WHAT IS EVOLUTIONARY FITNESS FOR?

Mississippi State University, 11/6/2015

Charles H. Pence

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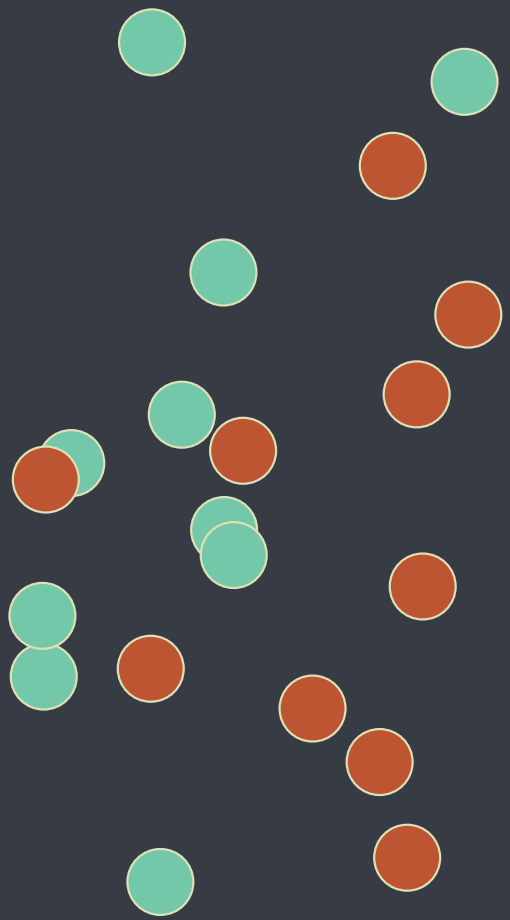
NATURAL SELECTION



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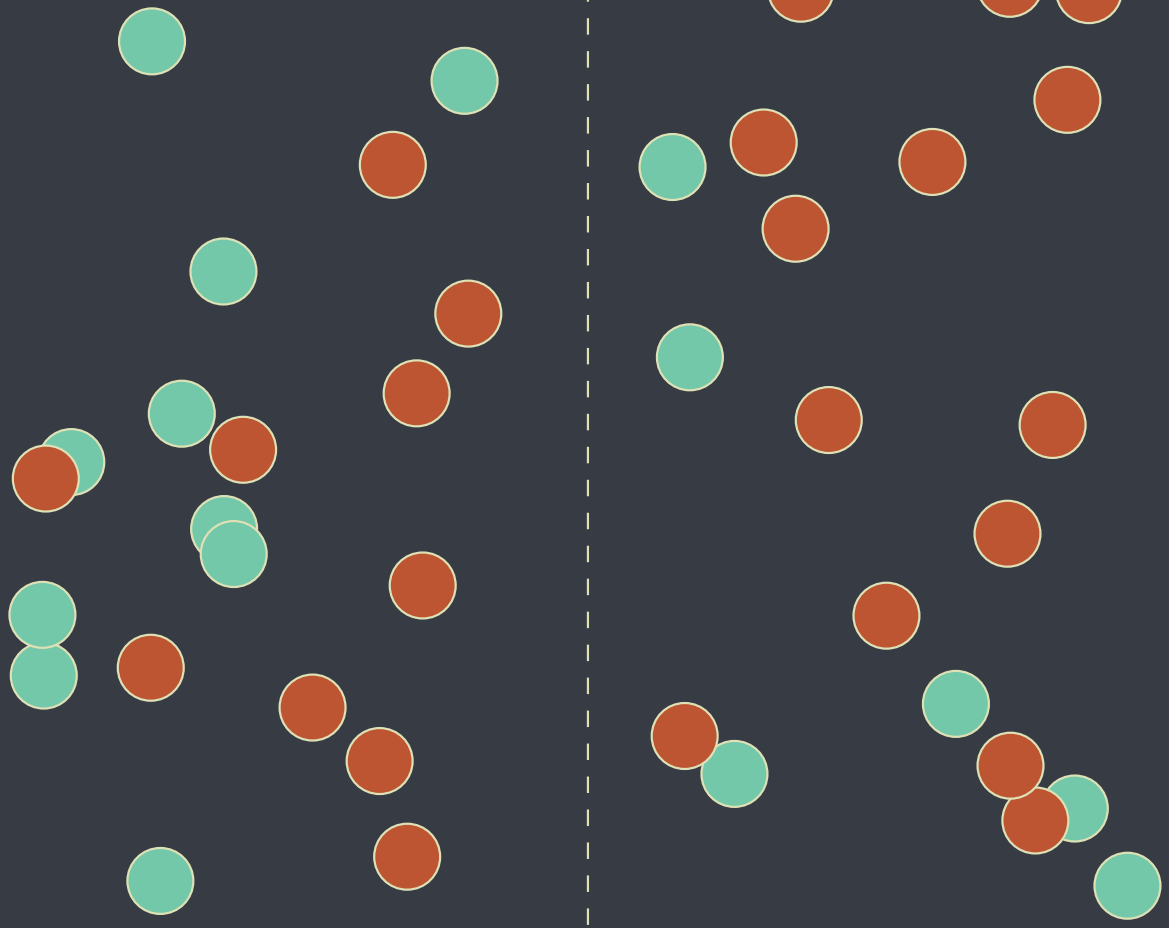
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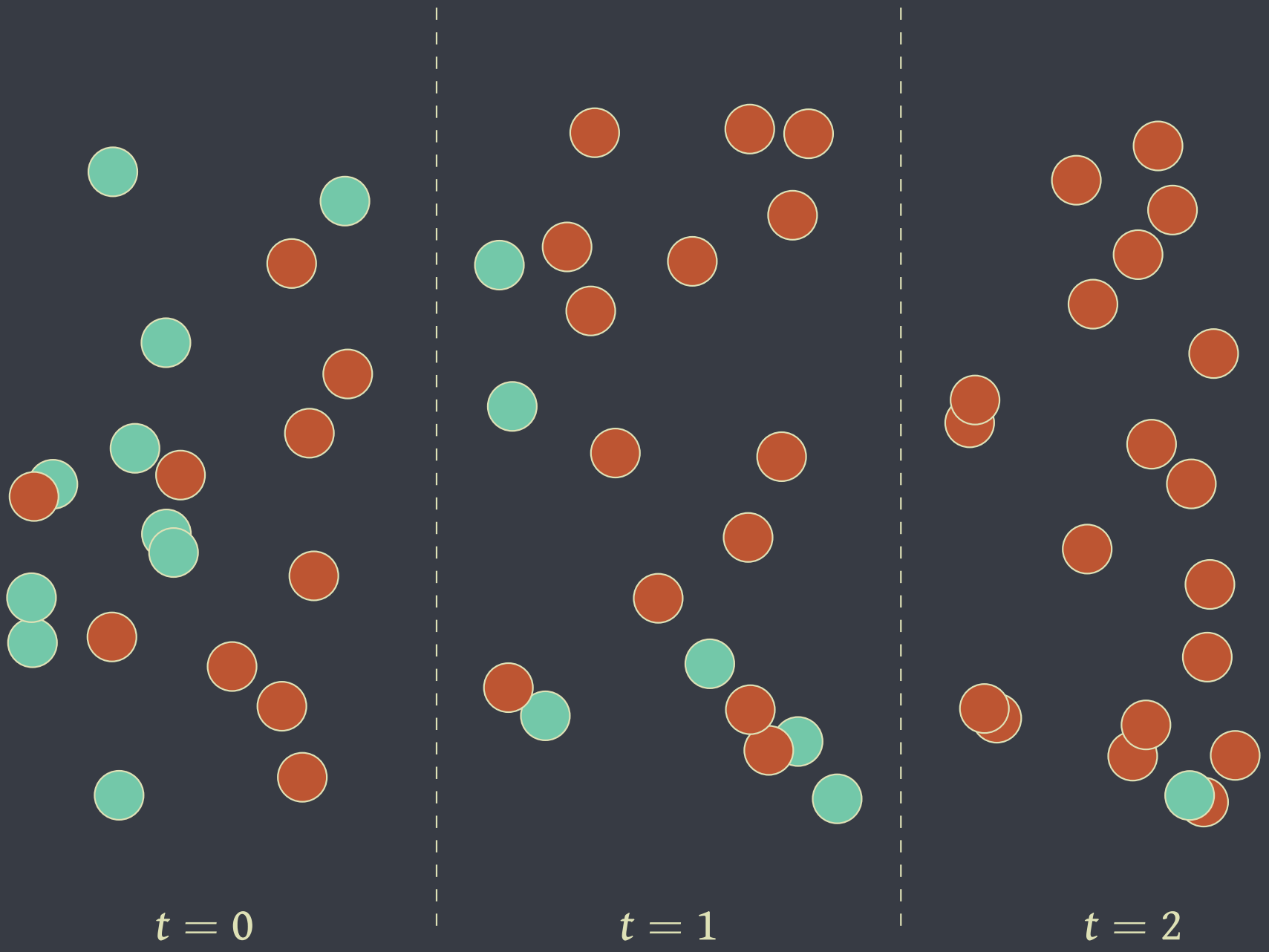
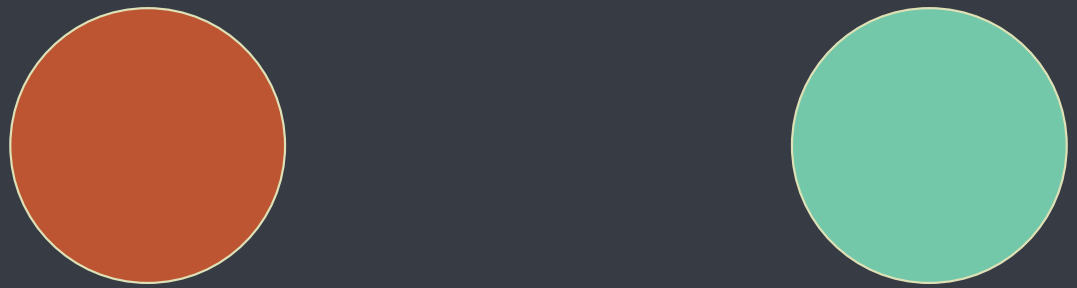
$t = 1$


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

FITNESS



Orange organisms leave more offspring than teal organisms.

Orange organisms leave more offspring than teal organisms.

A circle: *the tautology problem*

Orange organisms will probably (are disposed to) leave more offspring than teal organisms.

THE PROPENSITY INTERPRETATION OF FITNESS

ROBERT N. BRANDON

ADAPTATION AND EVOLUTIONARY THEORY*

There is virtually universal disagreement among students of evolution as to the meaning of adaptation. (Lewontin, 1957).

Much of past and current disagreement on adaptation centers about the definition of the concept and its application to particular examples: these arguments would lessen greatly if precise definitions for adaptations were

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THE PROPENSITY INTERPRETATION OF FITNESS*

SUSAN K. MILLS AND JOHN H. BEATTY†

Indiana University

The concept of "fitness" is a notion of central importance to evolutionary theory. Yet the interpretation of this concept and its role in explanations of evolutionary phenomena have remained obscure. We provide a *propensity* interpretation of fitness, which we argue captures the intended reference of this term as it is used by evolutionary theorists. Using the propensity interpretation of fitness, we provide a Hempelian reconstruction of explana-

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Adaptation and Environment

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Rethinking the Propensity Interpretation:
A Peek Inside Pandora's Box[1]

JOHN BEATTY[a] and SUSAN FINSEN[b]

[a] *Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, MN 55455, U.S.A.*
[b] *Department of Philosophy, California State University at San Bernadino, San Bernardino, CA 92407, U.S.A.*

Introduction

Over the past ten years, the propensity interpretation of fitness has attracted a number of proponents[2] and a few, persistent detractors.[3] Here, two previous supporters turn critics, to acknowledge and reframe some old problems, and to introduce some additional difficulties. We are not sure whether a radically revised interpretation of fitness is necessary. But it does seem to us that certain gross oversimplifications of the propensity interpretation deserve more serious attention.

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CHAPTER FIFTEEN

The Two Faces of Fitness

ELLIOTT SOBER

THE JOURNAL OF PHILOSOPHY

VOLUME XCIX, NO. 2, FEBRUARY 2002

The Two Faces of Fitness

ELLIOTT SOBER

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. (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.... (56)

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

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

THE CLAIM

Causal fitness can be made to survive counterexamples against it, but at a cost.

It's not clear just what predictive fitness is supposed to predict.

CAUSAL FITNESS

Brit. J. Phil. Sci. **57** (2006), 627–653

Natural Selection as a Population-Level Causal Process

Roberta L. Millstein

ABSTRACT

Recent discussions in the philosophy of biology have brought into question some fundamental assumptions regarding evolutionary processes, natural selection in particular. Some authors argue that natural selection is nothing but a population-level, statistical consequence of lower-level events (Matthen and Ariew [2002]; Walsh et al. [2002]). On this view, natural selection itself does not involve forces. Other authors reject this purely statistical, population-level account for an individual-level, causal account of natural selection (Bouchard and Rosenberg [2004]). I argue that each of these positions

Brit. J. Phil. Sci. **57** (2006), 627–653

Why the Causal View of Fitness Survives*

Jun Otsuka, Trin Turner, Colin Allen, and Elisabeth A. Lloyd[†‡]

We critically examine Denis Walsh's latest attack on the causalist view of fitness.

Brit. J. Phil. Sci. **57** (2006), 627–653

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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.

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

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- **Multi-generational life histories**

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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**

Can plausibly be saved from counterexamples

Results in a potential metaphysical mess

PREDICTIVE FITNESS

What is our inferential basis for determining the values of predictive fitness?

“Darwinian fitness” in basic population genetics:

$$\frac{p_t}{q_t} = w^t \cdot \frac{p_0}{q_0}$$

Expected number of offspring:

$$A(O, E) = \sum P(Q_i^{OE}) Q_i^{OE}$$

Fitness Property	Inferential Basis	Sample
Individual fitness, relativizing to environmental conditions	One individual life-history	Very small, unrepresentative
Individual fitness, including similar/clonal organisms	A small number of life-histories in similar environmental conditions	Small, likely unrepresentative

Fitness Property	Inferential Basis	Sample
Trait fitness, including environmental and pleiotropic effects	One trait-history	Very small, unrepresentative
Trait fitness, including similar traits	A small number of trait-histories in similar environmental conditions	Small, likely unrepresentative

Fitness Property	Inferential Basis	Sample
Type fitness, natural populations	A moderate number of type-histories in similar environmental conditions	Moderately-sized, possibly representative
Type fitness, experimental evolution	A huge number of type-histories in nearly identical environmental conditions	Large and representative, high-quality predictions

Best-case (long-term experimental evolution): great inferential basis

Almost all natural populations: poor inferential basis

Another test case: chaotic population dynamics

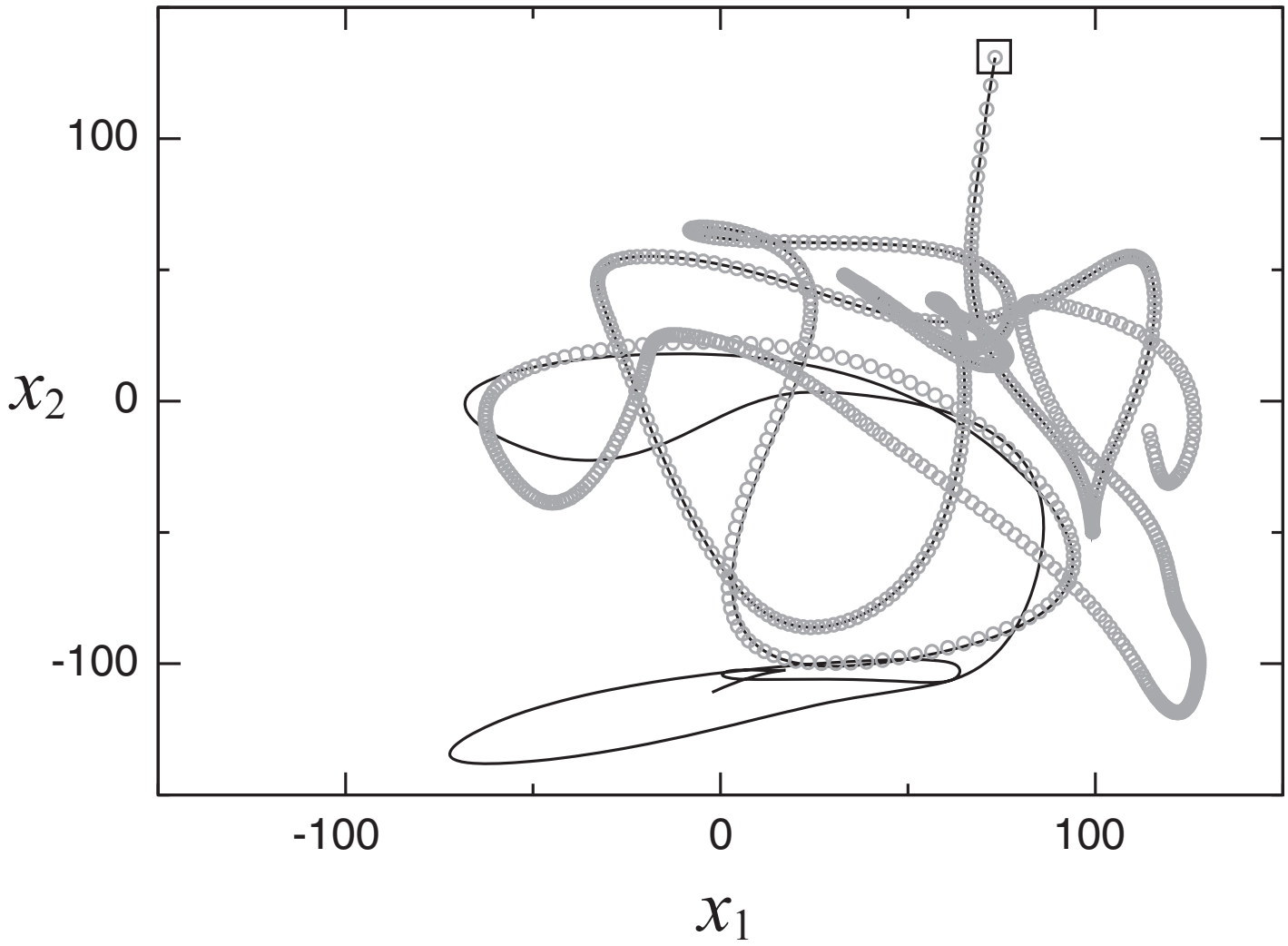
Assumption of most models of fitness: non-chaotic population dynamics

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

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

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

"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...." (D&I, 1368)



Doebeli and Ispolatov (2014), fig. 5

Surely there's no way to define predictive fitness in these scenarios?

"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." (Grant 1997)

Chaotic population dynamics: Common, and render predictive fitness meaningless

Predictive fitness isn’t very predictive after all

THE MORAL

Causal fitness can be saved from counterexamples at the cost of being made metaphysically problematic

Predictive fitness … isn’t

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.

QUESTIONS?

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