It's Okay to Call Genetic Drift a "Force"

PSA 2012, San Diego, California

Charles H. Pence

charles@charlespence.net

University of Notre Dame
Program in the History and Philosophy of Science
Department of Philosophy

The Plan

- What is genetic drift?
- What is the force interpretation?
- First problem: The direction of drift
- Second problem: Inertial states and deviations

The Plan

- What is genetic drift?
- What is the force interpretation?
- First problem: The direction of drift
- Second problem: Inertial states and deviations

The goal: Both the problems are solvable; it really is okay to call genetic drift a “force.”

What is Genetic Drift?

"What most of the phenomena so designated have in common is one or another biological form of random or indiscriminate sampling, and consequent sampling error." (Beatty, 1992)

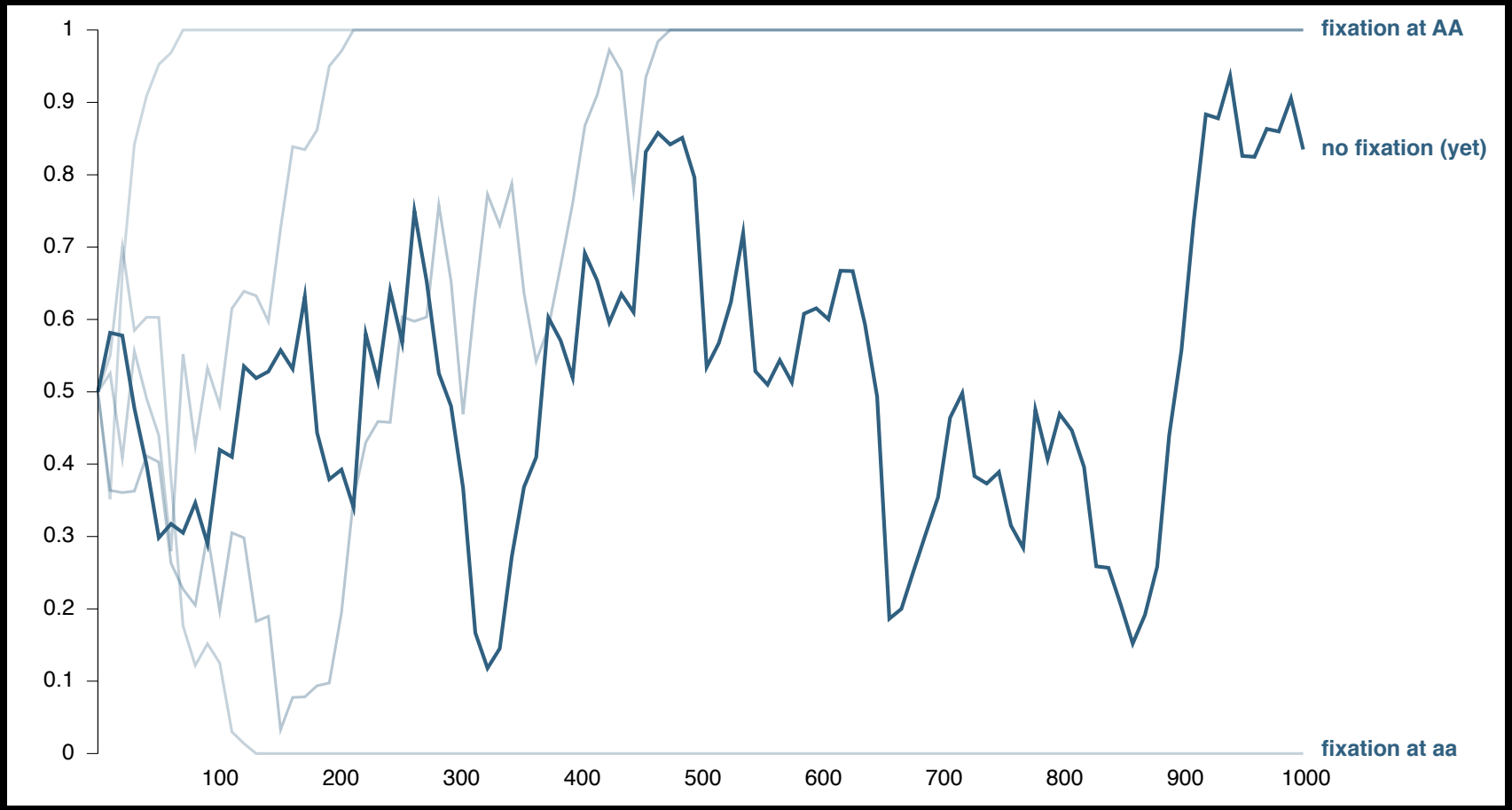
1. Random Mendelian segregation
2. Random fluctuations in equally fit types
3. Causes that fail to differentiate based on fitness ("lightning strikes")
4. The "founder effect": random geographic splitting of a group (possibly)
5. The cause of *any* non-adaptive variation (possibly)

What is Genetic Drift?

"What most of the phenomena so designated have in common is one or another biological form of random or indiscriminate sampling, and consequent sampling error." (Beatty, 1992)

1. Random Mendelian segregation
2. Random fluctuations in equally fit types
3. Causes that fail to differentiate based on fitness ("lightning strikes")
4. The "founder effect": random geographic splitting of a group (possibly)
5. The cause of *any* non-adaptive variation (possibly)

Random Mendelian Segregation

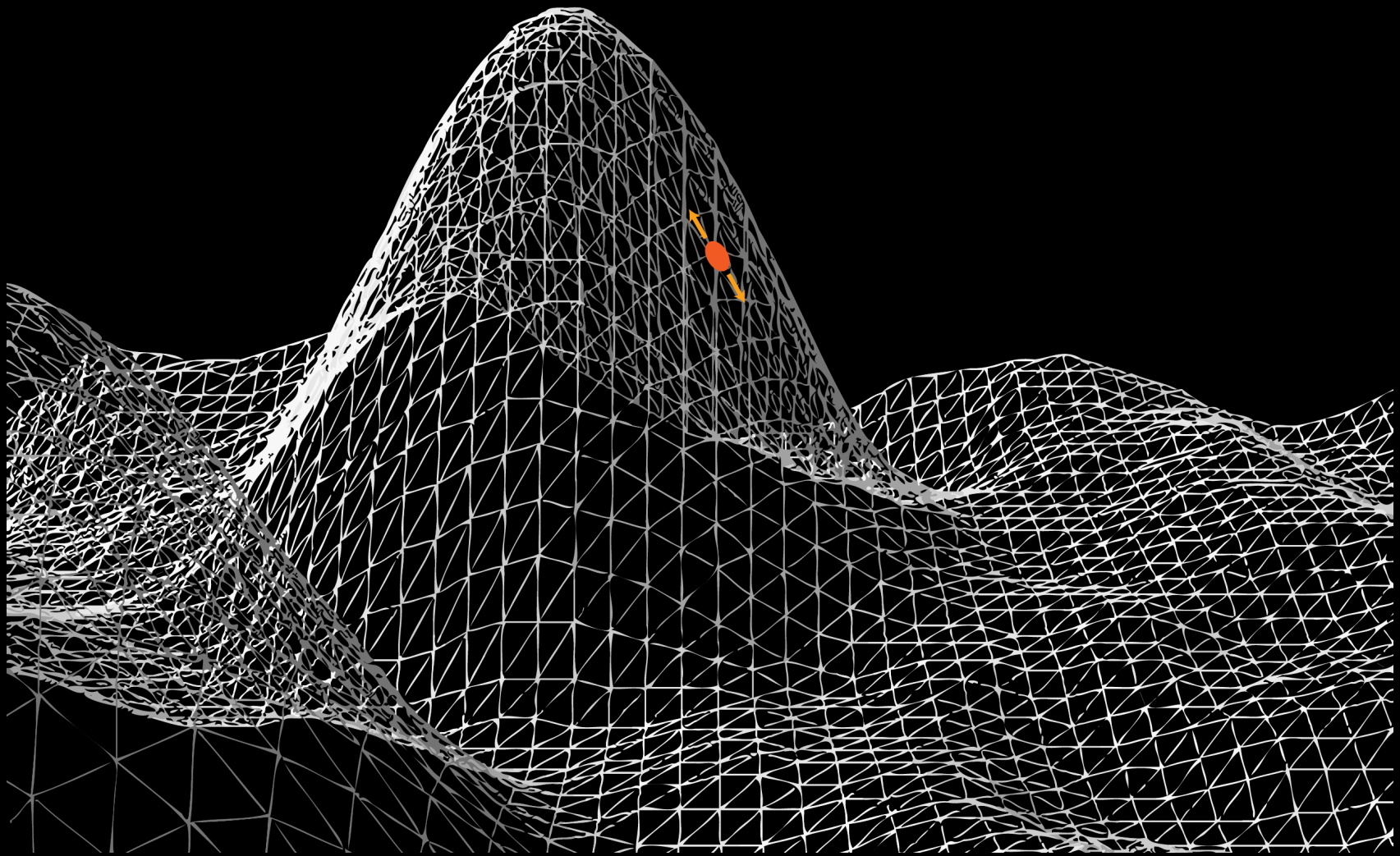


Five simulations of a heterozygous population ($N = 100$) undergoing only genetic drift (no selection or mutation)

The Force Interpretation

"[E]volutionary biology has also developed a theory of *forces.* This describes the *possible causes* of evolution. The various models provided by the theory of forces describe how a population will evolve if it begins in a certain initial state and is subject to certain causal influences along the way." (Sober, 1984)

The Force Interpretation



The Direction of Drift

"In any case, drift is not the sort of thing that can play the role of a force – it does not have predictable and constant direction." (Matthen and Ariew, 2002)

"Consider first the idea that a force has both a magnitude and a direction. Drift has a magnitude that can be probabilistically predicted prior to the fact, and can be quantitatively accessed after the fact. But drift definitely does not have a direction." (Brandon, 2006)

A First Response: Stephens

"Drift does have a direction – it serves to eliminate heterozygosity." (Stephens, 2004)

A First Response: Stephens

"Drift does have a direction – it serves to eliminate heterozygosity." (Stephens, 2004)

But:

- Is "homozygosity-space" sufficiently well-defined to support defining directions for forces? (Filler, 2009)
- Is this "direction" really what genetic drift is intended to describe?

A Second Response: Filler

Take two criteria for forcehood from the literature on forces (Filler, 2009):

- Forces must have a "mathematically *specific* magnitude"
- Forces can "unify a wide array of seemingly disparate phenomena"

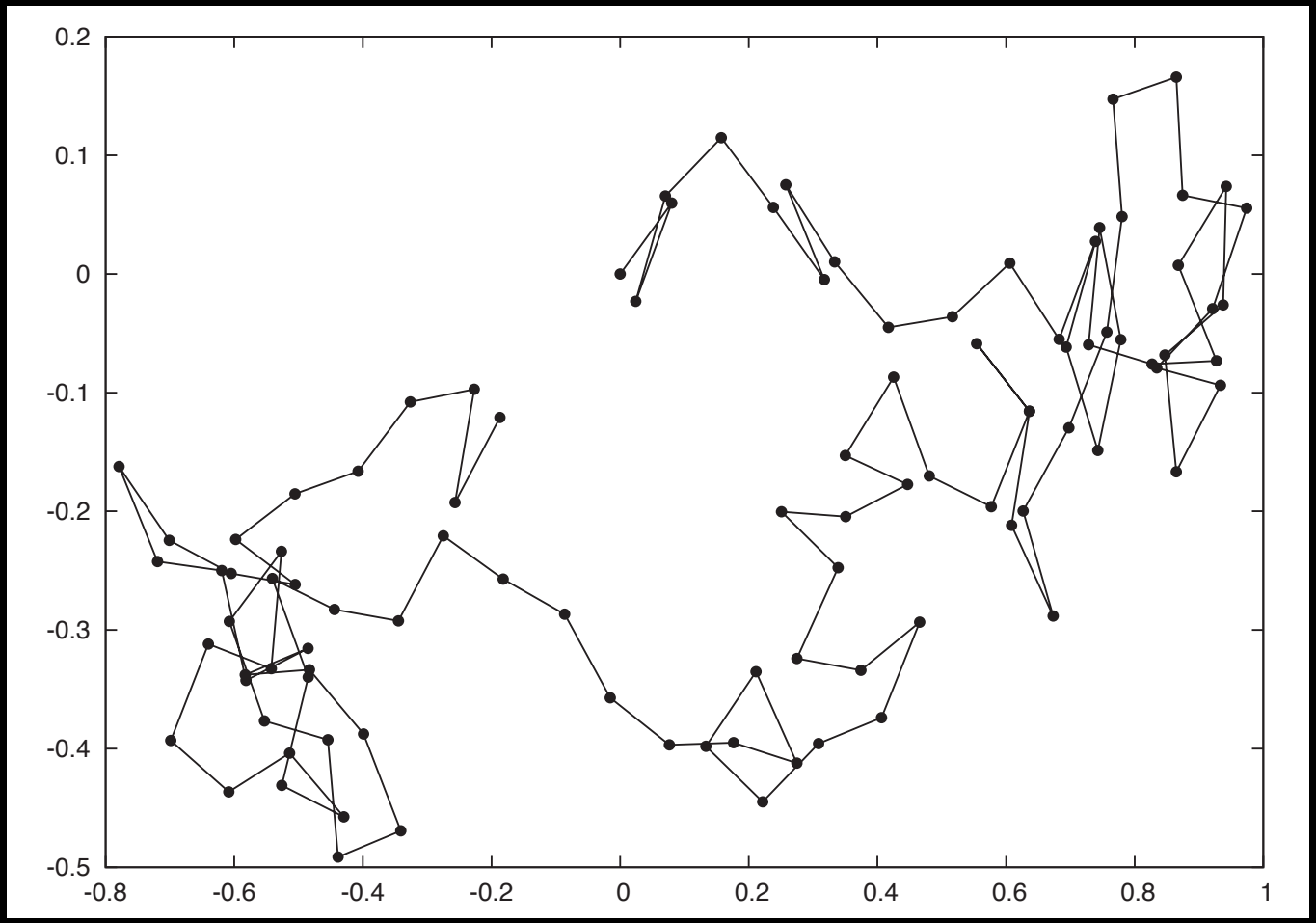
A Second Response: Filler

Take two criteria for forcehood from the literature on forces (Filler, 2009):

- Forces must have a "mathematically *specific* magnitude"
- Forces can "unify a wide array of seemingly disparate phenomena"

Can we find a way to salvage the force metaphor that runs less risk of being ad hoc?

Brownian Motion



Simulation of a particle released at $(0, 0)$ undergoing Brownian movement (after Perrin, 1909)

Brownian Motion

$$m\frac{d^2x}{dt^2} = -6\pi\mu a\frac{dx}{dt} + X$$

$-6\pi\mu a =$ damping coefficient

$X =$ random variable

Possible Objections

- Reject both Brownian motion and genetic drift as forces?

Possible Objections

- Reject both Brownian motion and genetic drift as forces?
  - Not “giving up” complete predictability

Possible Objections

- Reject both Brownian motion and genetic drift as forces?
  - Not “giving up” complete predictability
  - Fully able to model these systems

Possible Objections

- Reject both Brownian motion and genetic drift as forces?
  - Not “giving up” complete predictability
  - Fully able to model these systems
  - Stochastic forces often *already* countenanced (by Brandon, Matthen and Ariew)

On Inertial States and Deviations

Maudlin (2004) on "quasi-Newtonian" theories: when is "nothing happening," and when is a system "deviating" from that inertial trajectory?

Brandon (2006; McShea and Brandon, 2010): Drift is "part and parcel of a constitutive process of any evolutionary system," a "default-causal" explanation, while mutation, selection, and migration are "special" forces. Thus drift is not a force.

Two Force Interpretations

	Sober	Brandon
Inertial state	Hardy–Weinberg equilibrium	Genetic drift
Special forces	Drift, selection, mutation, etc.	Selection, mutation, etc.

Why is Drift Inertial?

- Drift is necessarily going to act in any circumstances in which evolution itself is possible.

Why is Drift Inertial?

- Drift is necessarily going to act in any circumstances in which evolution itself is possible.
- But what about Newtonian gravitation? Is it equally "constitutive?"

Why is Drift Inertial?

- Drift is necessarily going to act in any circumstances in which evolution itself is possible.
- But what about Newtonian gravitation? Is it equally "constitutive?"
- Response: we can build test cases where we eliminate gravity.

Why is Drift Inertial?

- Drift is necessarily going to act in any circumstances in which evolution itself is possible.
- But what about Newtonian gravitation? Is it equally "constitutive?"
- Response: we can build test cases where we eliminate gravity.
- But the same holds for drift:
  - A test mass "at infinity," undergoing no gravitational acceleration, versus
  - A "drift-free" evolving population – infinite, but with both selection and mutation

Conclusions

- Problem: Drift cannot be a force, because forces must have specifiable directions
  - Solution: We already countenance stochastic forces, such as Brownian motion
- Problem: Drift is a “first-law” inertial condition, not a “second-law” special force
  - Solution: Drift is no more “constitutive” of evolving systems than gravity is of Newtonian systems
- Overall: The force metaphor lives to fight another day

Questions?

charles@charlespence.net

A Drift-Free Population

- Four types: A, B, C, and D
- Population: Infinite, equally distributed (initially)
- Reproduction: Each individual produces exactly 1 offspring and then dies, if it survives to reproductive age
- Heredity: Clonal, with a slight mutation rate
- Selection: Types C and D have a 10% chance of dying before reproductive age

Results: C and D die off (thanks to selection); no bottlenecks or finite population size; all probabilistic or stochastic influences are *selection* or *mutation,* not drift. In the limit: roughly half A and half B (modulo the mutation rate).