# Fitness and Prediction in Evolutionary Theory

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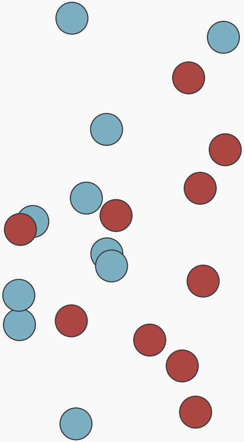
# Outline

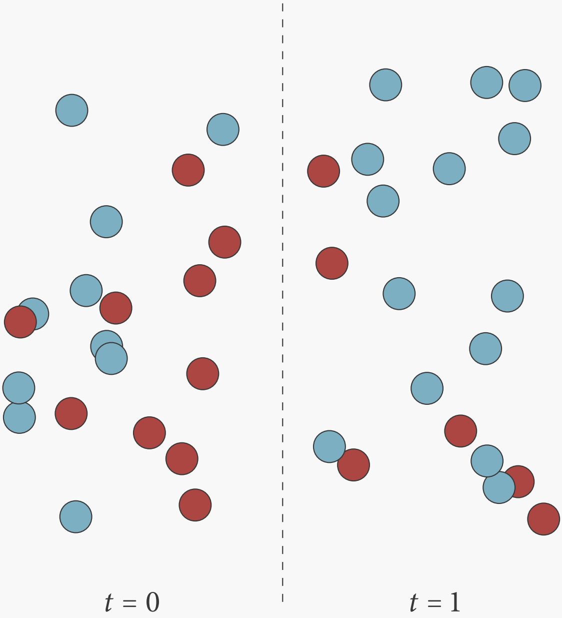


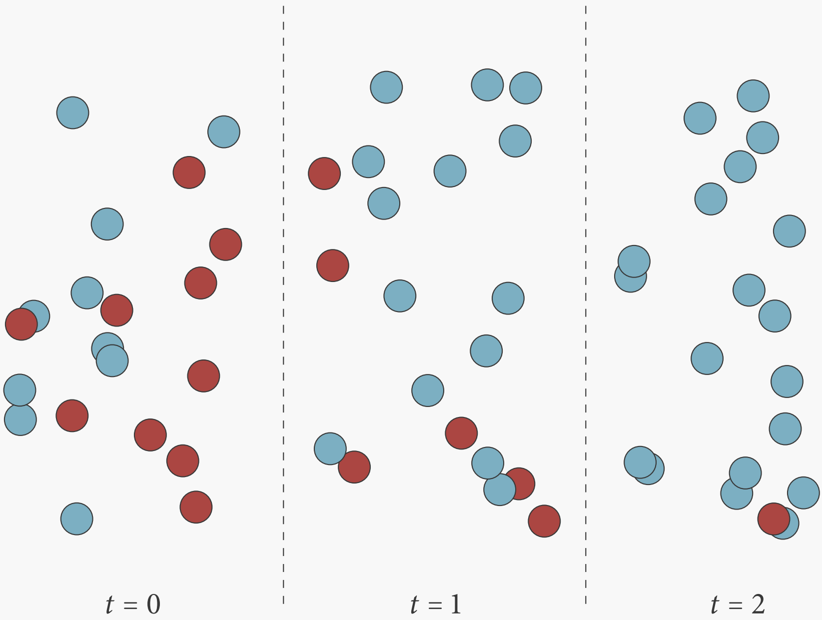
The take-home: A common conceptual analysis of fitness in the philosophy of biology is mistaken.

# Natural Selection

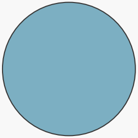


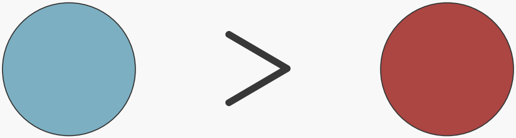
$t = 0$


$t = 0$
$t = 1$


$t = 0$
$t = 1$
$t = 2$

# Fitness





Blue organisms leave more offspring than red organisms.

~~Blue organisms leave more offspring than red organisms.~~

A circle: *the tautology problem*

Blue organisms will probably (are disposed to) leave more offspring than red organisms.

# The Propensity Interpretation of Fitness

THE JOURNAL OF PHILOSOPHY

VOLUME XCIX, NO. 2, FEBRUARY 2002

## TWO WAYS OF THINKING ABOUT FITNESS AND NATURAL SELECTION*

The concept of fitness is, Philip Kitcher[1] says, "important both to informal presentations of evolutionary theory and to the mathematical formulations of [population genetics]" (*ibid.*, p. 50). He is absolutely right. The difficulty is to harmonize these very different

# Two Notions of Fitness

# Matthen and Ariew (2002)

[F]or many this notion of an organism's *overall competitive advantage traceable to heritable traits* is at the heart of the theory of natural selection. Recognizing this, we shall call this measure of an organism's selective advantage its *vernacular fitness.* According to one standard way of understanding natural selection, vernacular fitness – or rather the variation thereof – is a *cause* of evolutionary change. (p. 56)

# Matthen and Ariew (2002)

Fitness occurs also in equations of population genetics which predict, with some level of probability, the frequency with which a gene occurs in a population in generation $n + 1$ given its frequency in generation $n$. In population genetics, *predictive fitness* (as we shall call it) is a statistical measure of evolutionary change, the *expected* rate of increase (normalized relative to others) of a gene … in future generations. … (p. 56)

Causal (vernacular) fitness: general (causal) notion in natural selection

Predictive (mathematical) fitness: predict future representation from central tendency/expected value

# Matthen and Ariew (2002)

[N]atural selection is not a process driven by various evolutionary factors taken as forces; rather, it is a statistical "trend" with these factors (vernacular fitness excluded) as predictors. These theses demand a radical revision of received conceptions of causal relations in evolution. (p. 57)

# The Claim

*Contra* Matthen and Ariew, predictive fitness is not a fruitful way to understand fitness in biology.

By extension, neither is the dichotomy between causal and predictive fitness.

It fails in a way that should lead us to question not only the predictive-causal dichotomy, but the relationship between short-term and long-term evolutionary processes.

# Predictive Fitness

Standard view: predictive fitness tracks something like a central tendency extracted from the distribution of outcomes of interest

# Matthen and Ariew (2002)

The basic principle of statistical thermodynamics is that less probable thermodynamic states give way in time to more probable ones, simply by the underlying entities participating in fundamental processes. [. . . ] The same is true of evolution. (p. 80)

# Lewontin (1974)

When we say that we have an evolutionary perspective on a system or that we are interested in the evolutionary dynamics of some phenomenon, we mean that we are interested in the change of state of some universe in time. […] *The sufficient set of state variables for describing an evolutionary process within a population must include some information about the statistical distribution of genotypic frequencies.* (pp. 6, 16; orig. emph.)

Among other reasons, this is to be useful for grounding medium- to long-term predictions about evolutionary change in fitness comparisons.

Naturwissenschaften (2009) 96:1313–1337
DOI 10.1007/s00114-009-0607-9

REVIEW

# The predictability of evolution: glimpses into a post-Darwinian world

**Simon Conway Morris**

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REVIEW

## The predictability of evolution: glimpses into a post-Darwinian world

Simon Conway Morris

Vol 461 | 29 October 2009 | doi:10.1038/nature08480 nature

ARTICLES

## Genome evolution and adaptation in a long-term experiment with *Escherichia coli*

Jeffrey E. Barrick[1]*, Dong Su Yu[2,3]*, Sung Ho Yoon[2], Haeyoung Jeong[2], Tae Kwang Oh[2,4], Dominique Schneider[5], Richard E. Lenski[1] & Jihyun F. Kim[2,6]

**The relationship between rates of genomic evolution and organismal adaptation remains uncertain, despite considerable interest. The feasibility of obtaining genome sequences from experimentally evolving populations offers the opportunity to investigate this relationship with new precision. Here we sequence genomes sampled through 40,000 generations from a**

# Fitness Maximization

One way to get these predictions:

Evolution as a process that maximizes fitness over time

# Birch (2016)

Neither [of the approaches surveyed] establishes a maximization principle with biological meaning, and I conclude that it may be a mistake to look for universal maximization principles justified by theory alone. (p. 714)

But this isn't the only way to generate predictions. What about building predictions from the PIF itself?

# From Causal to Predictive

How should defenders of the PIF respond to M&A's emphasis on predictive fitness?

# Millstein (2016)

Fitness is an organism's propensity to survive and reproduce (based on its heritable physical traits) in a particular environment and a particular population over a specified number of generations. That is what fitness *is*. […] Expected reproductive success is not the propensity interpretation of fitness and it never was; it was just one way of trying to grapple with probability distributions and assign fitness values. (p. 615)

*Brit. J. Phil. Sci.* **64** (2013), 851–881

# A New Foundation for the Propensity Interpretation of Fitness

Charles H. Pence and Grant Ramsey

ABSTRACT

The propensity interpretation of fitness (PIF) is commonly taken to be subject to a set of simple counterexamples. We argue that three of the most important of these are not counterexamples to the PIF itself, but only to the traditional mathematical model of this propensity: fitness as expected number of offspring. They fail to demonstrate that a new mathematical model of the PIF could not succeed where this older model fails. We then propose a new formalization of the PIF that

The basic idea: Define the propensity interpretation in terms of facts about the possible lives an organism (with a given genotype, in a given environment) could have lived.

$$F(G,E) = \exp\left(\lim_{t\to\infty} \frac{1}{t} \int_{\omega\in\Omega} \Pr(\omega) \cdot \ln(\phi(\omega,t))\, d\omega\right)$$

Having our cake and eating it, too:

- Gives you a mathematical model…
- …that's grounded in a specific dispositional property

Can we draw any conclusions about the quality of predictions from the Pence & Ramsey model?

$$F(G,E) = \exp\left(\lim_{t\to\infty} \frac{1}{t} \int_{\omega\in\Omega} \Pr(\omega)\cdot\ln(\phi(\omega,t))\,d\omega\right)$$

A long-run limit: perfect for prediction! But it relies on an assumption: non-chaotic population dynamics

Question: How common *is* non-chaotic dynamics in evolving systems?

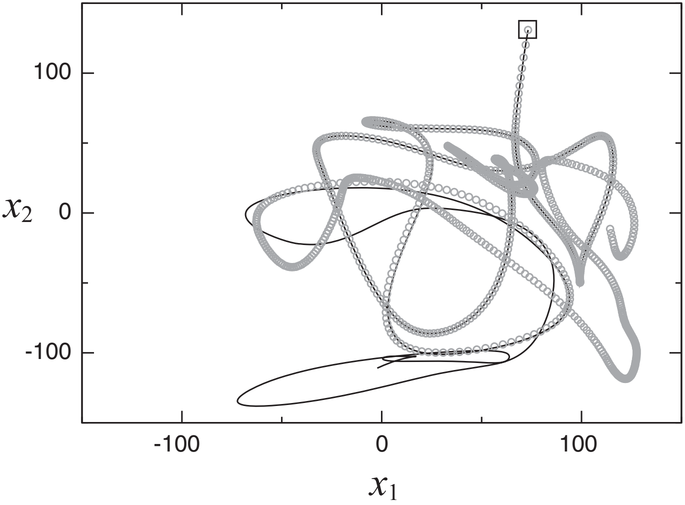
My assumption: Won't be able to answer this – model is far too general.

Approach of Doebeli & Ispolatov (2014): Investigate by simulating populations with two features:

1. Density-dependent selection pressures
2. High-dimensional phenotype space

# Doebeli & Ispolatov (2014)

Our main result is that the probability of chaos increases with the dimensionality $d$ of the evolving system, approaching 1 for $d \sim 75$. Moreover, our simulations indicate that already for $d \gtrsim 15$, the majority of chaotic trajectories essentially fill out the available phenotype space over evolutionary time.... (p. 1368)




Doebeli and Ispolatov (2014), fig. 5

What’s the real-world timescale here?

How does it relate to the rate of environmental change?

A surprising result at this level of generality. In cases where it holds, what kinds of fitness-based predictions would remain viable?


Way out →

# Grant (1997)

The invasion is exponential, but nonlinear dynamics of the resident type produce fluctuations around this trend. [Fitness] can therefore be most accurately estimated by the slope of the least squares regression of [daughter population size] on $t$. (p. 305)

Two major problems:

- Loses sight of the dynamics
- Offers poor predictions

Move the goalposts:

- Abandon all but short-term predictions
- Abandon predictive content; predict simply 'chaos'
- Abandon prediction, focus on statistical retrodiction

- Resuscitate central tendencies: poor predictions that ignore (interesting) dynamics
- Move the goalposts: loses the medium-to-long-term predictions cited above

# The Moral

Many uses of fitness:

- Mathematical parameter in models
- Causal property
- Proxies for strength of selection in populations
- Statistical estimator for any of the above

Fitness concepts are far more complex than a dichotomy between two simple roles for fitness.

What's the relationship between short-term and long-term evolutionary processes?

Complete continuity, all the way to the long run? Unlikely.

Complete continuity, all the way to the long run? Unlikely.

Medium-term continuity? Threatened by these results!

# Questions?

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$$F(G, E) = \exp\left( \lim_{t \to \infty} \frac{1}{t} \int_{\omega \in \Omega} \Pr(\omega) \cdot \ln(\phi(\omega, t))\, d\omega \right)$$

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- Multi-generational life histories
- Changing genotypes and environments over time

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- Multi-generational life histories
- Changing genotypes and environments over time
- Disposition (propensity) defined over modal facts about other possible lives of organisms

State space of possible lives: $\Omega : \{f : \mathbb{R} \to \mathbb{R}^n\}$

Cardinality, though, is too big! $N(\Omega) = 2^{2^{\aleph_0}}$

Can still define a $\sigma$-algebra $\mathcal{F}$ and a probability measure Pr if we restrict our attention to:

- continuous functions $\omega$,
- functions $\omega$ with only point discontinuities, or
- functions $\omega$ with only jump discontinuities

(Nelson 1959)

With that state space defined, we need three simplifying assumptions:

1. Non-chaotic population dynamics
2. Probabilities generated by a stationary random process
3. Logarithmic moment of vital rates is bounded

The last two are trivial in our context.

Then the following limit exists:

$$a = \lim_{t \to \infty} \frac{1}{t} E_w \ln(\phi(t)),$$

with $E_w$ an expectation value (Tuljapurkar 1989). Fitness is the exponential of this quantity $a$, and is equivalent (under further simplifying assumptions) to net reproductive rate and related to the Malthusian parameter.