What Role for Fitness?

Deep South Philosophy of Biology, 4/1/2017

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Outline

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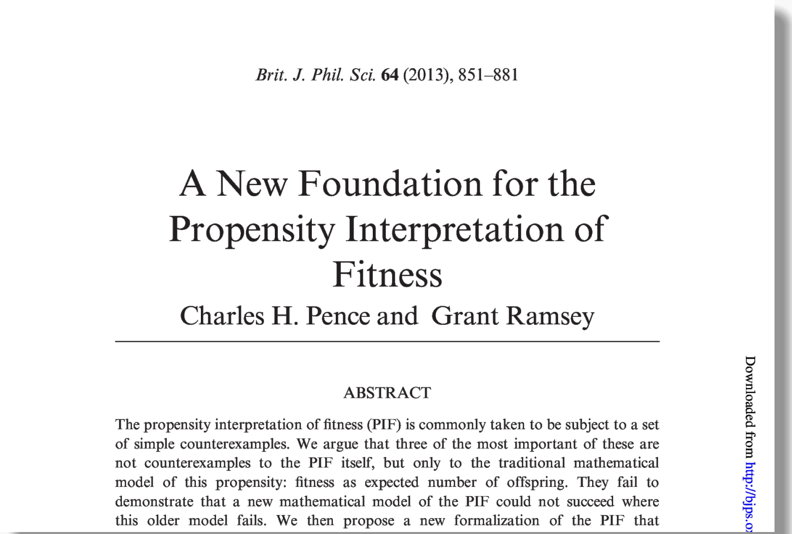

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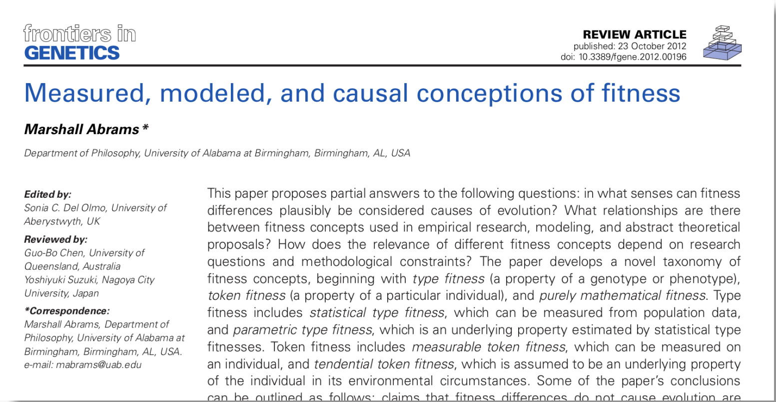
A New Foundation for the Propensity Interpretation of Fitness

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



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Measured, modeled, and causal conceptions of fitness

Marshall Abrams *

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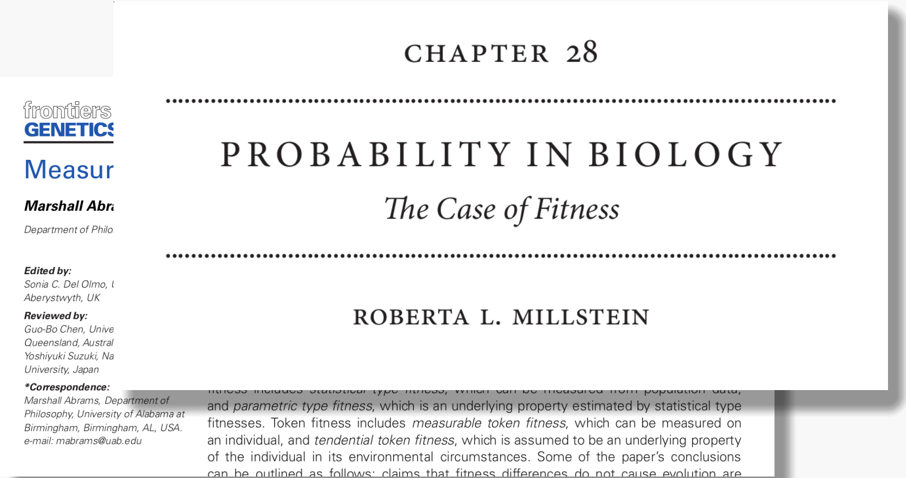
This paper proposes partial answers to the following questions: in what senses can fitness differences plausibly be considered causes of evolution? What relationships are there between fitness concepts used in empirical research, modeling, and abstract theoretical proposals? How does the relevance of different fitness concepts depend on research questions and methodological constraints? The paper develops a novel taxonomy of fitness concepts, beginning with *type fitness* (a property of a genotype or phenotype), *token fitness* (a property of a particular individual), and *purely mathematical fitness*. Type fitness includes *statistical type fitness*, which can be measured from population data, and *parametric type fitness*, which is an underlying property estimated by statistical type fitnesses. Token fitness includes *measurable token fitness*, which can be measured on an individual, and *tendential token fitness*, which is assumed to be an underlying property of the individual in its environmental circumstances. Some of the paper's conclusions can be outlined as follows: claims that fitness differences do not cause evolution are



CHAPTER 28

PROBABILITY IN BIOLOGY

The Case of Fitness

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Natural selection and the maximization of fitness

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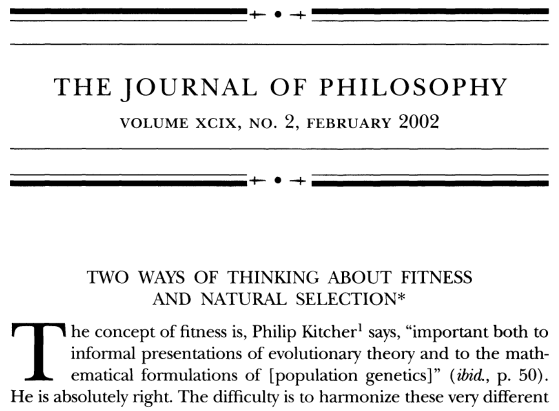
ABSTRACT

The notion that natural selection is a process of fitness maximization gets a bad press in population genetics, yet in other areas of biology the view that organisms behave as if attempting to maximize their fitness remains widespread. Here I critically appraise the prospects for reconciliation. I first distinguish four varieties of fitness maximization. I then examine two recent developments that may appear to vindicate at least one of these varieties. The first is the 'new' interpretation of Fisher's fundamental theorem of natural selection, on which the theorem is exactly true for any

Why are philosophers of biology interested in fitness?

What, in the philosophy of biology, is fitness *for*?



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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 the philosophy of biology.

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

While often unappreciated, a number of recent publications on fitness also cast doubt on the utility of the causal-predictive dichotomy.

Predictive Fitness

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

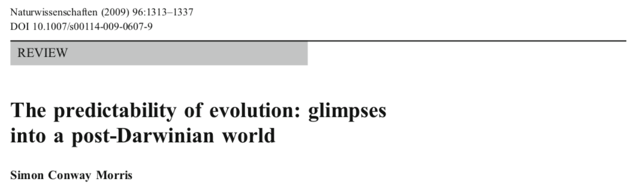
Matthen and Ariew (2002)

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.



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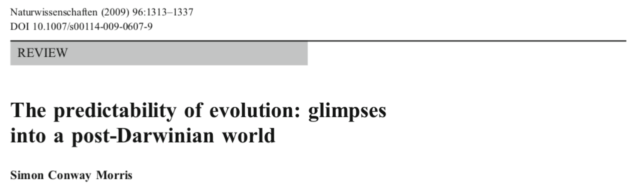
REVIEW

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

From Causal to Predictive

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?

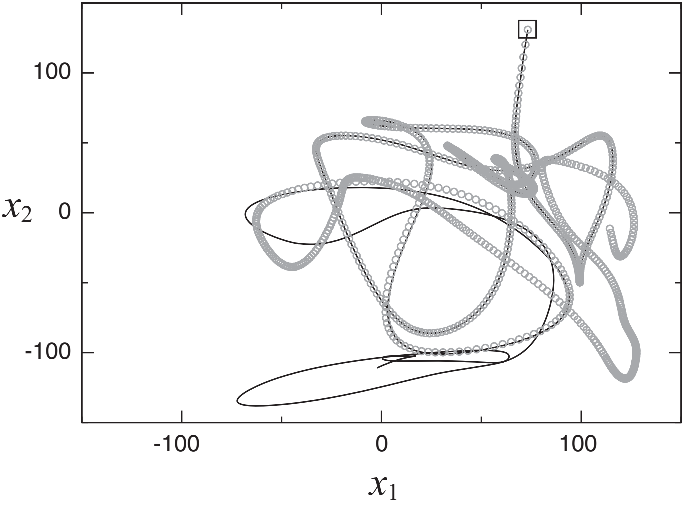
My assumption: Won't be able to answer this – model is far too general.

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?

Ways 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

Connections

Abrams (2012)

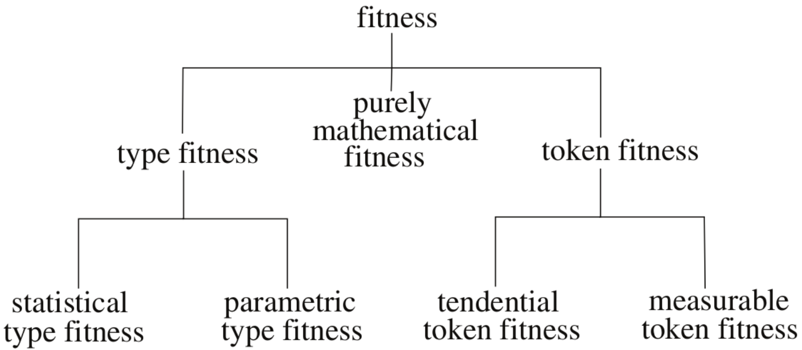


FIGURE 1 | Classes of fitness concepts defined in the text. Lines connect classes to their subclasses.

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)

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… As for the best way to compare probability distributions, I leave that to mathematicians and mathematical biologists. (pp. 615–6)

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.

So what is mathematical fitness for?

So what is mathematical fitness for?

Of course, analyzing biological models is a great project, and worthwhile in its own right.

Deriving *mathematical* models from our *causal* structures can give us confidence that the structure we are describing *really is a model of fitness.*

Deriving *mathematical* models from our *causal* structures can give us confidence that the structure we are describing *really is a model of fitness.*

I think this is the way to interpret the results in Pence and Ramsey (2013), as well as a number of other propensity-interpretation papers.

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

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

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

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

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

- continuous functions ω,
- functions ω with only point discontinuities, or
- functions ω 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.