

Selection: How Differential Persistence Accumulates Structure

IDE-011 · Fundamental Ideas

Concept essays for The Universe and Its Observers

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Article Abstract

Selection is what happens when variants of something differ in how well they persist or reproduce in a given setting, and when that difference is passed on. Three conditions do the work: variation, differential success, and heritability of whatever makes the difference.[2] Where all three hold, structure can accumulate with no foresight and no designer, because each generation starts from a population already shifted by the last. This article states the conditions precisely, argues that fitness is a relation between a variant and a context rather than a property a variant carries, and sets out what else moves frequencies: drift, which is sampling, and mutation, which supplies variation without being directed by need.[4,5] It closes on what has to be named before selection language is exported outside biology.

In 60 Seconds

Selection requires three things and not one. There must be variation among entities, those variants must differ in how many descendants or copies they contribute, and the difference must be inherited by whatever comes next; strip away any one and the process stops.[2] Price showed that the resulting change can be written exactly as a covariance between a trait and relative fitness plus a transmission term, which is an accounting identity rather than a mechanism: it holds whatever the biology is, and it tells you where to look rather than what happened.[3] Fitness itself is relational. Relative fitness is defined against a population mean.[6] Selection is also not the only thing that changes frequencies. Finite populations drift by sampling alone, and much molecular variation appears to be shaped that way.[5] And variation arrives before the filter: bacterial resistance mutations exist in the culture before the phage is added.[4]

Why This Question Matters

Selection is the most exported idea in biology, and most of the trouble comes from using the word without the conditions. A claim that some outcome was selected for is a claim that variants existed,

differed in success, and passed the difference on, and each of those can be checked or found missing. Skipping them turns an explanatory mechanism into a way of saying that whatever exists must be there for a reason. The same discipline matters when the language travels to culture, markets or algorithms, where the three conditions are sometimes satisfied and sometimes only gestured at.

1. The Three Conditions

Lewontin put the requirements in the form that has held since: a population shows variation among its members, the variants differ in fitness, and fitness is heritable.[2] He states them for individuals and phenotypes and then generalises them explicitly, noting that no particular mechanism of inheritance is specified and that the principles apply equally to genes, organisms, populations and species, which is why the same schema can in principle apply to other replicating systems.[2]

Each condition is a separate empirical claim. Variation can be absent because a trait is fixed in the population. Differential success can be absent because the variants do equally well in the environment that actually obtains. Heritability can be absent because the difference is acquired: an organism that grows larger on a rich diet does not thereby produce larger offspring, and the population does not shift.

Darwin's argument discusses heritable variation, struggle and differential survival, and natural selection.[1]

Where That Leaves Us

Selection needs variation, differential success and heritability, and each is a separate claim that can fail. The schema fixes no particular level, and Lewontin applies it equally to genes, organisms, populations and species, which is what lets it travel. Once the three conditions hold, the next question is what quantity actually changes and how much, and that requires being precise about the word fitness.

2. Fitness Is a Relation, Not a Property

Price derived an exact expression for the change in the mean value of a trait across a generation: it equals the covariance between the trait and relative fitness, plus a term for how faithfully the trait is transmitted.[3] The result is worth stating carefully because it is often overread. It is an identity, true by construction for any population that can be partitioned this way, so it is not evidence that selection occurred and it contains no biology of its own.

What it does supply is a decomposition. If the mean shifted, either it covaried with fitness or transmission was biased, and the two can be examined separately. That is a genuine gain, and it is also the reason the equation recurs in arguments about levels of selection, where the same covariance can be computed at the level of individuals and of groups.

The relational character of fitness follows from the same place. Relative fitness is defined against a population mean.[3,6]

Where That Leaves Us

The Price equation gives an exact decomposition of change into a covariance with fitness and a transmission term, and its status as an identity is what makes it a tool rather than evidence. That leaves open how much of observed change selection is responsible for at all.

3. Selection Is Not the Only Thing That Happens

Frequencies change in finite populations even when variants are equally successful, because each generation is a finite sample of the last. This is drift, the random sampling of variants in a finite population, and the effective population size determines the rate of change in composition that drift causes: the smaller it is, the larger the fluctuation, and the more likely a variant is to be lost or fixed for no reason connected to its effects.[7]

Kimura argued that a large share of molecular-level change may result from the random fixation, through genetic drift, of neutral or nearly neutral mutations.[5] The claim was contested when made and its scope is still debated, but the structural point is now standard: the observation that a variant became common is not by itself evidence that it was advantageous.

This is why selection is a hypothesis rather than a default. Demonstrating it requires showing the differential success, not just the outcome, and the alternatives that have to be excluded include drift, linkage to something else that was selected, and the possibility that the trait is a by-product of a constraint rather than a target.

Where That Leaves Us

Drift changes frequencies by sampling alone, and its strength rises as populations shrink, so prevalence is not evidence of advantage. Kimura's argument made that a working assumption at the molecular level rather than a curiosity. If selection filters variation, the remaining question is where the variation comes from and whether the filter helps produce it.

4. Variation Comes First, and Is Not Directed by Need

It would be economical if organisms produced the variants they needed. Luria and Delbrück designed an experiment that decides the question. If resistance to a phage arises only in response to exposure, the number of resistant colonies across replicate cultures should follow one statistical distribution; if resistant mutants arise spontaneously before exposure, early mutations produce large clones and the variance across cultures should be far greater.[4]

The observed distributions were of the second kind. Resistance mutations were present in the cultures before the phage was ever introduced, and the phage selected among them rather than inducing them. The experiment is worth dwelling on because it converts a question that sounds philosophical into a measurable difference between two distributions.

The general form of the result is that variation and selection are separate steps with separate causes. Mutation supplies candidates without regard to what would be useful; the environment then filters what was already there. This is what makes selection an explanation of apparent design rather than a restatement of it, because the appearance of purpose is produced by a filter acting on undirected material.

Where That Leaves Us

Luria and Delbrück turned the question of whether variation is directed into a difference between two distributions, and the answer was that resistant mutants pre-existed the phage. Variation and selection are therefore separate steps with separate causes, which is exactly what lets a filter produce apparent design. Whether that schema transfers outside biology is the last question.

5. Exporting the Idea

The schema is substrate-neutral in principle, and analogies to culture, markets, immune repertoires and optimization algorithms are sometimes exact and sometimes decorative. The way to tell is to name the three conditions in the case at hand: what varies, what determines differential success, and what carries the difference forward.

Some cases pass cleanly. An immune repertoire generates diversity and then amplifies the lineages that bind, with the difference inherited by the descendants of the amplified cell. A genetic algorithm builds all three conditions in by construction. Others do not: a cultural practice may spread without any mechanism that transmits the property responsible for its spread, in which case the third condition fails and what is happening is diffusion rather than selection.

Two failure modes recur. One is treating persistence as evidence of fitness, which assumes what was to be shown. The other is leaving the environment unspecified, which makes the claim untestable because fitness has no value until the setting is named. Both are avoided by the same discipline: state the population, the variation, the filter and the channel of inheritance.

Where That Leaves Us

Selection language transfers only where the three conditions can be named in the case at hand, and the usual failures are treating survival as proof of advantage and leaving the environment unstated. Naming what varies, what filters and what carries the difference forward is the whole discipline. IDE-012 takes up a different question about carried structure: how a state can stand for something else at all.

What We Know, and How

- Selection requires variation, differential success and heritability of the difference; the schema fixes no particular level and is applied equally to genes, organisms, populations and species, which is why it can apply to other replicating systems.[1,2]
- The Price equation decomposes change in a mean trait into a covariance with relative fitness plus a transmission term; it is an identity, so it organizes an explanation rather than providing one.[3]
- Relative fitness is defined against a population mean.[3,6]
- Variation is supplied before and independently of the filter: resistant bacterial mutants are present before the selecting agent is applied, as the fluctuation test shows.[4]

What We Still Don't Know

- What fraction of observed molecular variation is effectively neutral, which remains contested and varies by organism, genomic region and population size.
- How often and under what conditions selection acting above the level of the individual makes a measurable difference, as opposed to being redescribable at a lower level.

- Which cultural and technological analogies satisfy the heritability condition in a way that supports quantitative prediction rather than a qualitative narrative.

What Could Change Our Minds

- A repeat of the fluctuation test showing colony-count distributions consistent with mutations arising only after exposure, under conditions excluding phenotypic delay and residual pre-exposure growth, would overturn the claim that variation precedes the filter.[4]
- A demonstrated case in which a trait's mean changed across generations with zero covariance between the trait and relative fitness and no transmission bias, correctly measured, would contradict the Price decomposition and indicate an error in how the population was partitioned.[3]
- Systematic evidence that fixation rates at sites with no detectable fitness effect depart from the predictions of drift given the effective population size would force revision of the neutral account of molecular change.[5]

If You Remember Only One Thing

Selection is variation plus differential success plus inheritance of the difference; without all three named, calling something selected explains nothing.

Related Articles

- IDE-012 — Representation
- IDE-007 — Emergence
- IDE-010 — Feedback

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