

It's Okay to Call Genetic Drift a “Force”

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The Plan

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

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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)

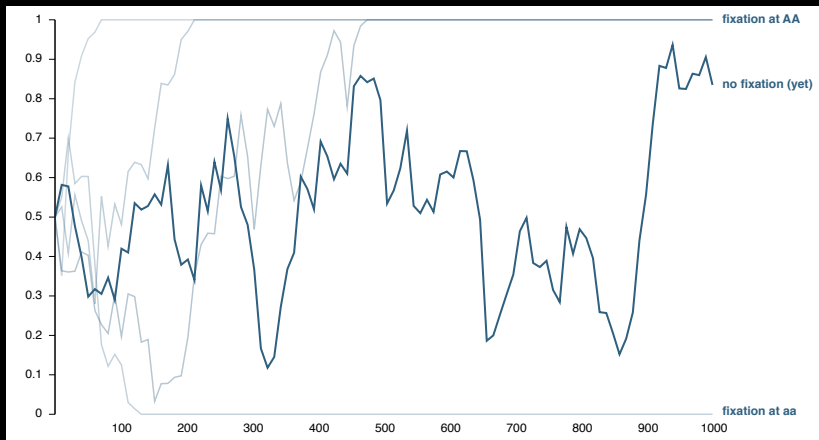
1. Random Mendelian segregation
2. Random fluctuations in equally fit types
3. Causes that fail to differentiate based on fitness (“lightning strikes”)
4. The “founder effect”: random geographic splitting of a group (possibly)
5. The cause of *any* non-adaptive characters (now outdated)

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Random Mendelian Segregation

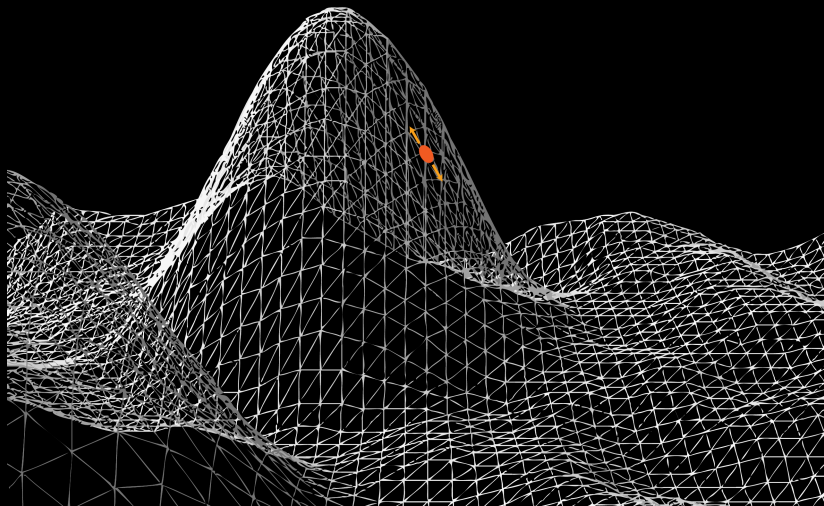


Five simulations of a heterozygous population ($N = 100$) undergoing only genetic drift (no selection or mutation)

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)

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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”

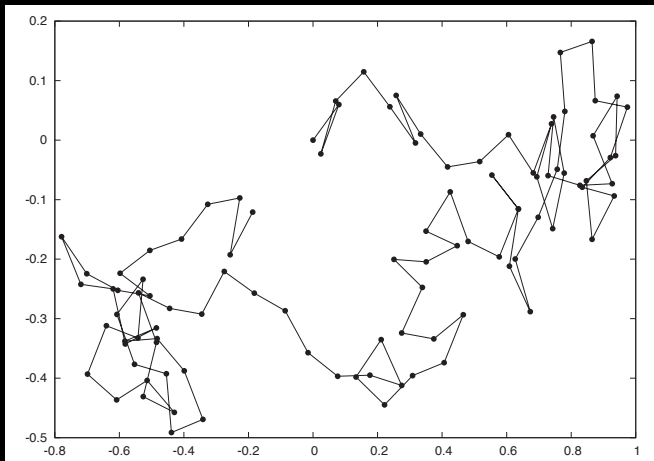
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Can we find a way to salvage the force metaphor that runs less risk of being ad hoc?

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

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- 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.

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- 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

Two Force Interpretations

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

Drift as Mechanism

- Barros (2008): Drift features in, at best, *ex post* mechanistic explanations
- Darden: The mechanistic view should consider drift not to be a mechanism

Metatheoretical Diversity

- Causal interpretations:
 - Force explanations
 - Causal process explanations
 - Mechanistic explanations
- Statistical interpretations

Where Next?

- Forces vs. processes vs. mechanisms
 - Drift: a process, a force, *not* a mechanism
 - Multi-level mechanisms
- An example of drift-as-force?

Questions?

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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).