

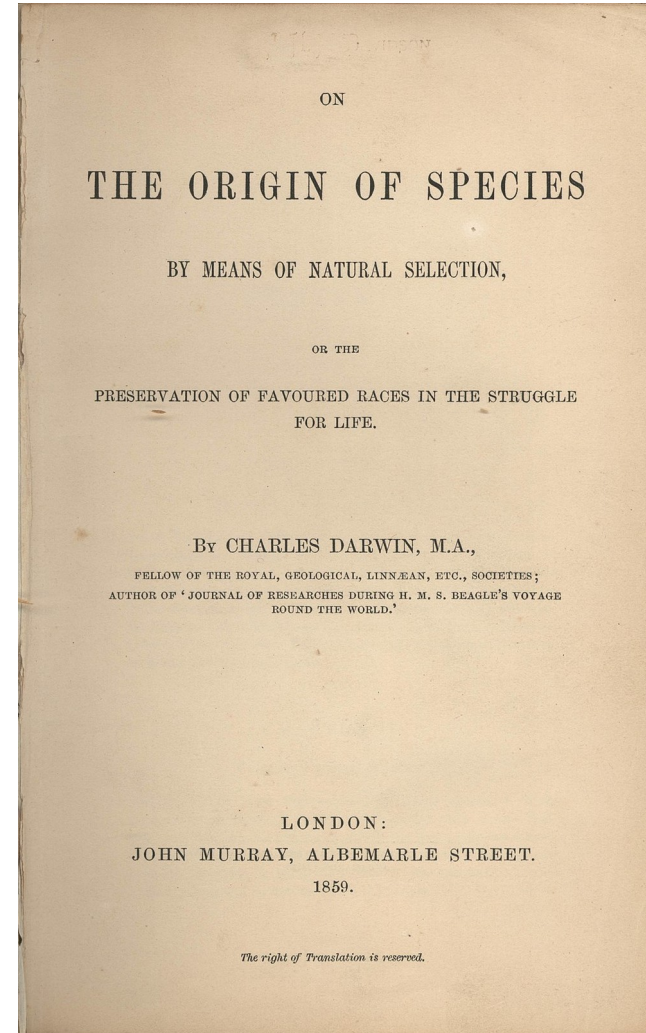
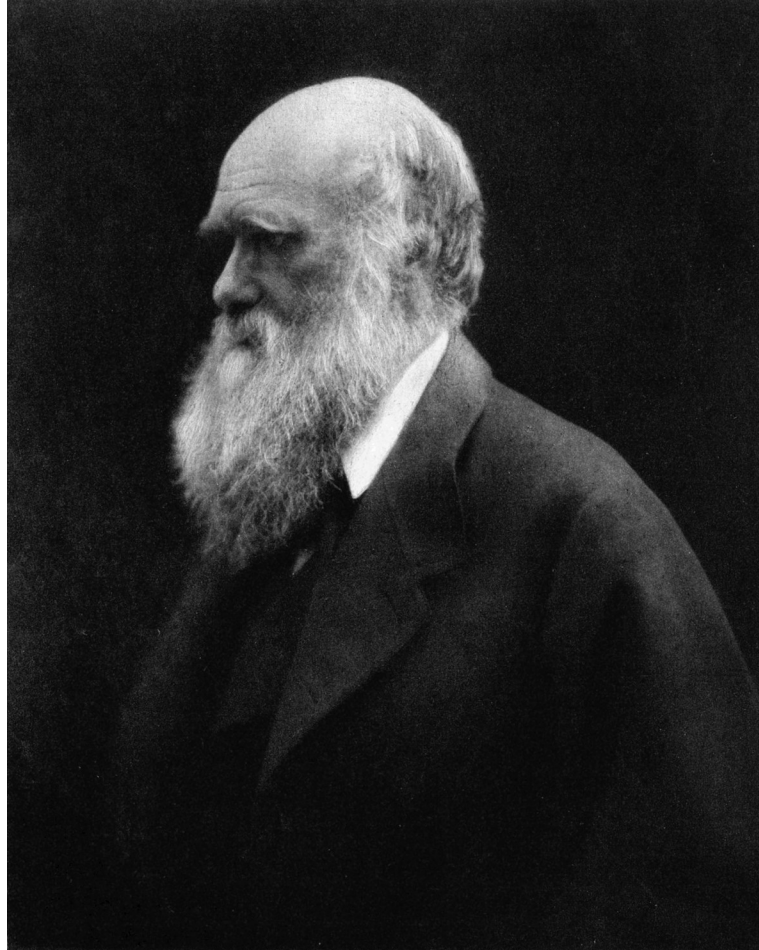
Are 165 years of adaptationism enough?

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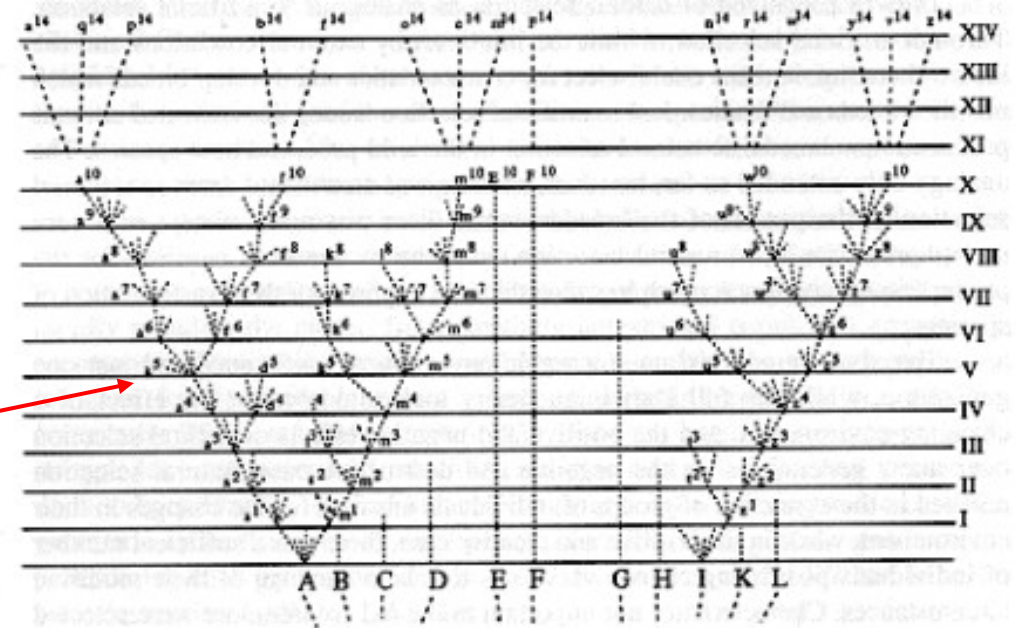


November 2024: 165 years since *The Origin of Species*



The Darwinian core of 1859 - variation

- Relevant variation has an *infinitesimal* impact on the phenotype
- Variation is *ever-present* and *undirected*
- Variation is *not reduced* by selection
- No clear distinction between *speciation* and *adaptation*



Natural selection as a *creative process*

- ***If*** variation is infinitesimally small and undirected (like a clay) all evolution is guided by natural selection
- ***Therefore*** generative processes (“mutations”) are *irrelevant*
- The *sculptor/composer analogy*



Selection acts on an unlimited buffet of variation



If variation was limited...

We would have this...



Instead of this.



Adaptationism

How biologists see organisms



If the driver of evolutionary change is natural selection acting on malleable clay-like variation...

- Finalistic interpretations of the evolutionary process are difficult to avoid (*teleology*)
- Because every trait in organisms is the result of selection and, therefore, *must have an end (adaptationism)*

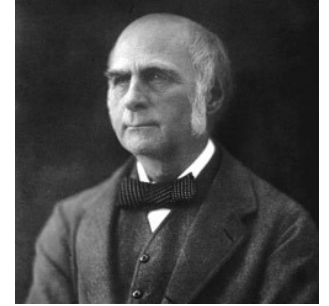
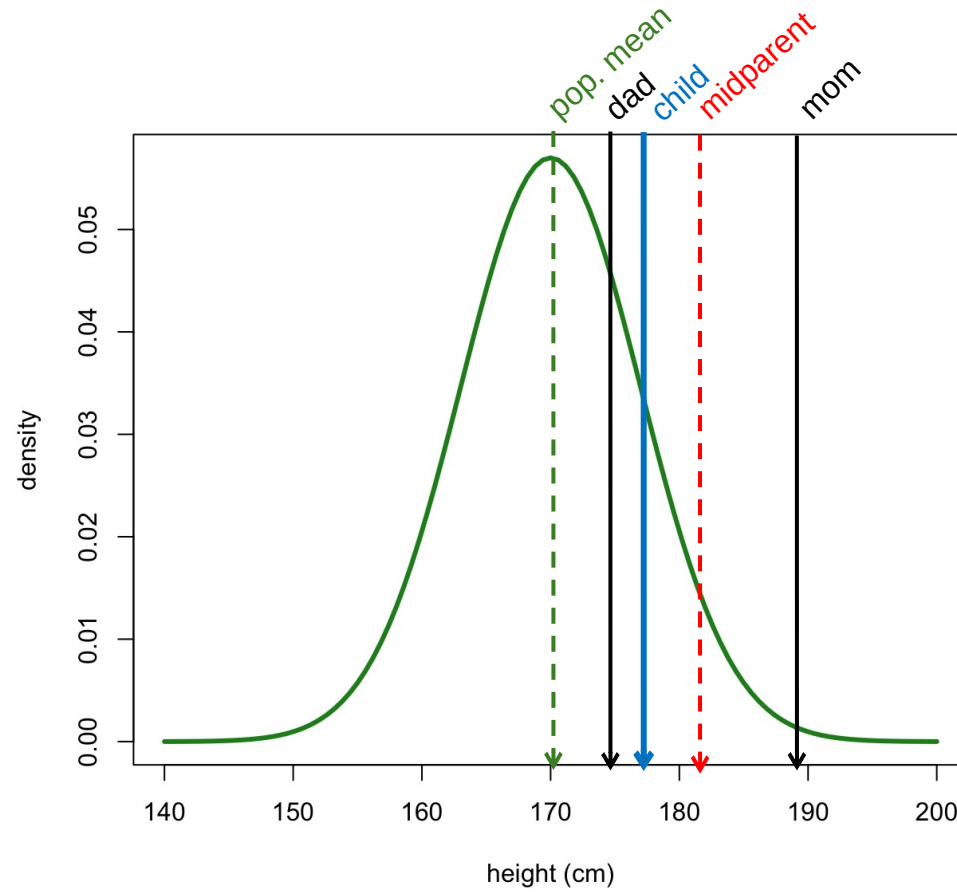
purposeful agent (natural selection)



amorphous matter (variation)

Darwinian theory was met with strong criticism by early geneticists: Galton

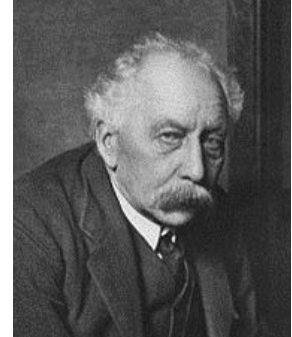
- Although Galton's works are pre-mendelian, he observed that traits tend to regress to the *population mean* in offspring
- It was as if the population mean acted like a magnet
- Thus, it would be much harder for natural selection to change traits



Francis Galton (1822-1911)

Criticisms by early geneticists: Bateson

- Bateson vigorously opsed the relevance of Darwin's infinitesimal hypothesis
- He also criticized the significance of adaptation



William Bateson (1861-1926)

"[...] I feel quite sure that we shall be rightly interpreting the facts of nature *if we cease to expect to find purposefulness* wherever we meet with definite structures or patterns."

Bateson, 1909

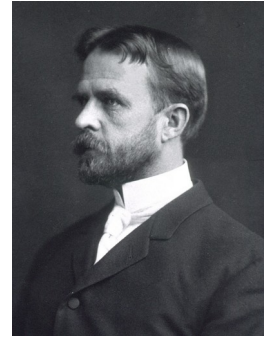
Criticisms by early geneticists: Morgan

- Morgan believed that adaptation had little scientific value

“There is a suspicion that morphologists, who have been the most ardent students of adaptation, *have often appealed to imaginary rather than known agencies in accounting for the evolution of adaptations.*”

Morgan, 1932

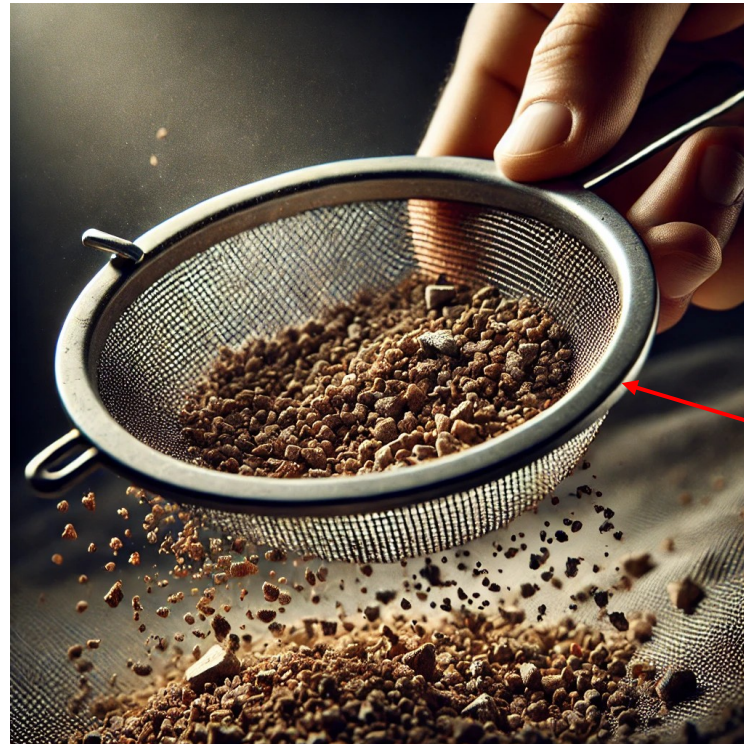
- He clearly understood that Darwinian evolution required variation to be directed by selection itself



Thomas Morgan (1866-1945)

Criticisms by early geneticists: de Vries

- Used the *sieve* as an analogy for natural selection
- Natural selection is simply an eliminatory process of the variation created (*negative selection*)

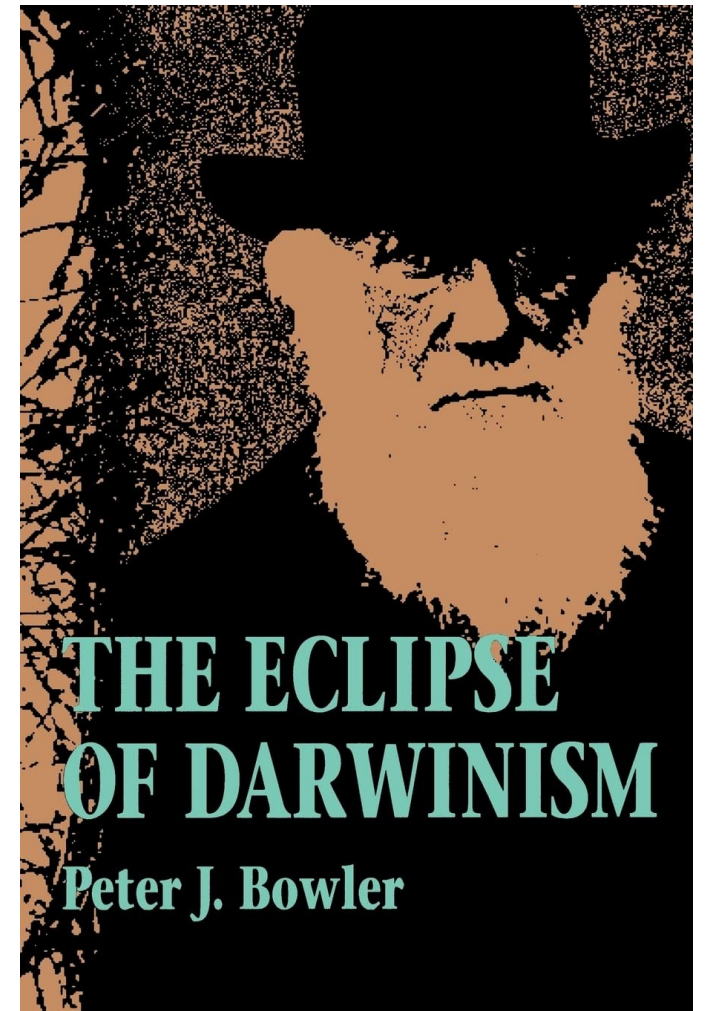


Hugo de Vries (1848-1935)

natural selection

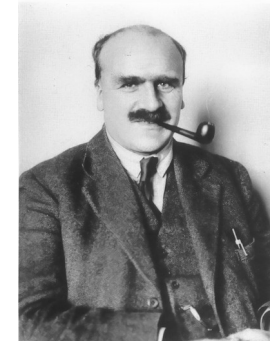
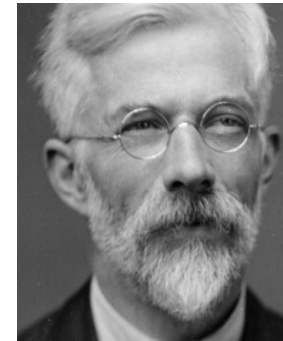
The “eclipse” of natural selection (1875-1930)

- The term was coined by Julian Huxley (1942) and later confirmed by historians of biology (Bowler, 1983)
- But who reintroduced natural selection as a creative agent?



Revival of natural selection in 1930s

- After the works by Fisher and Haldane:
 - Mathematically, it was shown that response to selection can be rapid
 - Even small differences in fitness can overcome mutation pressure
- Thus, *generative processes are secondary* in determining the rate of evolution



Ronald Fisher (1890-1962) John Haldane (1892-1964)

Evolutionary Synthesis resurrected the 'sculptor/composer' analogy

- Random mutations *provide* the raw material for evolutionary change by natural selection
- Mutations with small impact on the phenotype are more important (infinitesimal thinking)
- Thus, the primary driver of evolution is natural selection. *Selection initiates* evolutionary changes

This is the standard interpretation of the Synthesis

Incorrect hypotheses regarding the origin and inheritance of variation

- During 1930-1950, biologists had a limited understanding of the *processes generating variation* in populations
- Their models on the genotype-phenotype mapping were unrealistic
- No understanding of the molecular nature of evolutionary innovations

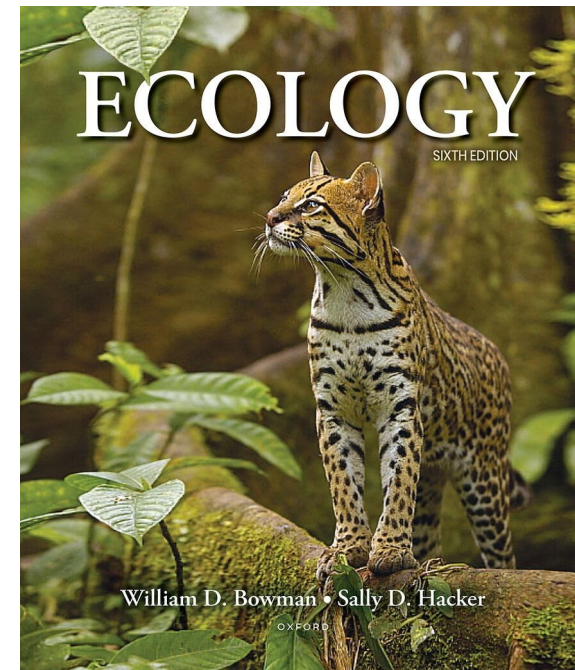
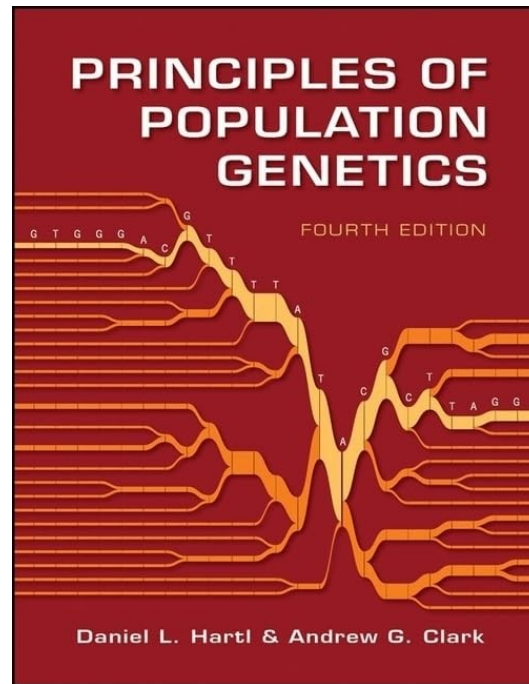
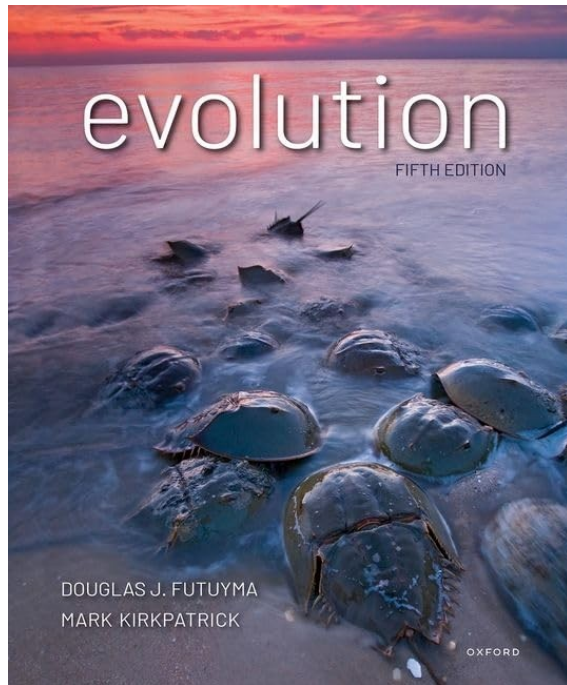


Ernst Mayr (1904-2005) T Dobzhansky (1900-1975)

"A temporary suspension of the mutation process, even if it could be brought about, would have no immediate effect on evolutionary plasticity. Rapidly evolving groups need not have high mutation rates, nor should evolutionary stasis be taken as evidence of insufficient mutability."

Dobzhansky, 1970

Yet, evolutionary biology textbooks still maintain this standard interpretation



The importance of *generative processes* and *constraints* (physico-chemical or structural) are secondary, at best

Does it explain the evolution of life on Earth?

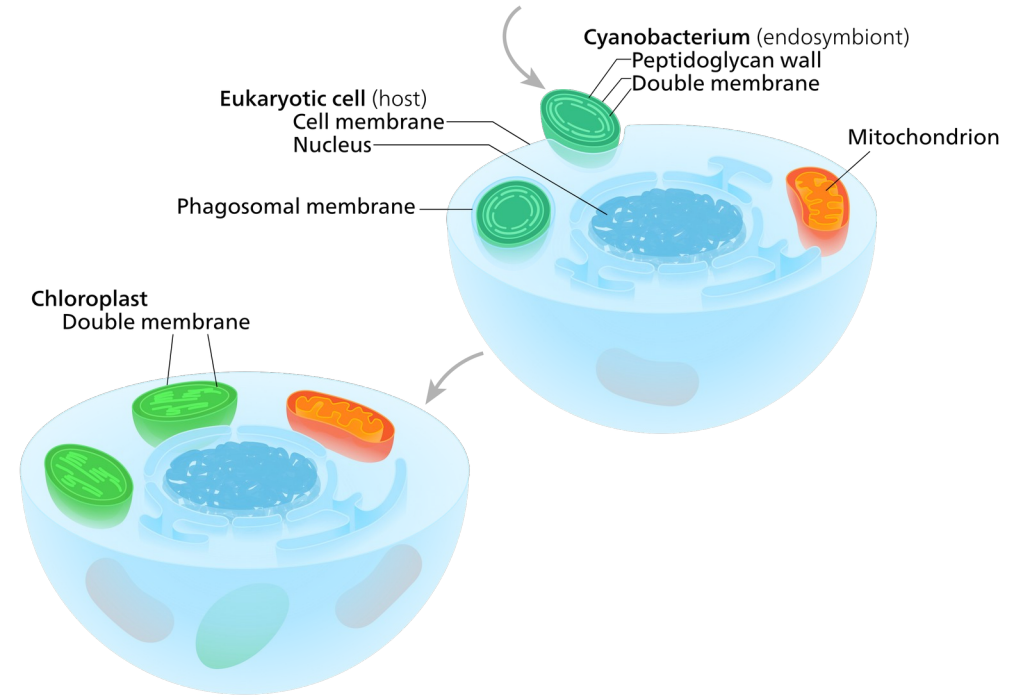
Generative processes across the ToL: Horizontal gene transfer

- HGT is so common in both Bacteria and Archaea that the concept of a fully dichotomous Tree of Life is blurred
- In prokaryotes, between 15% and 40% of the genome was not inherited vertically
- Several eukaryotic genes were acquired horizontally

The “statistical Tree of Life”

Generative processes across the ToL: symbiosis

- Endosymbiosis occurred *multiple times* during the evolution of life on Earth
 - Argard Archaea + Alphaproteobacteria
 - (Argard archaea + Alphaproteobacteria) + Cyanobacteria
- And it was not restricted to events over >1 billion years ago



Paulinella chromatophore

Primary symbiotic event ~90 Ma

These evolutionary novelties were not anticipated by the Synthesis

- These examples suggest that variation itself dictates the possible outcomes of the evolutionary process
- Natural selection was not creative agent, because variation had a primary role in initiating the change

natural selection



non clay-like
variation

Have we been blinded by adaptations ever since Darwin?

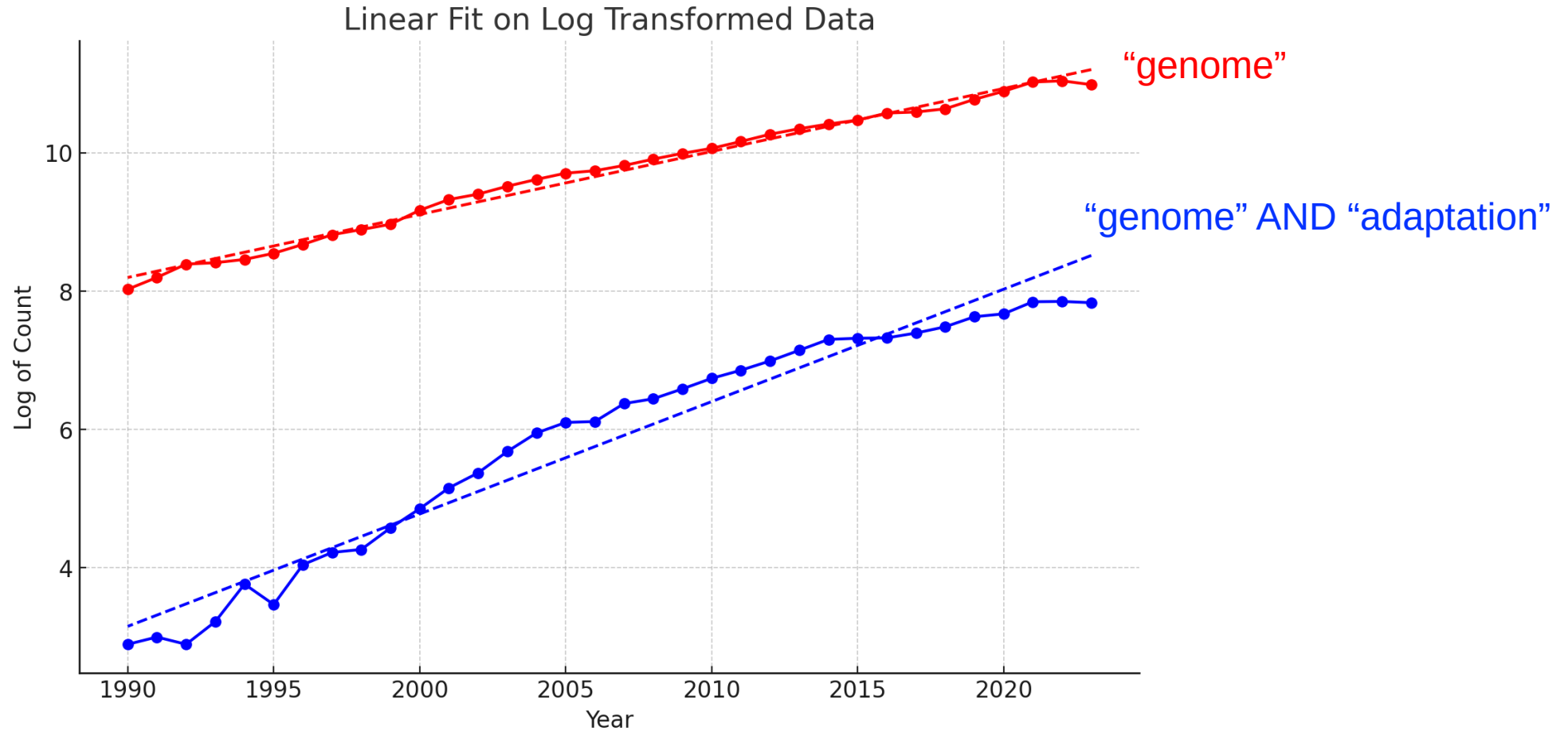
- Focus on adaptations makes evolutionary biology *the study of the things that have gone right*
- Little focus on what is deleterious, useless, historically contingent, physico-chemically constrained (*because, in principle, they should not exist – adaptationist view*)



perfectly sculpted organism

adaptationist view

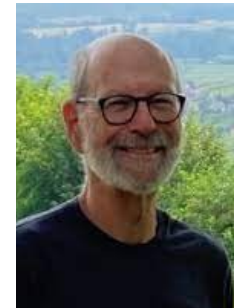
Maybe you are exaggerating a bit...



Source: Scopus, as of September 12th 2024

What is *adaptation*?

- Although common in everyday use, the term has multiple meanings. Sober has recognized at least three:
 1. Adaptation is simply a trait that resulted from the action of natural selection (pan-selectonism)
 2. Adaptation is a trait that was *selected for the same function* along *several generations* (historical)
 3. Adaptation is any trait that increases fitness (ahistorical)



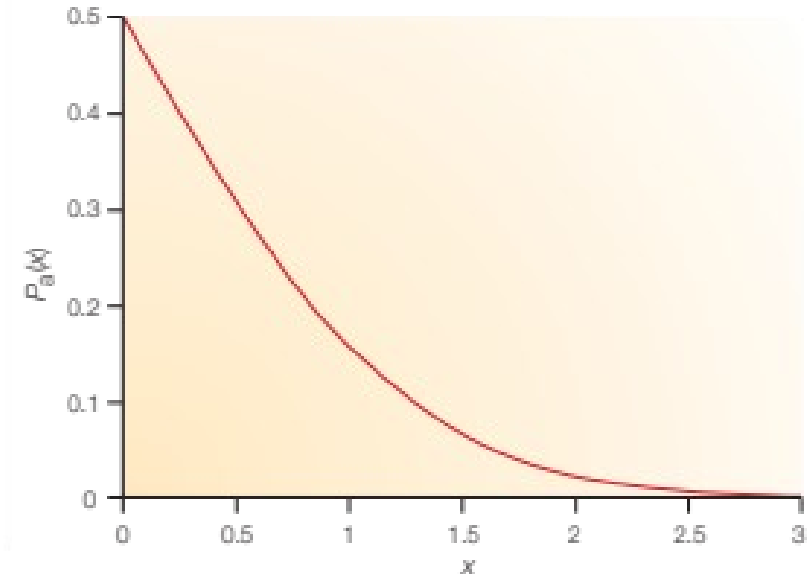
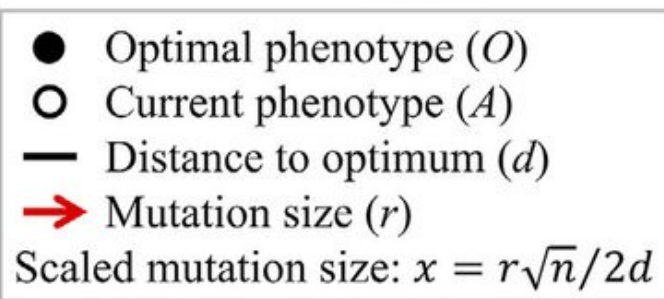
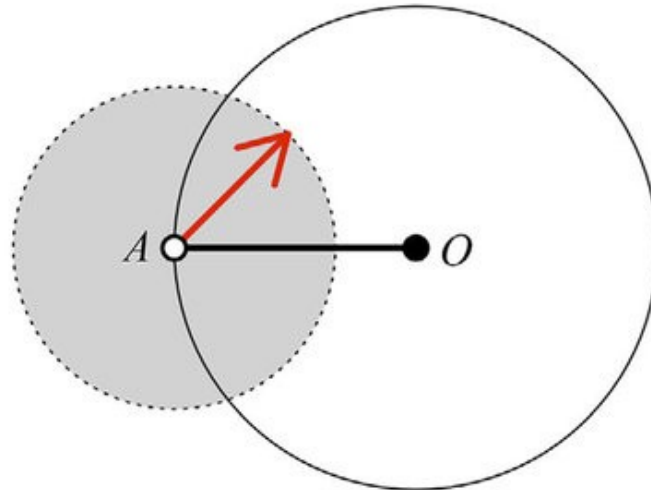
Genetics and the theory of adaptation

- In evolutionary genetics, the *historical* concept is widely adopted.
- Surprisingly, few theoretical studies has investigated the *genetics of adaptation*
- Famous exceptions include Fisher (1930), Kimura (1983) and Orr (1998)

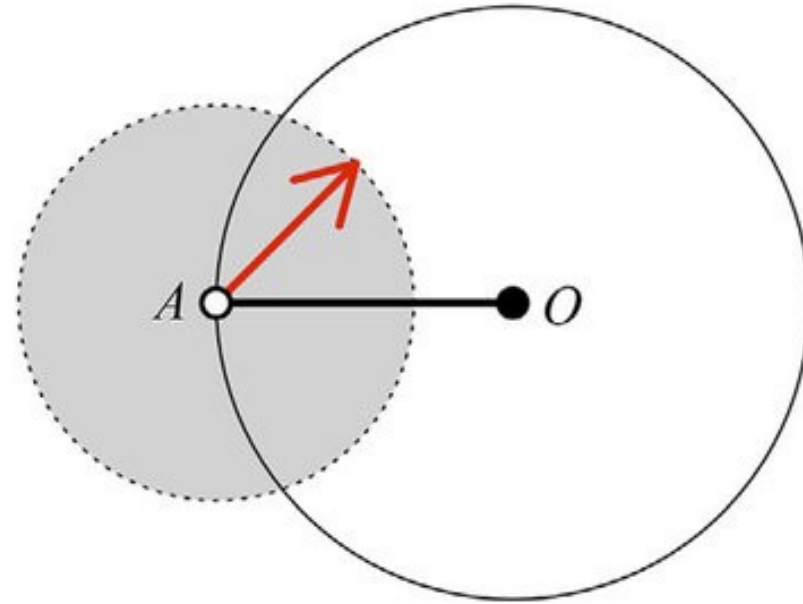


Fisher (1930) – Geometric model of adaptation (*Genetical Theory of Natural Selection*, pp. 38-41)

- The smaller the effect size of a mutation, the greater the probability of it contributing to *optimization*
- This should confirm Darwin's infinitesimal hypothesis



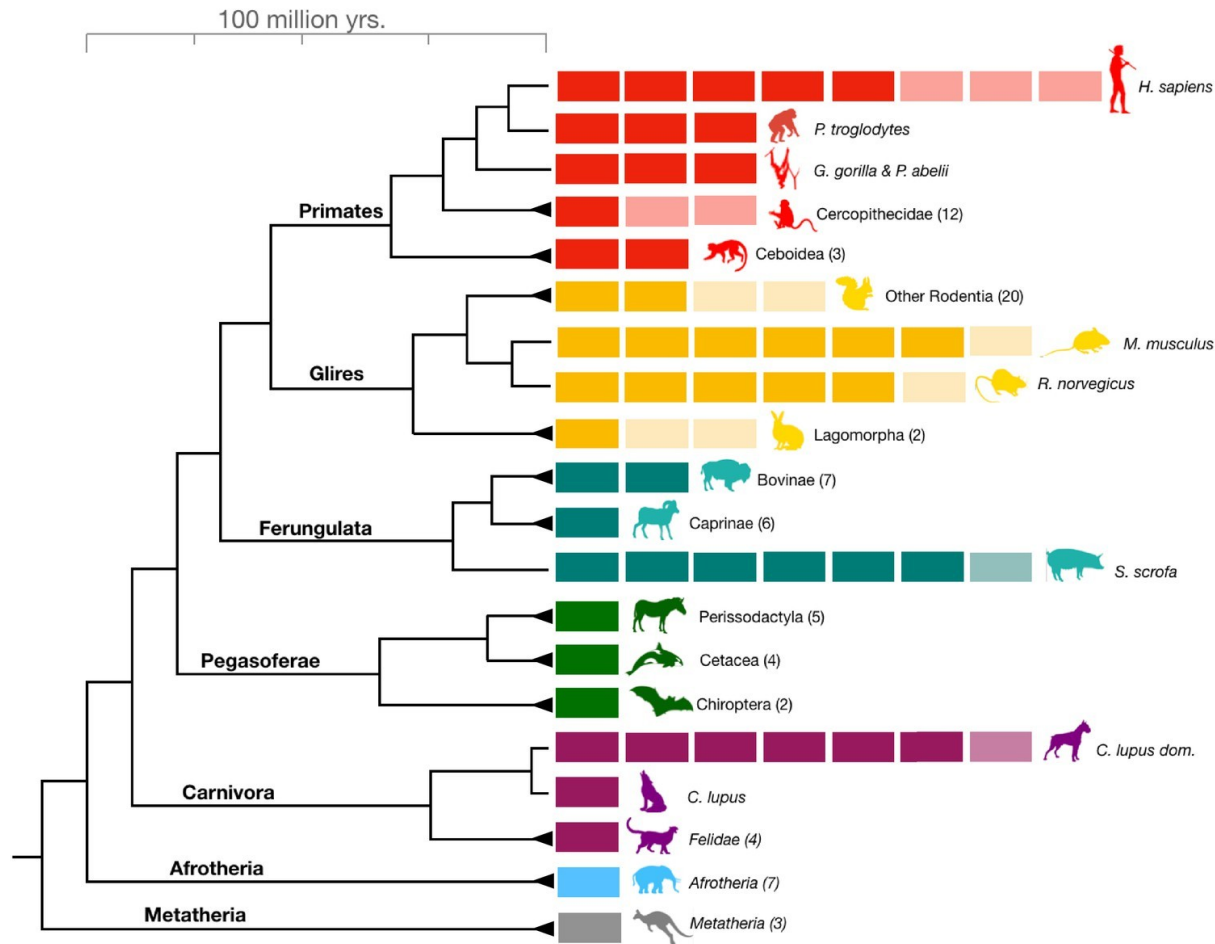
Genetics of adaptation – What does *optimal phenotype* mean?



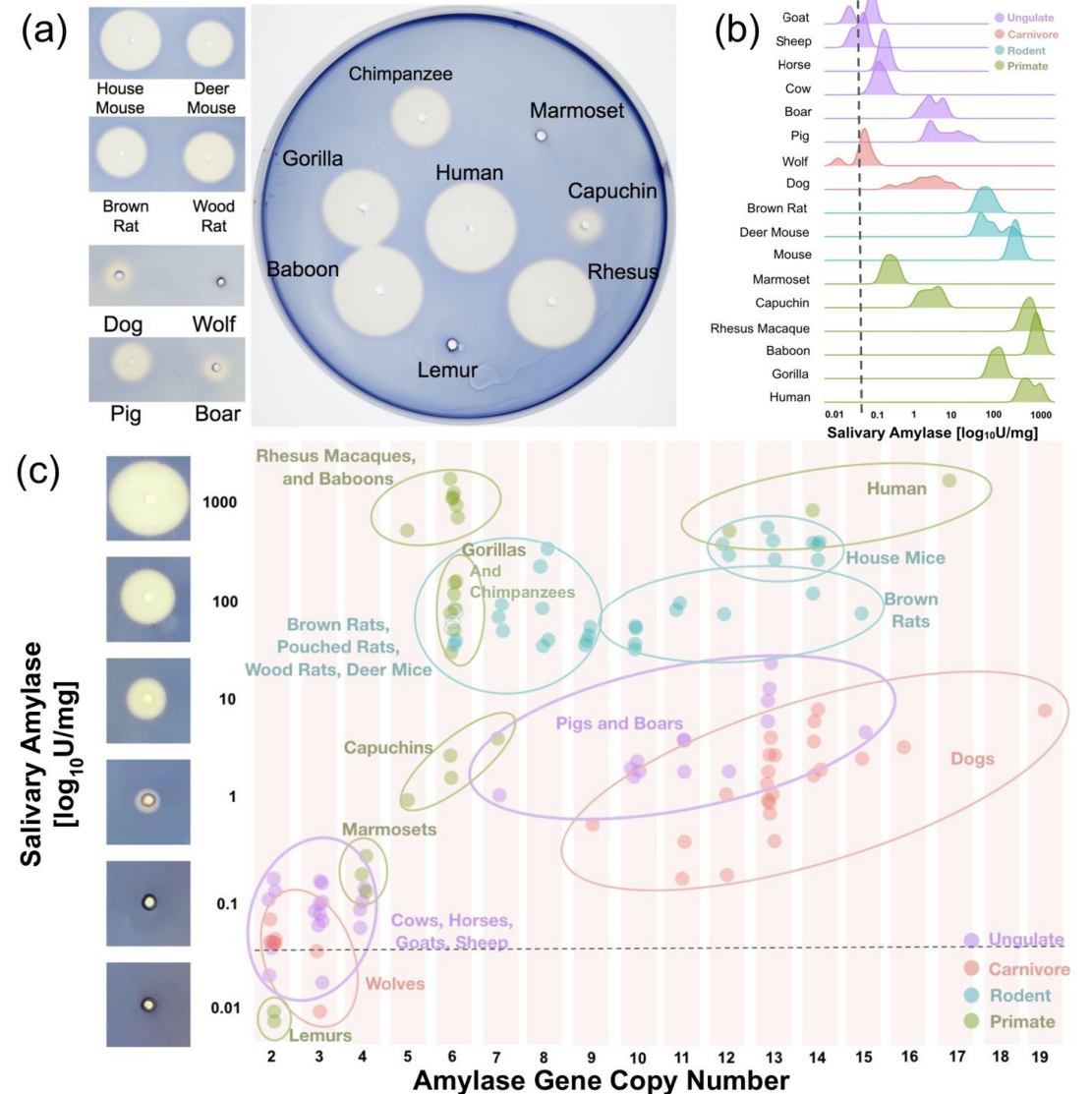
Is the future guiding the past?
(finalism)

- Optimal phenotype (O)
 - Current phenotype (A)
 - Distance to optimum (d)
 - Mutation size (r)
- Scaled mutation size: $x = r\sqrt{n}/2d$

Generative processes: *AMY1* gene – salivary amylase

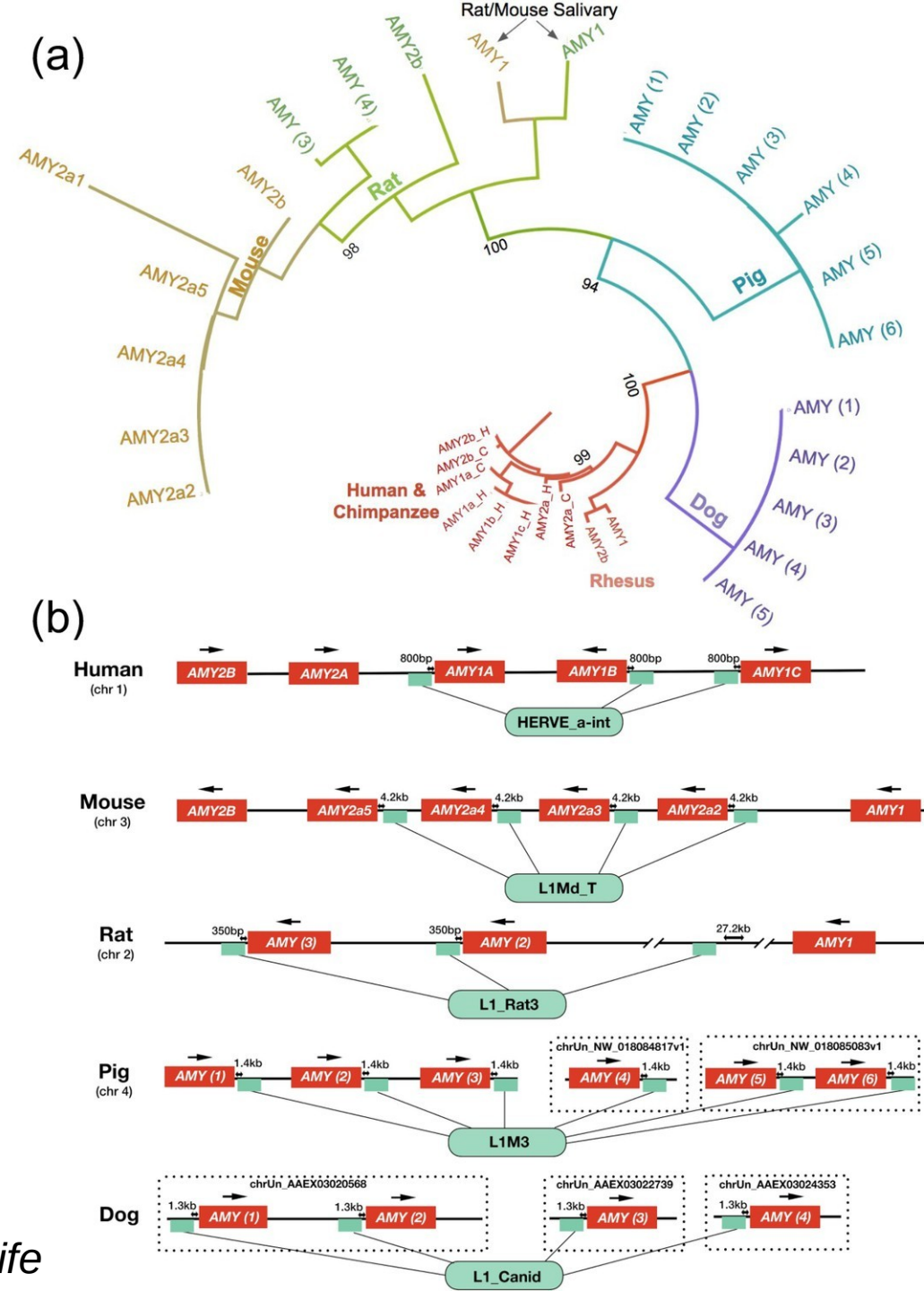


Pajic et al. (2019) *eLife*



But how?

- Salivary amylase gene duplication is facilitated by its genetic architecture
- Increased amylase function was enabled by retrotransposons
- Ignoring this makes AMY1 evolution appear teleological



Generative processes: p53 protein – the guardian of the genome

Peto's paradox: animals with larger bodies should not live longer due to a greater chance of developing cancer.

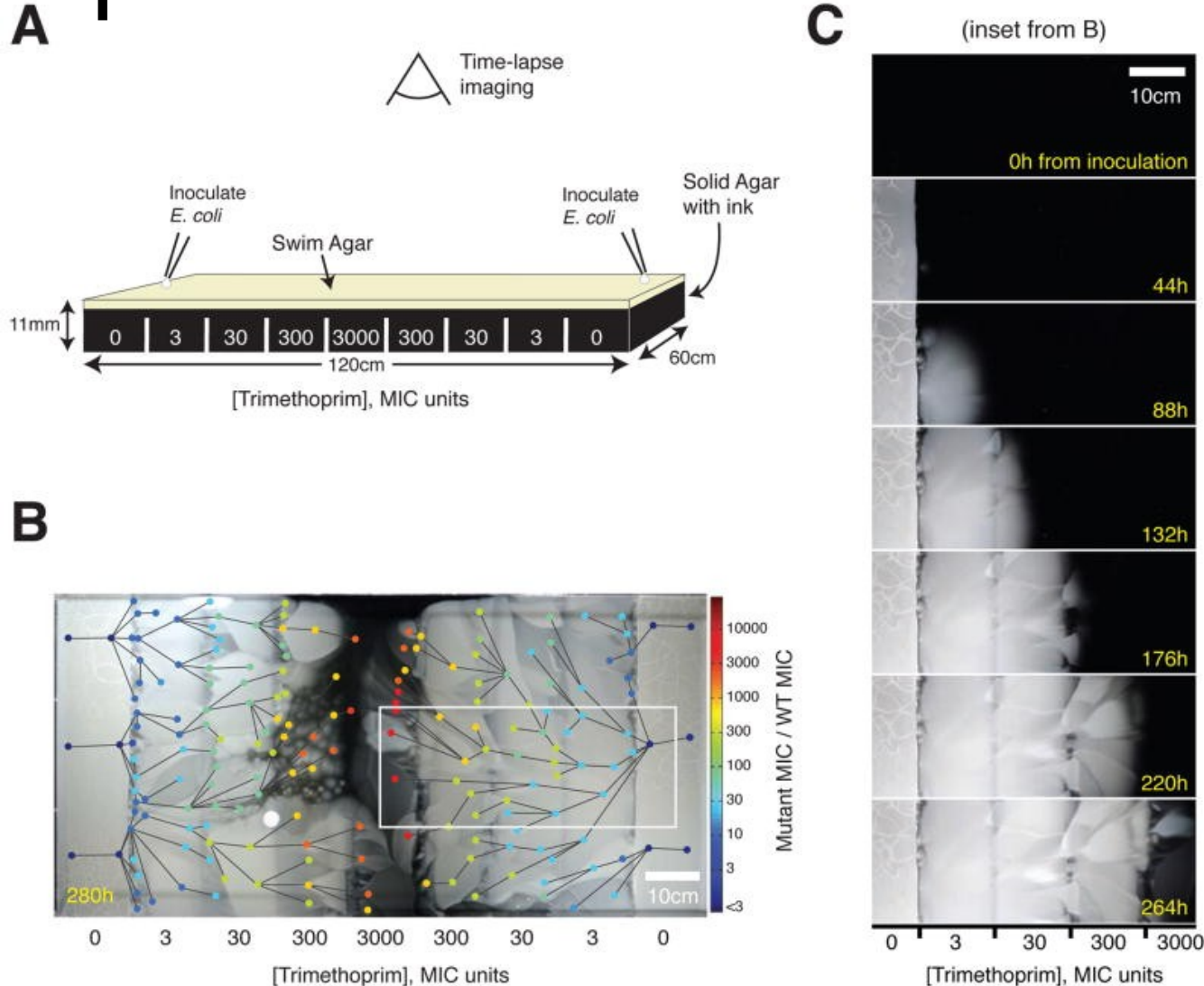
The p53 protein (*TP53* gene) halts the cell cycle when DNA damage is detected

However...

- Most copies are nonfunctional
- The largest living animal (blue whale) has a single copy of the TP53 gene
- The rate of retrogene insertion is higher in elephants (for every gene)
- Even if these extra copies are related to the larger bodies and lifespan of elephants, it is a consequence of higher retrogenization
- >17% of elephant genes have a copy number equal to or surpassing that of the *TP53* locus



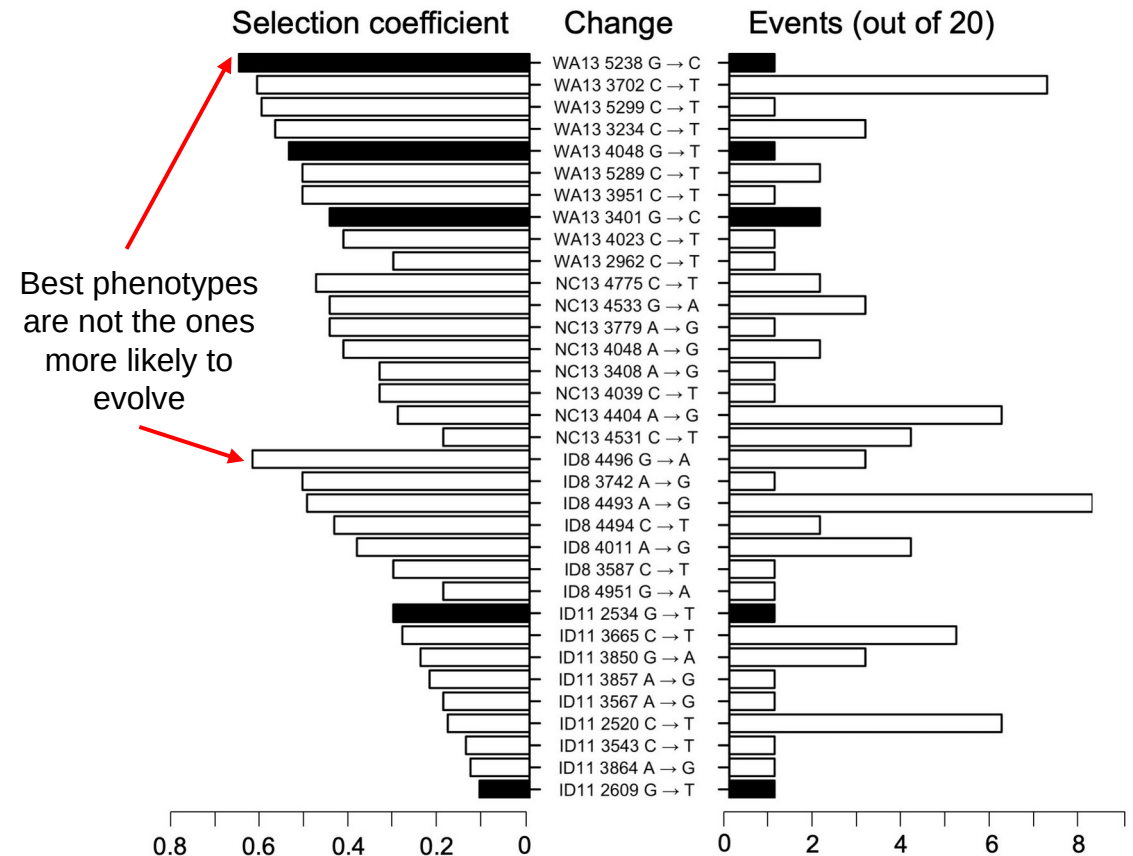
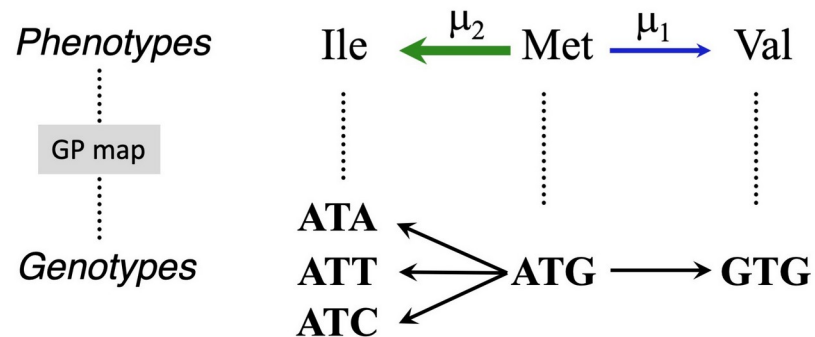
Time to evolutionary response depends on mutations



- The response to increasing antibiotic concentration had to wait for *de novo* mutations
- Some steps took longer than others
- Solutions differed between the two trials
- This is *not* expected under the interpretation of the Evol. Synth.

A “novel” highlighting the role of mutations: arrival-biased and niche-filling evolution

- Some mutations are more likely than others (arrival-biased)
- This creates a *bias in the introduction of variation* and the possibilities of evolutionary change

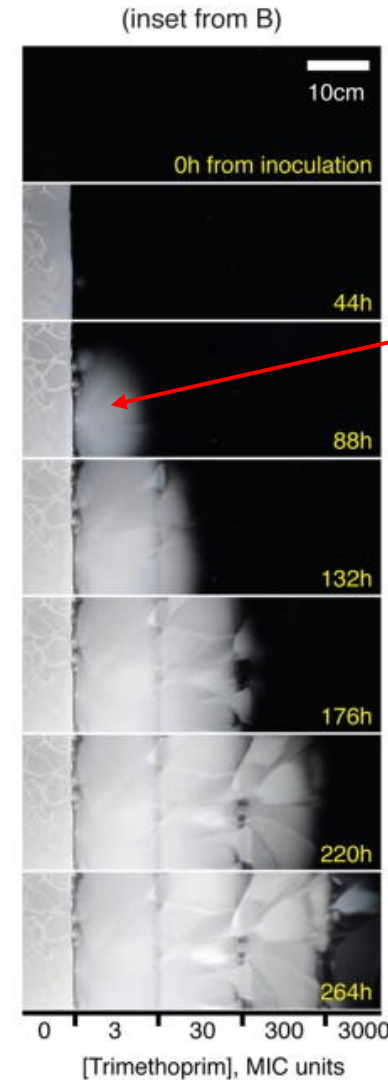


The niche-filling process



no building plan

Where can we go from here?



niche-filling

In this sense, evolution is mutation-driven

Why evolutionary biology “cancelled” the work of early geneticists?

- Early geneticists emphasized the role of mutations in evolution, particularly those with significant phenotypic impact
- These mutations are unique
- However, it was easier to model recurrent phenomena using infinitesimal effect mutations
- Modeling a historically contingent trajectory is more difficult



Adaptationism leaves evolutionary biology without *first principles*

the usual question in papers:

What has occurred since the organism needed this?

- By understanding the molecular basis of the various types of variation and their physical constraints, evolutionary analysis can be build on first principles

Given these properties (first principles), what can possibly occur?

Silver linings

- Technical developments (raw data)
 - High-throughput sequencing
- New methodological approaches
 - Mathematical models that incorporate arrival-bias and physical constraints
- New aims
 - Focus on understanding variation and its origin (similar to early geneticists)



Thanks to



Laboratório de
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