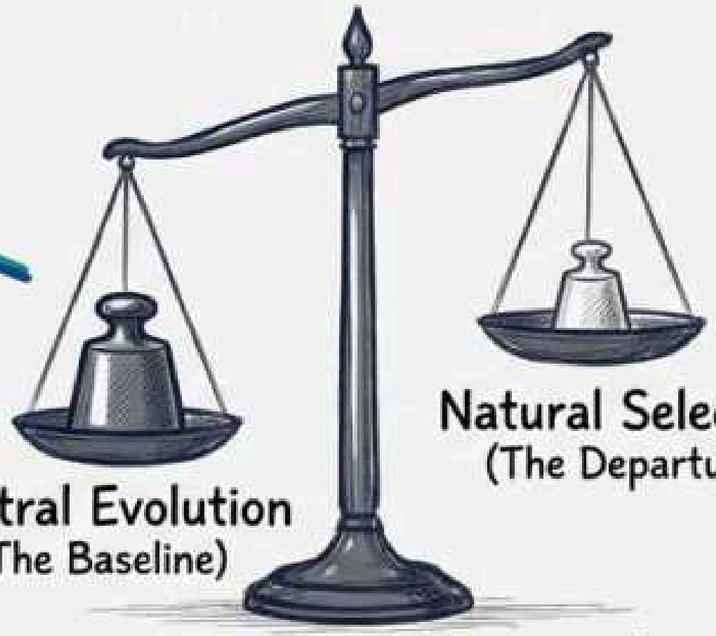
Detecting Natural Selection: The Three Arenas

¶ 4.1

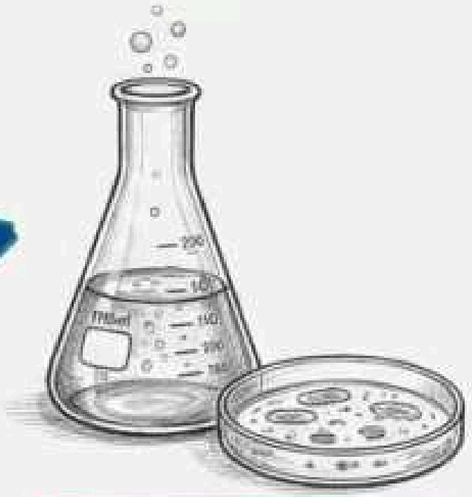


The Wild



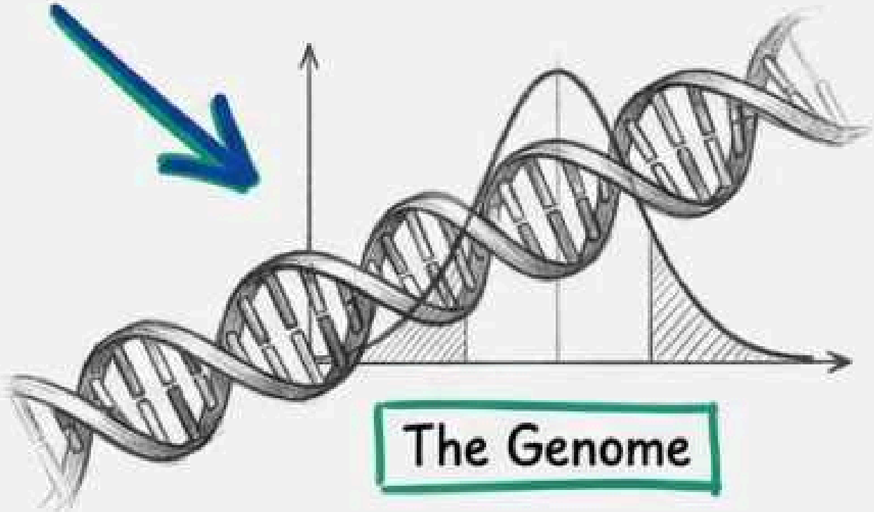
Neutral Evolution
(The Baseline)

Natural Selection
(The Departure)



The Laboratory

Claiming a trait was shaped by selection requires evidence. We must find its signature by observing departures from the neutral baseline.



The Genome

Observation in the Wild: The Daphne Major Drought

¶ 4.2

[Study begun by Peter & Rosemary Grant (1973) on a tiny Galapagos island.]

Pre-1977





1977: Severe Drought



Post-1977

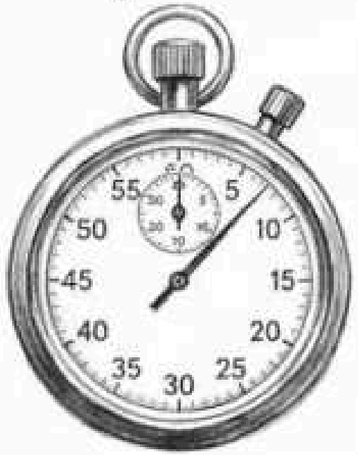


Birds with deeper beaks survived better →
Next generation had measurably deeper beaks.

Triangulating Darwin's Finches

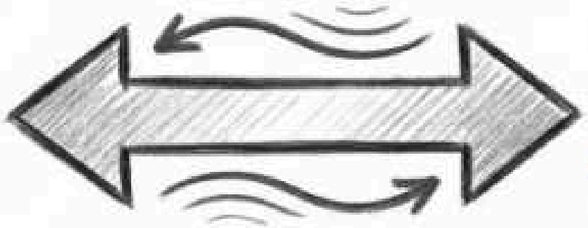
¶ 4.3

Speed



Selection can be measured in a single generation.

Direction



Selection can change direction (later wet years favored smaller beaks).

Mechanism



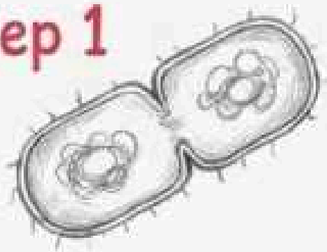
Because beak size is heritable, selection causes evolutionary change.

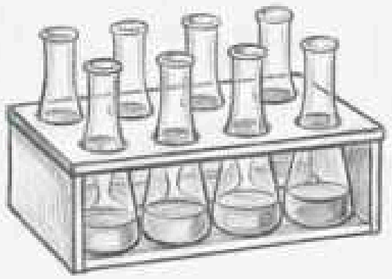
Decades of data turned these finches into the textbook example of evolution observed in action.

The Living Fossil Record

¶ 4.4

Step 1





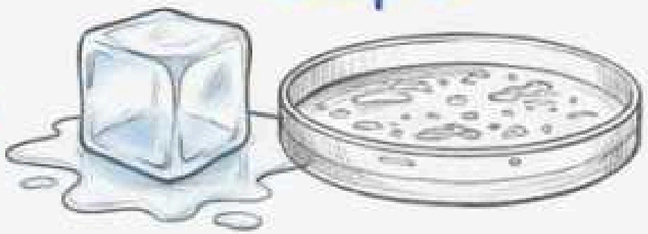
Richard Lenski's Long-Term Evolution Experiment, begun 1988

Step 2

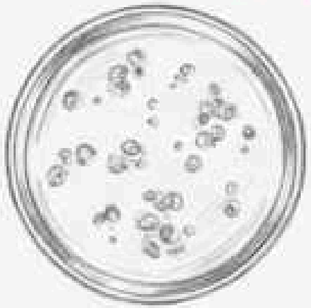


Samples frozen every 500 generations

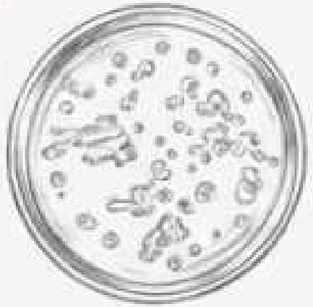
Step 3



Step 4



Ancestor

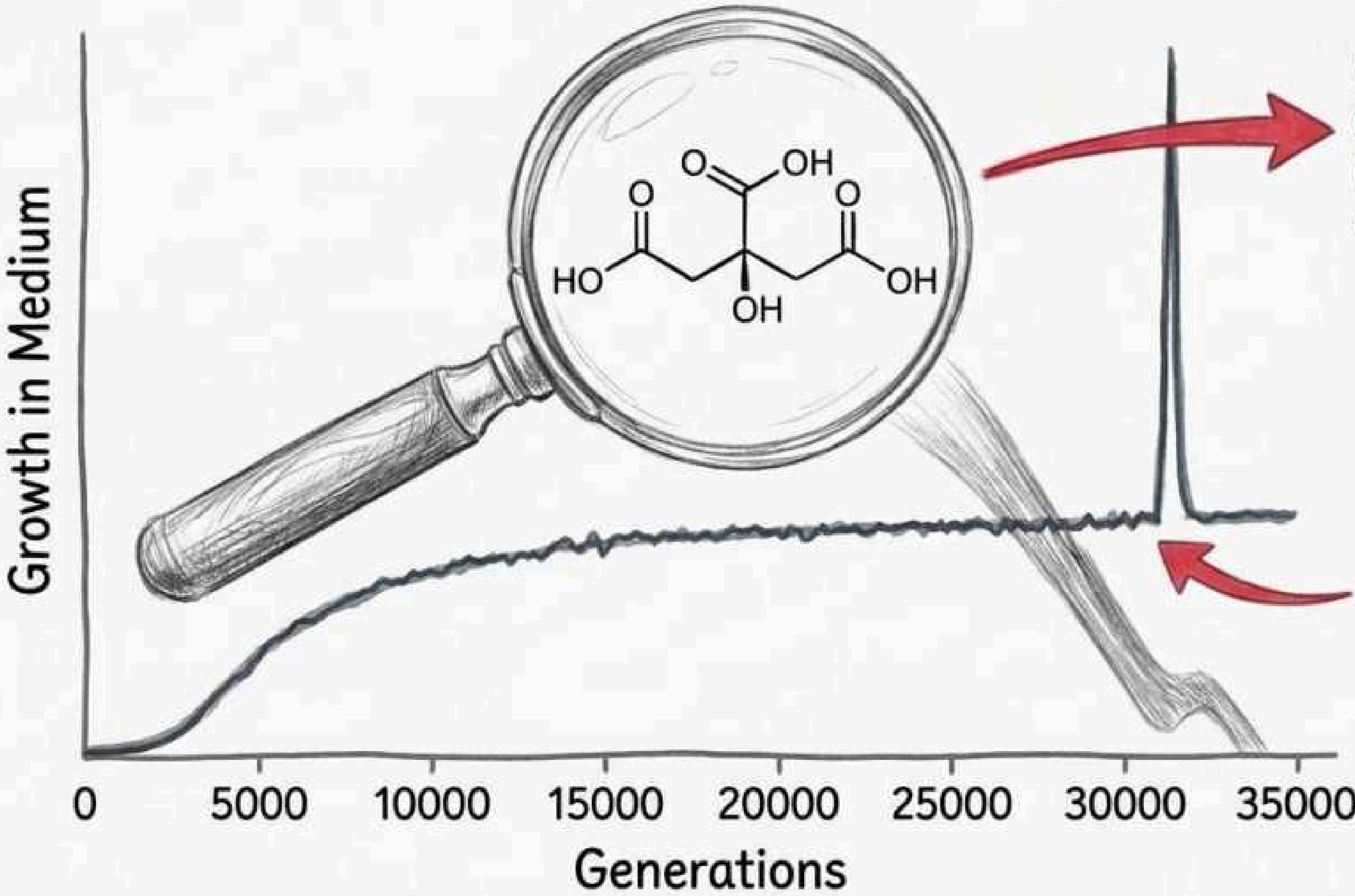


Descendant

Because frozen bacteria can be revived, researchers can compare ancestors and descendants side by side.

The Citrate Breakthrough

¶ 4.5



E. coli evolved the ability to use citrate (a chemical they normally cannot use in oxygen).

Dependent on earlier, potentiating mutations (Zachary Blount et al., 2008) — discovered by replaying evolution from frozen samples.

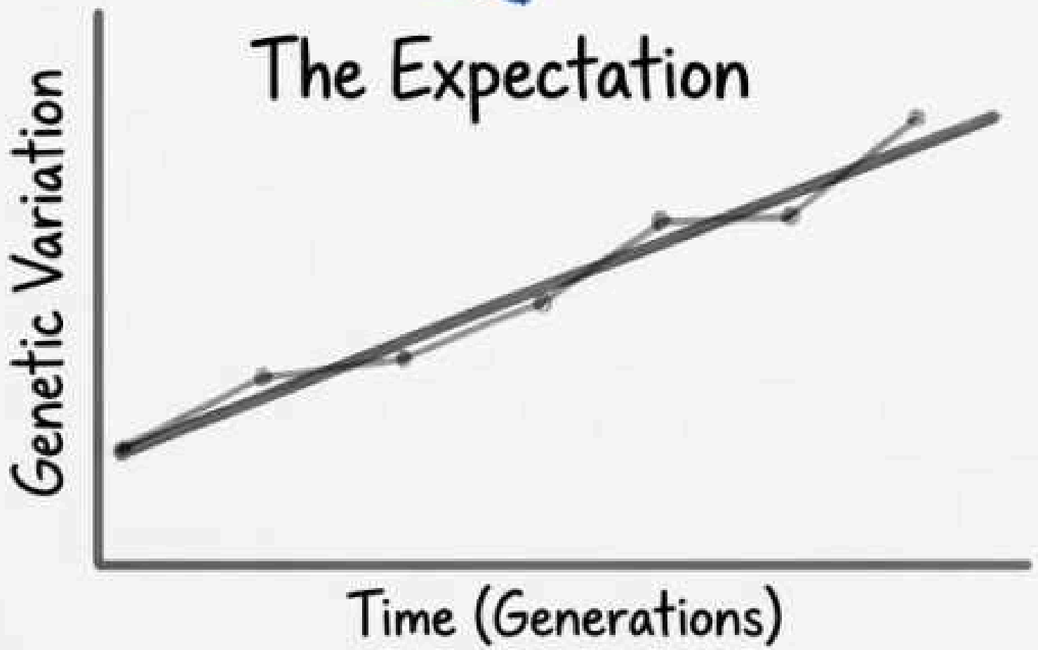
Defining the Neutral Baseline

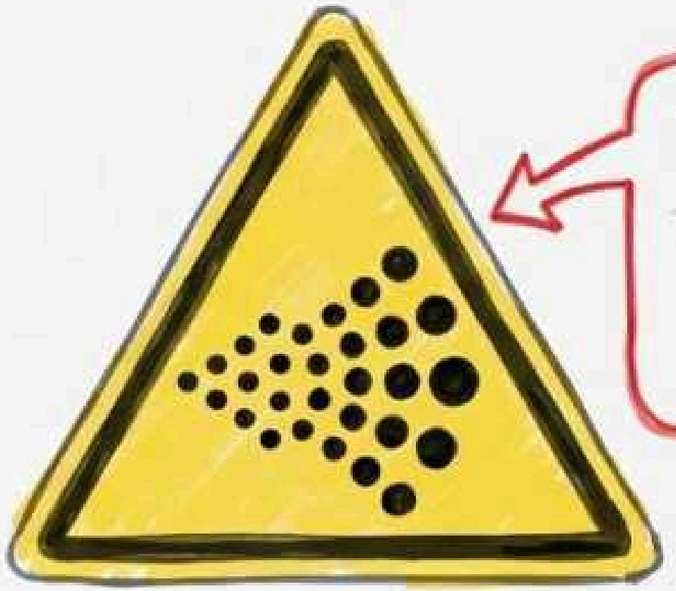
¶ 4.6

Mutation + Genetic Drift = Neutral Theory

Under neutral theory, patterns of genetic variation within and between species can be predicted.

The Expectation





CAUTION: Changes in population size can mimic the departures caused by selection. Tests must be interpreted carefully.

The Anatomy of a Mutation: Synonymous vs. Nonsynonymous

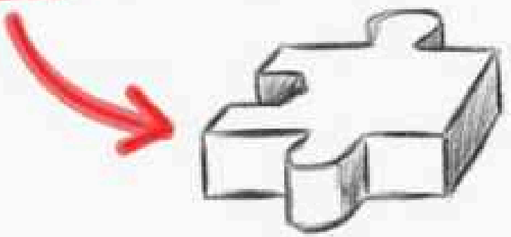
¶ 4.7

T-A-C-G-A-T-T-C-C-G-T



Synonymous (dS) → Mostly neutral, provides the baseline.

T-A-C-G-A-T-T-C-C-G-T



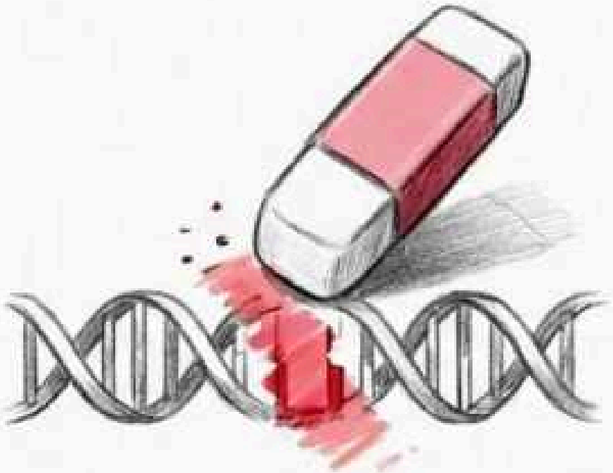
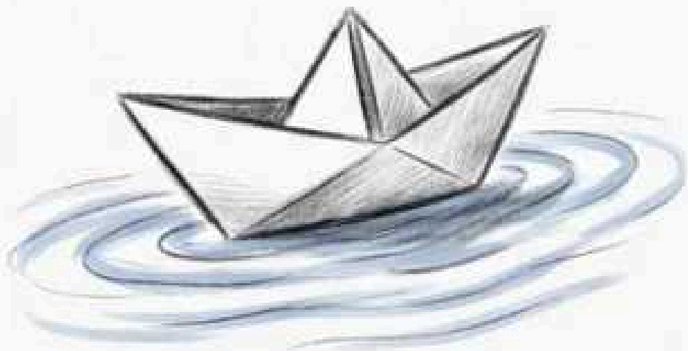
Nonsynonymous (dN) → Changes the protein.

$$\omega = \frac{d_N}{d_S}$$

Biologists compare the rate of protein-changing mutations to silent mutations to find selection.

Decoding the Omega Ratio

¶ 4.8

$\omega < 1$	$\omega \approx 1$	$\omega > 1$
Purifying Selection	**Neutral Evolution**	**Positive Selection**
		
Protein changes are actively removed by selection. This is the typical pattern for most genes.	The protein is evolving neutrally, drifting without strong selective pressure.	Protein changes are being actively favored. Often seen in genes for immune defense and reproduction.

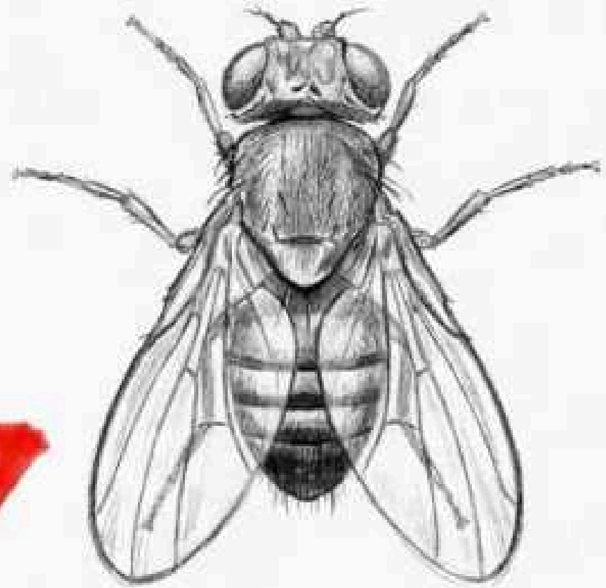
The McDonald-Kreitman (MK) Test

¶ 4.9

	Synonymous	Nonsynonymous
Within Species		Polymorphisms (P_n)
Between Species	Polymorphisms (P_s)	

Under neutrality, the ratio should be the same for both.

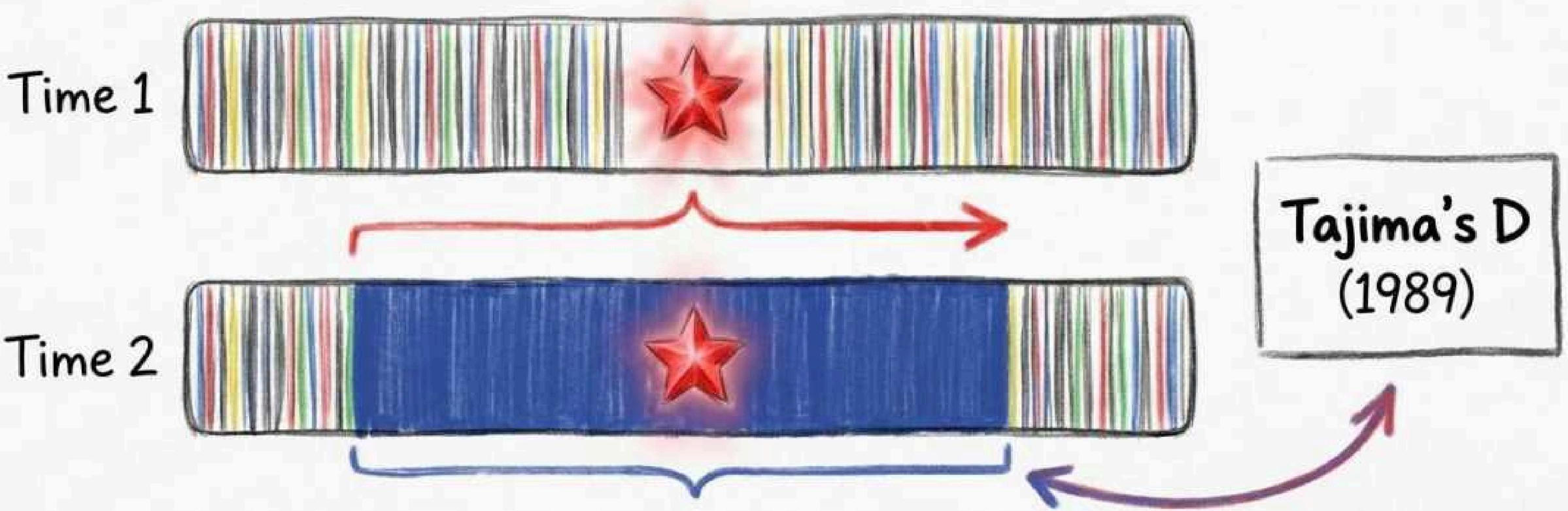
EXCESS



Proposed by John McDonald and Martin Kreitman in 1991. Finding an excess of nonsynonymous differences between species suggests positive selection drove those changes.

Selective Sweeps & Genetic Hitchhiking

¶ 4.10



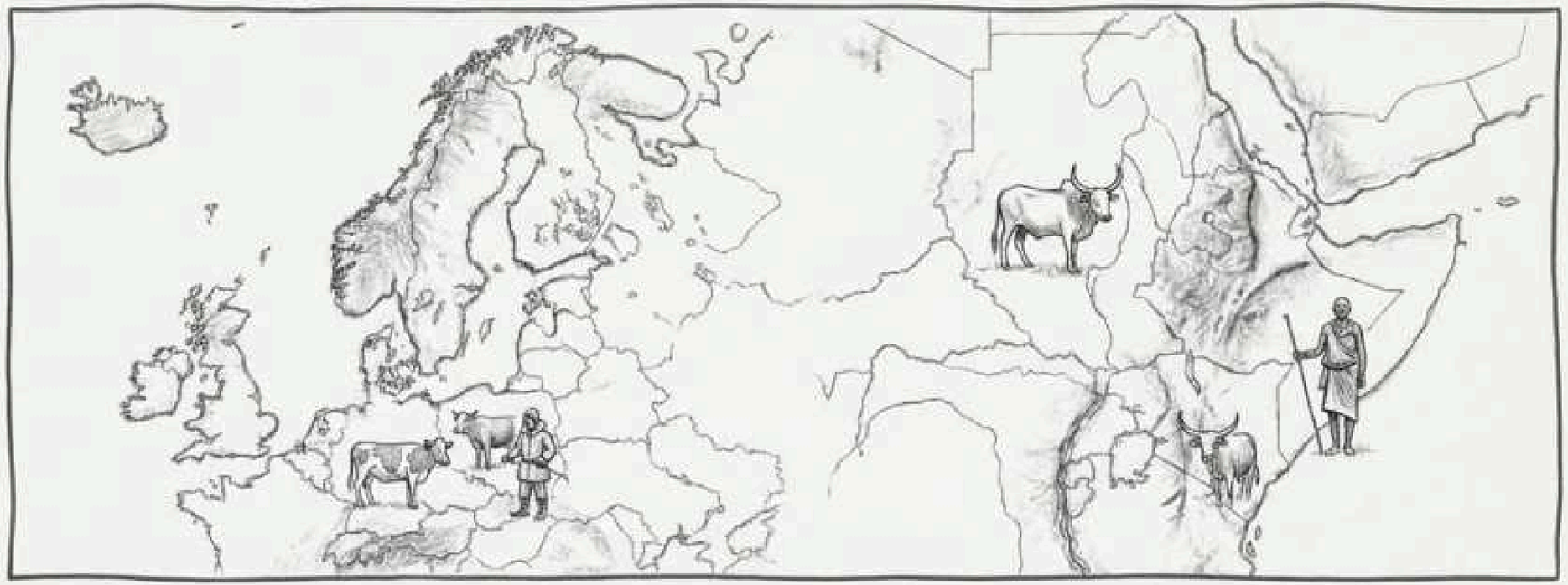
When a strongly favored mutation spreads quickly, it carries nearby DNA with it. The result is a Selective Sweep: a region with unusually low variation and an excess of rare variants.

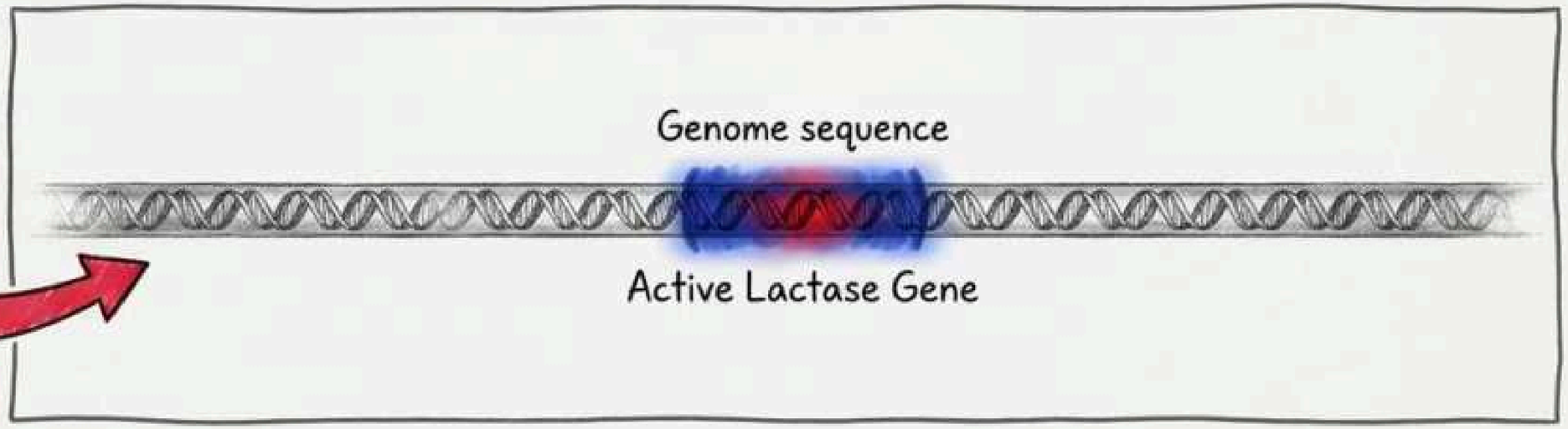
Note: Population growth can mimic this distortion.

Human Signatures: Lactase Persistence

¶ 4.11

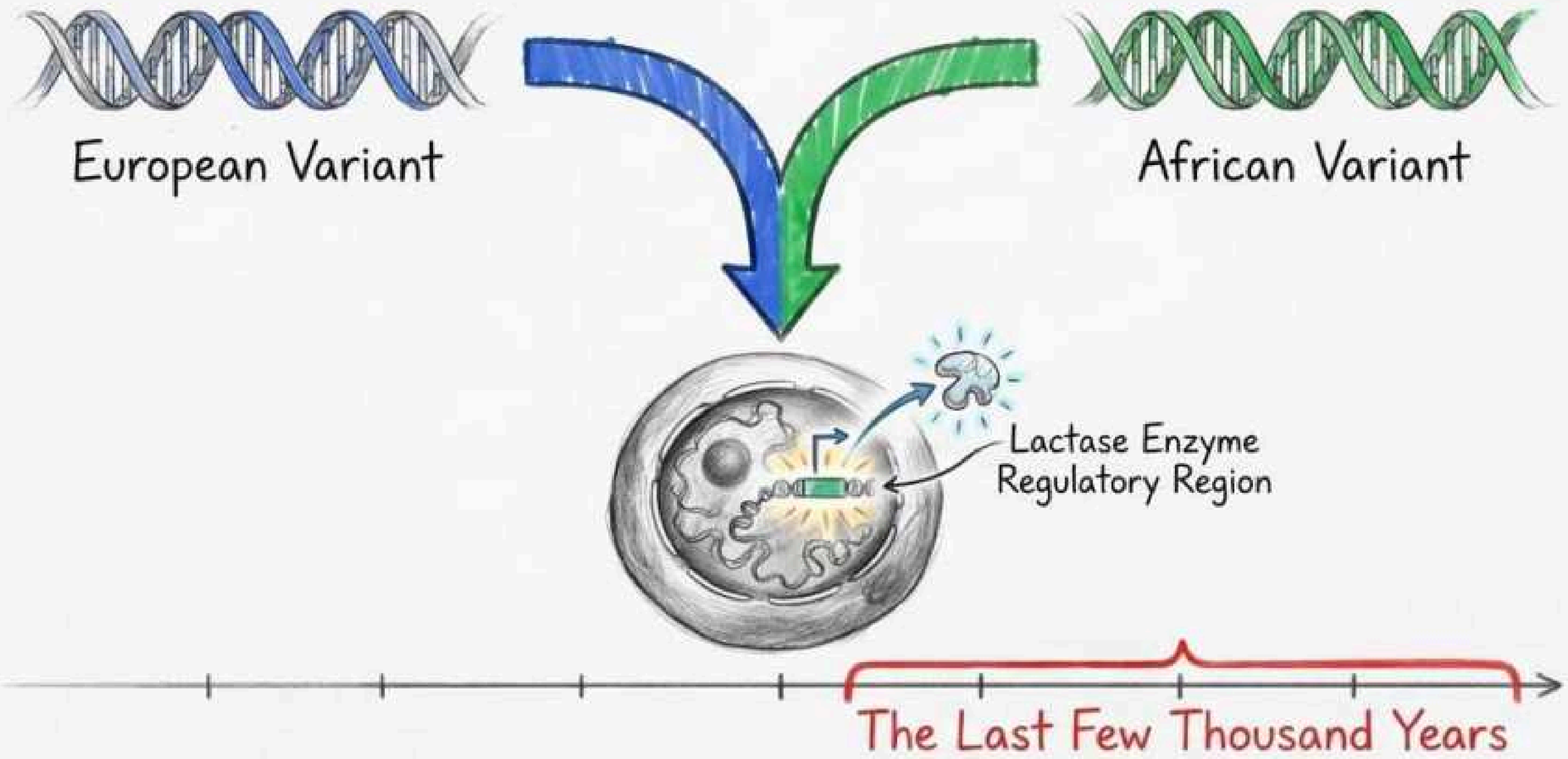
Most mammals lose the ability to digest milk sugar after weaning. In populations with a long history of dairy farming, variants keep the lactase gene active.





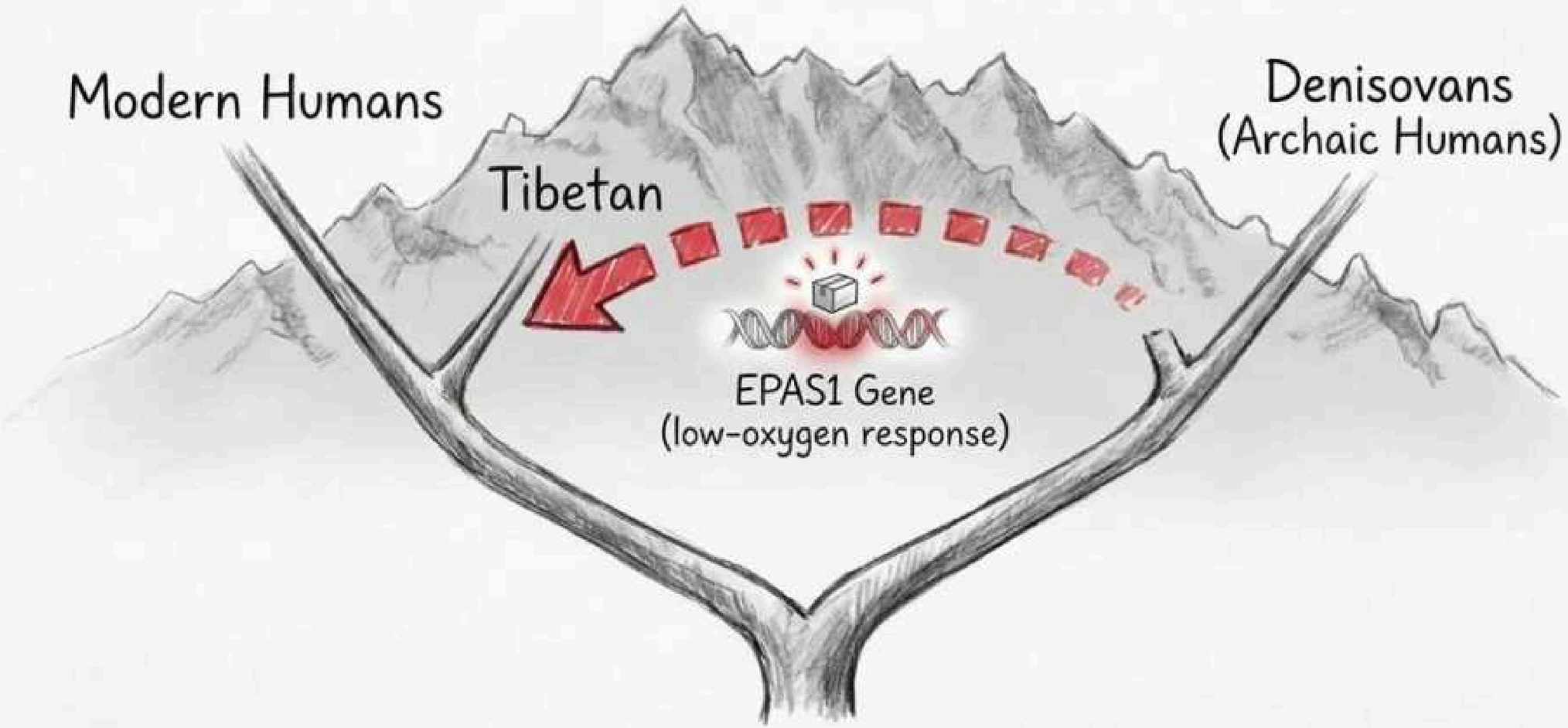
These variants sit on long stretches of unusually uniform DNA—the unmistakable mark of a recent selective sweep.

Molecular Convergent Evolution



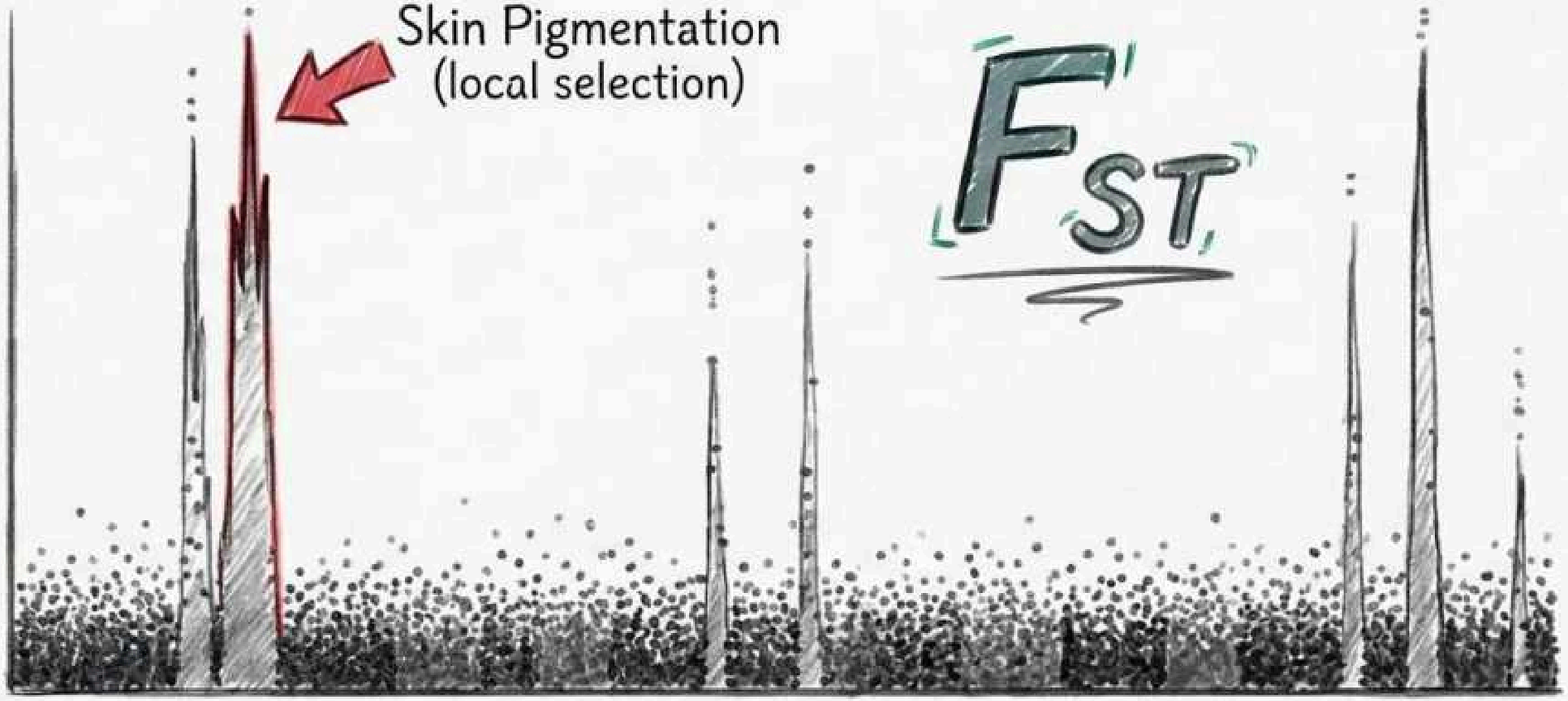
Different mutations in the same regulatory region evolved independently to keep lactase active. Ancient DNA shows the European variant became common surprisingly recently—long after dairy farming actually began.

Altitude Adaptation & Introgression



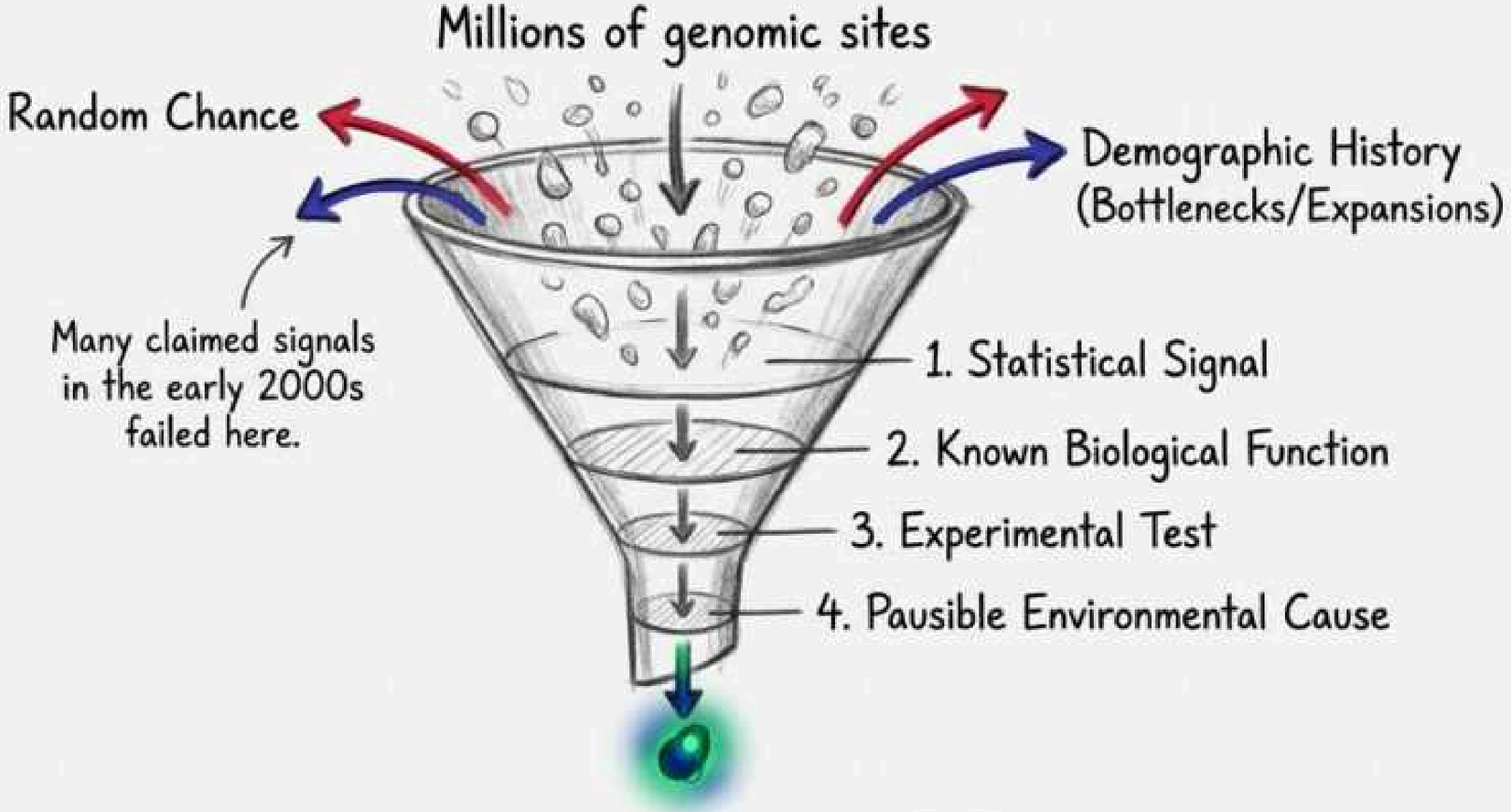
Tibetans live where oxygen is scarce. In 2014, Huerta-Sánchez, Nielsen, et al. showed that the EPAS1 gene was favored by selection after being borrowed from an extinct archaic population.

F_{ST} & Population Differences



The F_{ST} statistic measures how much genetic variation differs between populations. Researchers scan the whole genome for extreme outliers. For example, genes affecting skin pigmentation show massive differences due to strong local selection.

The Diagnostic Filter for True Selection



Genome scans have pitfalls. The strongest, most unassailable cases of selection require multiple overlapping lines of evidence to rule out demographic mirages.

Summary: The Evolutionary Biologist's Toolkit

Direct Observation (The Wild & Lab)



Galapagos Finch



E. coli culture

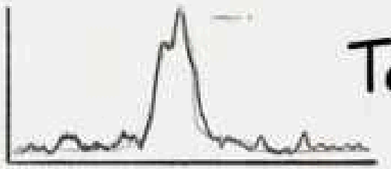
Selection can be measured rapidly and replayed.

DNA Signatures (The Genome)

ω

MK Test

Sample		
	24	2
	1	2x



Tajima's D

Neutrality provides the baseline; selection is the departure.

Human Adaptation (Our History)





Diet and environment leave permanent, detectable marks on our genome.

Next up: Populations, Ancestry, and Ancient DNA. →