

# The Evolutionary Synthesis and its Critics

“Nothing in biology makes sense except in the light of evolution.”

Dobzhansky, 1973, *American Biology Teacher*

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## At the End of the 19th Century Many Biologists viewed Natural Selection as Impotent

- Selection can only eliminate variants—it cannot produce anything.
- Variants must arise from somewhere else—mutation, etc.
  - The source of variation is the true cause of evolution
- “We are now standing at the deathbed of Darwinism, making ready to send the friends of the patient a little money to insure a decent burial. . .” (E. Dennert, *At the Deathbed of Darwinism*, 1904)

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## The Mendelian Alternative to Darwin

- Mendel had focused on individual factors responsible for observable traits (color, shape, etc.)
  - Alternative factors resulted in clearly distinct traits in organisms (green versus yellow peas)
- It seemed plausible that a change in one of these factors would result in a fundamental change in a trait of an organism
  - These might be large enough to yield transmutation
  - De Vries thought he had identified an instance in the Evening Primrose
- On this scenario, the origin of new species is due to mutation operating in one generation
  - Natural Selection, as a slow, gradual process, was claimed to play no role in the origin of species

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## Clicker Question

What fundamental change in conceptualization was required to bring Darwinian Natural Selection together with Mendelian Genetics

The recognition that genes reside on chromosomes

The recognition that many different genes could each produce small effects on a given trait

The recognition that each trait of an organism is governed by a different gene

The recognition that Natural Selection could only operate to eliminate variants

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## Bringing Mathematics to Bear on Mendelism: Hardy-Weinberg Equilibrium

- Punnett felt unhappy with his attempt to explain why recessive phenotypes still exist, and asked his cricket partner and Cambridge mathematician Godfrey Harold Hardy (1877-1947)
  - Question: what happens to a Mendelian mutation?
- Hardy's approach: Assumed a 2-allele case: **A** and **a**, with starting  $f = \mathbf{AA} = 0.49$ ,  $\mathbf{Aa} = 0.42$  and  $\mathbf{aa} = 0.09$  This gives an allele frequency of **A** = 0.7, **a** = 0.3
- He demonstrated that this ratio would remain constant from generation to generation provided:
  - Population is large
  - Mating is random
  - No selection: All offspring combinations are equally successful
  - No migration in or out of the population
  - Mutation rate has reached equilibrium
- The same result was independently derived by Wilhelm Weinberg (1867-1937), pediatrician in Stuttgart



## Pearson and Fisher

- The Biometricians (Galton, Pearson et al.—defenders of a Darwinian account based on gradual change through Natural Selection) had developed statistical tools to understand patterns of inheritance of traits such as height by assuming *continuous* distributions
  - But they did not have mathematical tools for dealing with discrete components such as Mendelian factors/genes
- These tools were developed by R.A. Fisher, who was initially snubbed by the Biometricians
  - "...Fisher...received an offer from Professor Pearson at the Galton Laboratory. Fisher's interests had always been in the very subjects that were of interest at the Galton Laboratory, and for five years he had been in communication with Pearson, yet during those years he had been rather consistently snubbed. Now Pearson made him an offer on terms which would constrain him to teach and to publish only what Pearson approved. It seems that the lover had at last been admitted to his lady's court—on condition that he first submit to castration. Fisher rejected the security and prestige of a post at the Galton Laboratory and took up the temporary job as sole statistician in a small agricultural research station [viz., Rothamsted Experimental Station] in the country." (Box, 1978, p. 61)





## Ronald Aylmer Fisher and *Population Genetics*

- Analyzed populations in terms of the genes of its members and investigated mathematically how gene frequencies will change over generations if selection is applied
  - That is, add selection to Hardy-Weinberg
- 1918: Fisher's first paper: "The Correlation between Relatives on the Supposition of Mendelian Inheritance."
  - Argued that discrete Mendelian genes were the focus of selection
  - That if many genes contributed to a given trait, one could account for the continuous variation the Biometricians observed
  - Opposed Darwin's and Pearson's view of blending inheritance, and Galton's "Laws"—genes are inherited as unitary entities
- In developing this analysis, Fisher made major contributions to the development of statistics, including the analysis of variance (ANOVA)

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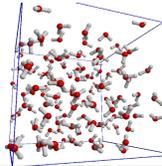
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## Fisher's project of Population Genetics

- Evolution occurs in large, virtually unlimited populations
- Variation and environmental change are random
- Selection produces a gradual shift in gene frequency
- Evolution leads inevitably to better adaptation
- Populations are simply collections of independent alleles combining and recombining every generation
  - These make independent contributions to fitness
- Aimed to make population genetics do for evolution what kinetic theory of gases did for temperature
  - Show how particles produce what appear to be continuous values for temperature




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## Discussion Question

By making Mendelian genes the units on which natural selection occurred, what fundamental problem that Darwin had struggled with finally had an answer?

The evidence that the earth had not been around long enough for Natural Selection to have produced current species

The fact that the fossil record was so incomplete that one could not show that intermediate forms had existed

Fleming Jenkin's demonstration that Darwin's proposed account of blending inheritance was incompatible with evolution by Natural Selection

The problem of showing how varieties could ever generate independent species

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## Genetical Theory of Natural Selection (1930)

- First half of book involved developing Fisher's concepts of genetics at the population level:
  - Idea of a "gene pool"
  - Fitness of alleles
  - Role of selection
- Fundamental theorem of natural selection: *The rate of increase of fitness of any organism is equal to its additive genetic variance in fitness at that time.*
  - Importance of *additive* (contrast: interactive) *variance*
  - Downplayed but did not deny "genetic residue" – linkage, epistasis (interaction between genes at different loci)
- Second half applied these principles to human breeding as an argument for *eugenic control* of reproduction (eliminating the "unfit" and promoting the more fit by providing an allowance for children proportional to income)

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## Fisher's Fundamental Theorem

"It will be noticed that the fundamental theorem .... bears some remarkable resemblances to the second law of thermodynamics. Both are properties of populations, or aggregates, true irrespective of the nature of the units which compose them; both are statistical laws; each requires the constant increase in a measurable quantity, in the one case the entropy of the physical system and in the other the fitness .... of a biological population .... Professor Eddington has recently remarked that 'The law that entropy always increases - the second law of thermodynamics - holds, I think, the supreme position among the laws of nature'. It is not a little instructive that so similar a law should hold the supreme position among the biological sciences." (Fisher 1930 *The Genetical Theory of Natural Selection*).

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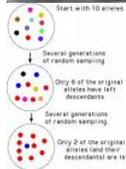
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## Sewall Wright's Alternative

- Early experience with animal breeding and development of a manual for cattle breeding for the U.S. Department of Agriculture
- Developed mathematical framework while at the University of Chicago
- Concluded that small, inbreeding groups were the key to evolution—**Shifting balance theory**
  - Gene frequencies could more easily become fixed (100%), frequently by chance (genetic drift)
  - Inbreeding would promote homozygosity and hence expose genes more effectively to selection
  - Each population would become adapted to a micro-niche, or would become extinct
  - Genes often interact in production of traits (epistasis), and fortuitous combinations more likely in small groups
  - Some migration & interbreeding between groups




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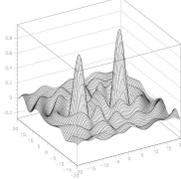
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## Adaptive landscapes



- The mathematical account Wright offered is much more complicated than that generated by Fisher
- Wright developed graphical ways of presenting his ideas
  - Peaks represent maximal adaptation
  - Valleys represent low adaptation
  - Sub-populations (demes) adapt by moving to a peak
  - If not at a peak, demes move to one or goes extinct
  - Only small populations could move through valleys to new peaks—hence small populations were the key to evolution
  - Competition both between organisms and between groups
  - Adaptive landscapes constantly changing due to:
    - External conditions
    - Activity of the organisms themselves



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## Fisher-Wright Dispute

- Fisher's and Wright's accounts make fundamentally different assumptions
  - Wright assumed that natural populations are sufficiently small, or divided into nearly isolated inbreeding groups
    - In such groups, genetic drift can be a critical factor
    - Natural selection one among several factors influencing evolution
  - Fisher assumed that natural populations are sufficiently large for Natural Selection to reliably promote the better adapted variants
    - Natural Selection is the overwhelming determiner of the course of evolution
- The conflict between Fisher and Wright turns on which mathematical model better describes our world
  - Each makes assumptions: the challenge is to determine which assumptions better fit the world
  - Settling this is not a job for theorists but researchers investigating natural populations

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## Field Studies of Evolution



- Russian tradition initiated by Chetverikov and continued by Dubinin studied large wild populations of *Drosophila melanogaster* collected in the Caucasus
  - Found large percentage (16%) of recessive lethals on 2<sup>nd</sup> chromosome
  - Natural populations are loaded with hidden genetic variability—population's *gene pool*
  - Since much of it is lethal, referred to as *genetic load*

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## From Theory to Field: Theodosius Dobzhansky



- Brought the Russian tradition to the US
- Unlike his more mathematically inspired predecessors, Dobzhansky's focus was the field (also true of Ernst Mayr and G. Ledyard Stebbins and of paleontologist G. G. Simpson)
- From the field he derived a very strong impression of both diversity and the adaptiveness of diverse forms to local circumstances
- Recognized the importance of variability:
  - "... the accumulation of germinal changes in the population of genotypes is . . . a necessity if the species is to preserve its evolutionary plasticity. . . . The environment is in a constant state of flux, and its changes...make the genotypes of the past generations no longer fit. . . . Hence the necessity for the species to possess at all times a store of concealed, potential, variability."

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## From Drift to Selection

- In 1937 (*Genetics and the Origin of Species*) Dobzhansky viewed much of the variability as non-adaptive and thus likely due to drift
  - Defined evolution as "a change in the frequency of an allele within a gene pool."
  - Emphasized isolating mechanisms for differentiating populations
- By 1951, he downplayed drift and emphasized selection
  - But a broadened conception of the power of selection not just in winnowing but in promoting particular traits
  - Result: balance selection—heterozygote superiority
- Increased emphasis on selection referred to as the "hardening" of the synthesis

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## Discussion Question

One of the questions confronting Darwin was how did Natural Selection results in new species. Has population genetics answered that question?

Yes. In large populations Natural Selection can drive populations to be sufficiently different that they no longer are parts of the same species

Yes. By allowing Natural Selection to remove some forms while promoting others, gaps emerge between populations that make them into different species

No. Natural selection in large populations will only lead to varieties, not new species. Something else is needed for generating species

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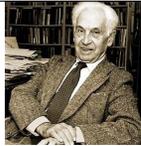
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## Geographic Isolation and Species



- From his field work with birds in New Guinea and the Solomon Islands, Ernst Mayr began to focus on geographical factors that separated populations
  - Within isolated individual populations, Natural Selection could promote different traits—resulting in isolating mechanisms that kept the new populations from interbreeding
- Emphasized the view that species should be view as populations of varying individuals
  - Separated when individuals are no longer able to reproduce

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## Dobzhansky's Isolating Mechanisms

1. Premating or prezygotic mechanisms:
  - (a) Ecological or habitat isolation.  
The populations concerned occur in different habitats in the same general region.
  - (b) Seasonal or temporal isolation.  
Mating or flowering times occur at different seasons.
  - (c) Sexual or ethological isolation.  
No attraction between the sexes of different species.
  - (d) Mechanical isolation.  
Physical non-correspondance of the genitalia of the flower parts prevents copulation or the transfer of pollen.
  - (e) Isolation by different pollinators.  
In flowering plants, related species may be specialized to attract different insects as pollinators.
  - (f) Gametic isolation.  
Female and male gametes are not attracted to each other. In organisms with internal fertilization, the gametes of one species may be inviable in other species: sexual ducts.
2. Postmating or zygotic isolating mechanisms:
  - (g) Hybrid inviability.  
Hybrid zygotes have reduced viability.
  - (h) Hybrid sterility.  
The  $F_1$  hybrids of one sex or both sexes fail to produce functional gametes.
  - (i) Hybrid break down.  
The  $F_2$  or backcross hybrids have reduced viability.

## The Synthetic Theory of Evolution

- International Conference on Genetics, Paleontology, and Evolution, Princeton, 2-4 January, 1947



Dobzhansky

Wright Muller Mayr Haldane

## Clicker Question

What is meant by calling a biological trait an adaptation?

The trait serves to enable its bearer to leave more offspring

The trait serves to enable its bearer to live longer

The trait enables its bearer to better satisfy the constraints imposed by its local environment

The trait is present in current organisms as a result of being selected in previous generations

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## Challenging the Hardening of the Synthesis



- In 1979 Stephen J. Gould and Richard Lewontin issued a stinging critique of adaptationism
- Traits might be adaptive without being adaptations (i.e., without having been the object of natural selection)
- More generally, traits can evolve without being adaptations
  - As a result of being linked with other traits that are being selected
  - As conserved traits due to existing *bauplan*
  - As a result of developmental constraints
- Adaptationist explanations are often *just-so* stories
  - Typically they are not subjected to rigorous tests
  - When found to be false, they are quickly replaced with another purported adaptationist explanation

## Spandrels of San Marco

- Spandrels are an inevitable consequence of mounting a dome on top of rounded arches
  - Once spandrels existed, they became places on which to present art
  - BUT, they were not included in the design as a place to put art
- Contention: biological traits are often spandrels, not products of selection



## Discussion Question

Infidelity is a common characteristic of human relationships. What selection factors might have favored it? Pick your favorite story or propose another

It results in a more diverse range of combination of genes than if all relationships were monogamous

It provides opportunities for humans to re-evaluate their partner choice and find better fit partners with whom to have children

It helps promote a higher rate of reproduction given that people get tired of the same partner

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## Bringing Development Back



- Before he developed the chromosomal theory of inheritance, Morgan's focus was on development (a project to which he returned late in his career)
- The evolutionary synthesis downplayed the significance of development for understanding evolution
  - Development is the unfolding of the organism according to the program laid out in the genes
  - Any noise in the expression of genes does not affect the genes themselves
- In pointing to developmental constraints Gould and Lewontin pointed to a potential relevance of development to evolution
- This has given rise to Evolutionary Developmental Biology (Evo-Devo) and the even more radical Developmental Systems Theory

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## Susan Oyama: Developmental Systems Theory



- Genes and Natural Selection are not sufficient to understand evolution
  - Rather, one should make the organism, and the developmental processes it undergoes, central
- "If development is to reenter evolutionary theory, it should be development that integrates genes into organisms, and organisms into the many levels of the environment that enter into their ontogenetic construction" (p. 113).
- Developmental System:
  - "a mobile set of interacting influences and entities" comprising "all influences on development" at all levels, including the molecular, cellular, organismal, ecological, social and biogeographical (p. 72).

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## Genes Just Part of the Replicator Story



- Parity Thesis:
  - “any sense in which genes code for phenotypic traits, program development, or contain developmental information can be equally well applied to other factors required for development” (Griffiths and Gray, 2000)
- Intracellular resources required for development
  - Membranes to serve as templates for synthesizing new membranes from proteins
  - Mitochondria for energy
  - Chromatin marking system regulating transcription
  - Cytoplasmic chemical gradients

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## Genes Just Part of the Replicator Story - 2

- Extracellular resources required for development
  - Bush fires for eucalyptus trees
- But, according to orthodox Darwinism, these are not part of inheritance
- “In line with this theoretical role, developmental systems theory applies the concept of inheritance to any resource that is reliably present in successive generations, and is part of the explanation of why each generation resembles the last.”
- Developmental system is a integrated system in which resources are made available to the developing organism




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## Niche Construction

- The standard view has been that the environment exists and selects among organisms that compete with each other
- But organisms can also modify environments in ways that create opportunities for themselves
- The selection forces operative in an environment are partly a product of the organisms' activities
  - not just something preset for the organism




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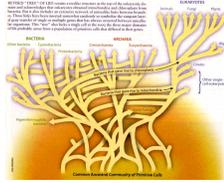
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## Promiscuous Genes

- Since Weismann in the late 19<sup>th</sup> century, the dominant view has been that genetic material is transferred only vertically from parents to offspring
- In bacteria, however, lateral gene transfer—transfer of genes from one organism to another is coming to be recognized as quite common
- It appears likely that eukaryotic cells (cells with internal organelles such as a nucleus and mitochondria) resulted from the combining of two prokaryotes (one becoming the mitochondrion or the chloroplast)
- This raises serious problems for the tree of life and accounts of evolution emphasizing transmission of genes from parents to offspring



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