combines genetic drift, migration and selection.

Genetic drift became an important evolutionary mechanism, enabling populations to cross valleys between peaks.

He also thought that most phenotypes were the results of epistasis and pleiotropy, in addition to additive genetic effects.

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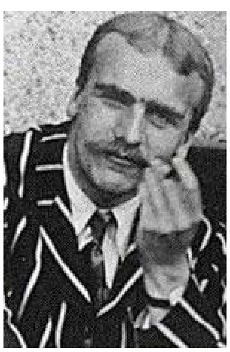
II. The Modern Synthesis: The Pioneers



J.B.S. Haldane

Fisher, Wright and JBS Haldane (1892-1964) invented population and quantitative genetics.

Haldane published 10 seminal papers between 1924-1934, “A mathematical theory of natural and artificial Selection 1-X”, summarized in his 1932 book *The Causes of Evolution.*

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II. The Modern Synthesis: Summary

Population genetics deals with traits controlled by one or a few loci – it is a mathematical theory and models the evolutionary changes of allele frequencies in populations due to mutation and selection.

Quantitative genetics deals with those traits controlled polygenically - it is a *statistical* approach which assumes that there are many loci involved, each with the same small additive effect on the trait. Mostly interested in effects of selection.

The first phase of the synthesis was accomplished through the development of these powerful tools and put the focus firmly on populations as units of evolution.

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III. The Modern Synthesis: Work on Natural & Laboratory Populations

Sergei Chetverikov

Theodosius Dobzhansky

Sergei Chetverikov (1880-1959) was an early proponent of evaluating evolution in natural populations.

His student Dobzhansky (1900-1975) was among the first in the US to apply the ideas of Fisher, Wright & Haldane to evolution in natural populations, in particular *Drosophila*.

Dobzhansky's *Genetics and the Origin of Species* (1937) was the first of a series of books conceived by Ernst Mayr to broaden the reach of evolutionary theory.

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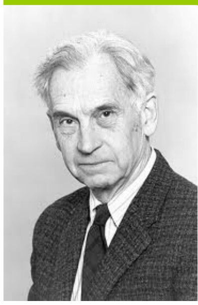
III. The Modern Synthesis: Work on Natural & Laboratory Populations


Ernst Mayr

Mayr (1904-2005), an ornithologist, wrote *Systematics and the Origin of Species* (1942) focused on species concepts.

Mayr developed the theory of peripatric speciation, i.e., new species are formed as small peripheral isolates of ancestral populations.


George Gaylord Simpson

G.G. Simpson (1902-1984) was a mammalian paleontologist. In 1944 he published *Tempo and Mode in Evolution*.

In the book he describes how macroevolutionary patterns can be produced by microevolutionary processes.

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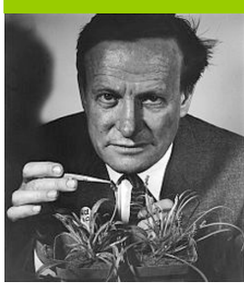
III. The Modern Synthesis: Work on Natural & Laboratory Populations


G. Ledyard Stebbins

Stebbins (1905-2000) was a botanist and geneticist.

In *Variation and Evolution in Plants* (1950), Stebbins brought botany in line with the ideas presented by the other architects of the Modern Synthesis.

Most of the book is oriented above the species level, not on population processes


Julian Huxley

Interestingly, the term *The Modern Synthesis*, was coined by Julian Huxley (1887-1975), a zoologist, as the title of his 1942 book *Evolution: the Modern Synthesis*.

In terms of true synthesis, Huxley's book is probably the best.

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III. The Modern Synthesis: Summary

The main tenets of this synthesis were (Mayr 1980):

1) gradual evolution is brought about by small genetic changes and recombination;
2) natural selection is the main evolutionary process acting on random variation within populations; and
3) evolutionary phenomena associated with macroevolution and speciation, are consistent with microevolutionary mechanisms.

In The evolutionary synthesis. Perspectives on the unification of biology

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IV. Outside The Modern Synthesis

There were a number of other prominent biologists of this period who are not typically included in the pantheon of the synthesists and we will talk about them as well during the course.

C.D. **Darlington** (1903-1981): pioneered the study of chromosomes, meiosis and the importance of crossing-over in evolution; an early sociobiologist

R.B. **Goldschmidt** (1878-1958): cytogenetics & evolution - theory of genes as independent regulators of complex systems; synthesis could not explain macroevolution, i.e., new species or body plans; macromutation – chromosomal changes, homeotic mutations

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IV. Outside The Modern Synthesis

I.I. **Schmalhausen**: saw evolution as modification of development and norm of reaction; importance of internal and external environments; stabilizing selection

Factors of Evolution (1949) – a much more developmentally oriented view of evolution than the main books of the synthesis

Jens **Clausen**: ecotypic variation; ecological genetics
Working with David Keck and William Heisey, he made massive transplant experiments across elevations in California.

He thought population genetic theory too simplistic; nature much more complex.

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IV. Outside The Modern Synthesis

Conrad Hal Waddington
(1905-1975)

C.H. **Waddington** (1905-1975): epigenetics (interactions of products of genes during development); canalization

3 problems with the theory:

1. adaptation – “Is it really … due solely to the selection of random variations?” points to plastic modifications that in some cases mirror genetic differences among populations.

2. Macroevolutionary gap – are the differences between species similar to the differences between populations or races within species?

3. Differences in evolutionary rates, e.g., stasis, radiation

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Some Open Questions for Evolutionary Biology I

What limits differences among individuals?

Contrast *Variability* (potential for trait to change) and *Variation* (observable differentiation)

How much variation can we attribute to random vs. directed forces? Nearly neutralists vs. selectionists

How are complex phenotypes coordinated?

The genotype → phenotype map

How do organisms solve the problem of changing environments?

Genetic polymorphism vs. phenotypic plasticity

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Some Open Questions for Evolutionary Biology II

How do novel phenotypes arise? Genetics, integration

How does a new species arise? What maintains it?

Why are some clades more successful than others?

Is macroevolution just a large scale version of microevolution?

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