Exploring the complicated role of evolutionary modeling in paleobiology

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Overview

- Two instances where evolutionary modeling meets human paleobiology

  1. Sequence evolution models behind molecular tests for natural selection

  2. Models of cooperation in connection with the evolution of human cognition and social behavior

- Conclusion: comparison and a coincidence

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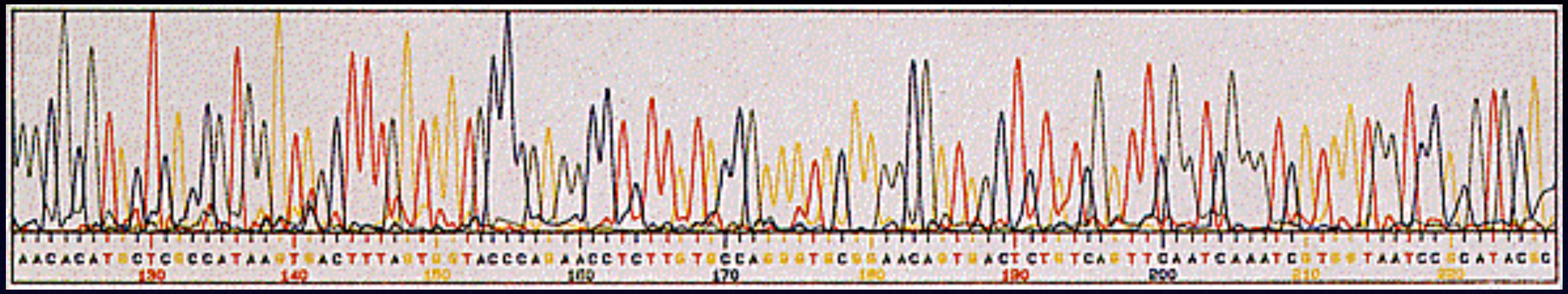
- The epistemic risk: such signatures may be ***artifactual***—they may cohere with some selection hypothesis but be produced by different causes

Molecular signatures



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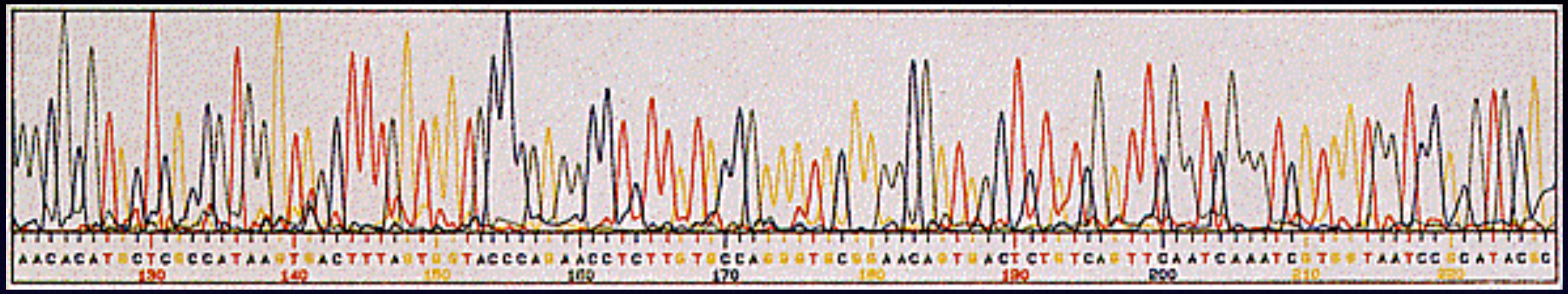

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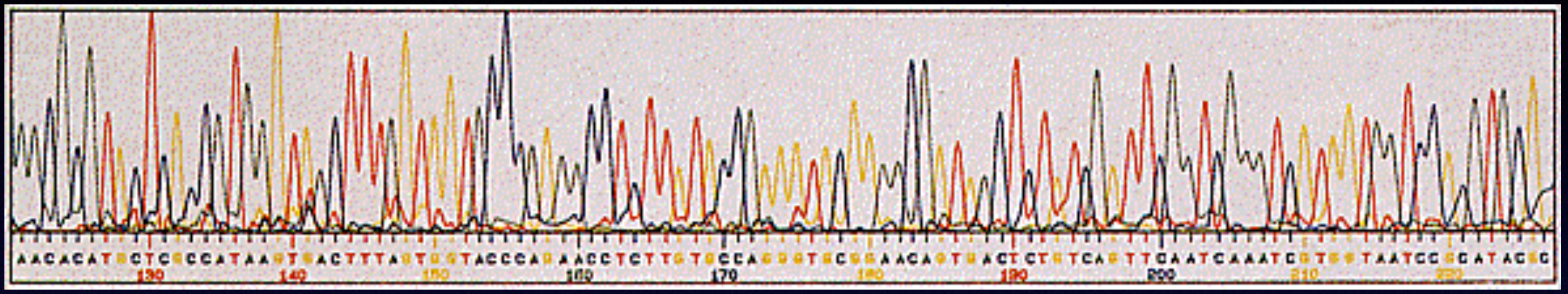

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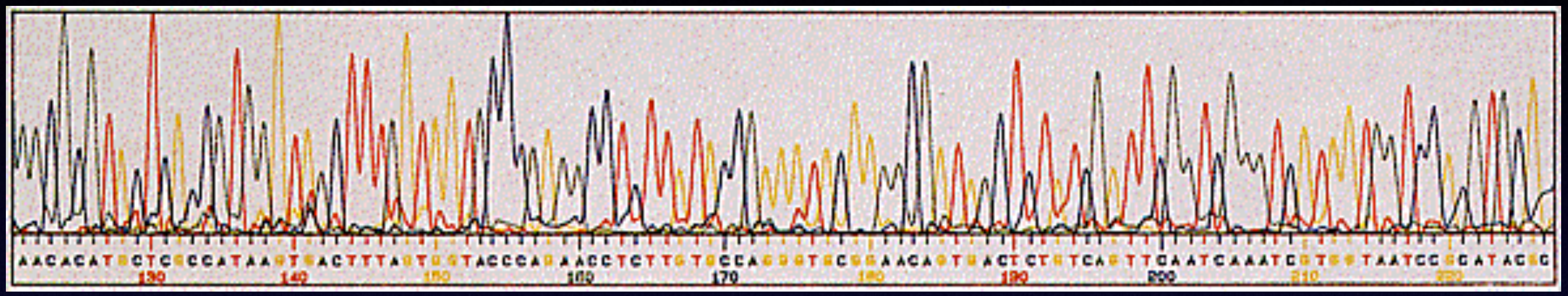

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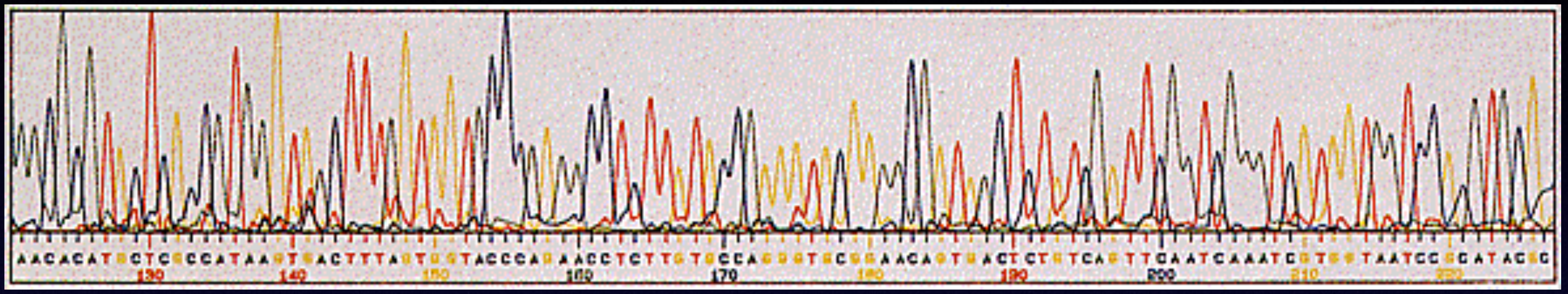

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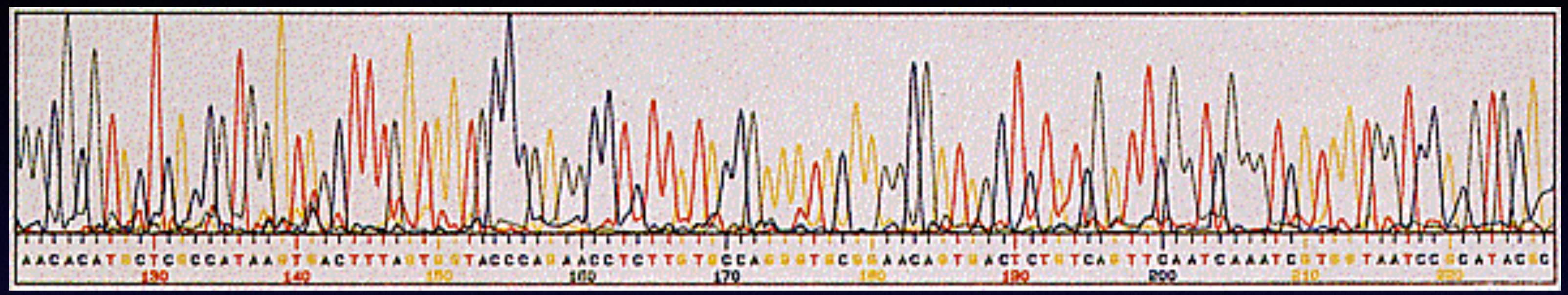

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    - *Ratio of nonsyn. to syn. substitution rates* (d_n/d_s)
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    - *Frequency spectrum*

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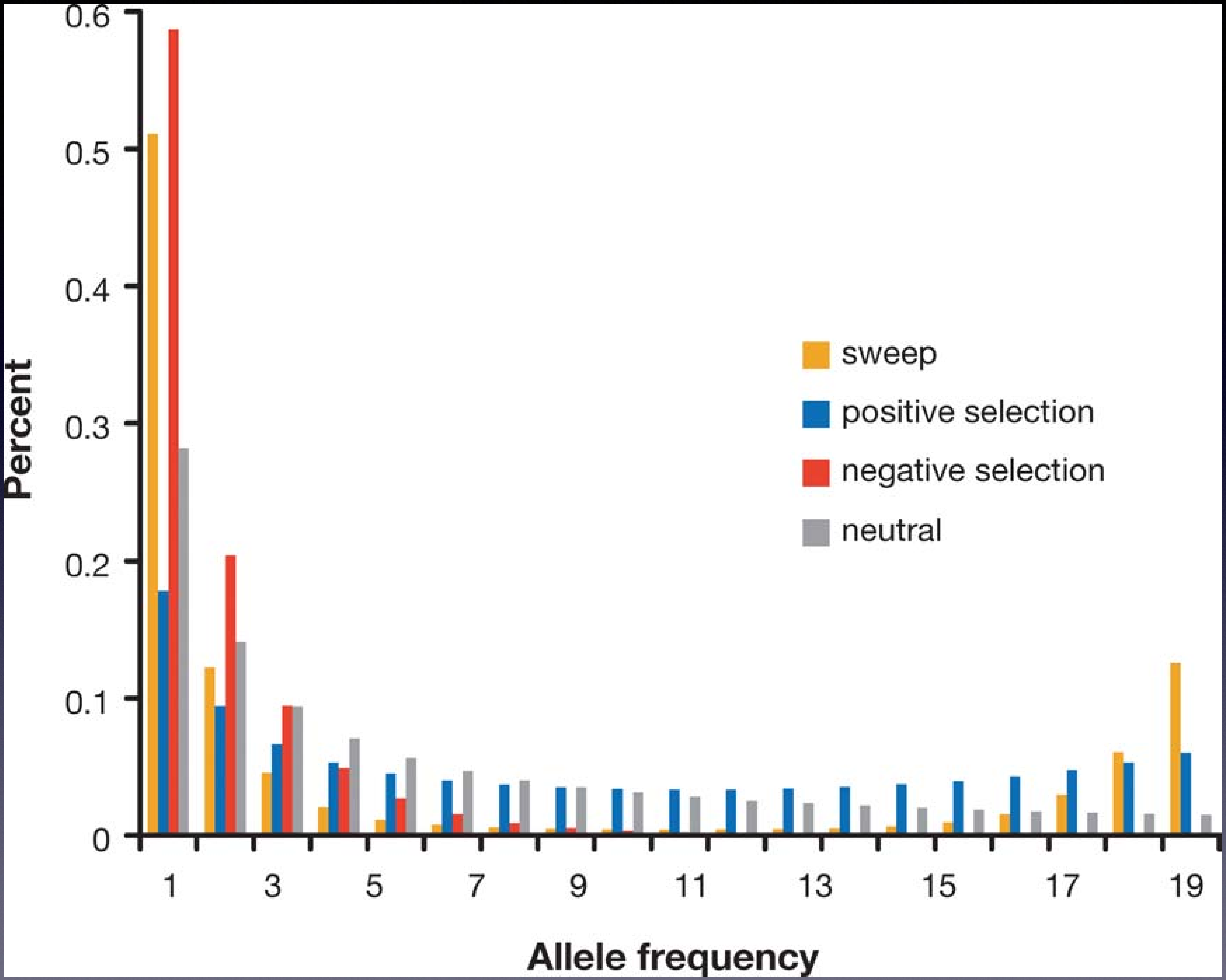
- *Frequency spectrum*: a distribution of the number of segregating sites that occur at a specific frequency in the sample data

Frequency spectrum

More precisely, the distribution of the number of sites *x* at some frequency across a sequence sample size of *n.*

$$x_i : \text{number of sites at frequency} = \frac{i}{n},$$
$$\text{for } i = 1, \ldots, n-1$$

$$E(x_i) \propto \frac{1}{i} \quad \text{and depends on} \quad \theta,\ \theta = 4N_e\mu$$



From Nielsen 2005 based on Sawyer & Hartl 1992

Signatures in the frequency spectrum

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- Tajima's D test (Tajima 1989) is a common statistical test for the frequency spectrum
  - Perhaps the most widely used test (Dietrich, pers. comm.)
  - Used extensively on human DNA (Carlson et al 2005; Nielsen et al 2005; Oleksyk et al 2010)

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  - Used extensively on human DNA (Carlson et al 2005; Nielsen et al 2005; Oleksyk et al 2010)
- Compares two different estimates of the neutral parameter where each estimate is sensitive to different features of the frequency spectrum
  - Number of segregating sites vs average number of pairwise nucleotide differences

Signatures in the frequency spectrum

- Tajima's D statistic compares the *difference* between the two estimates (normalized)

- Expectations:

$$Neutrality \Rightarrow D = 0$$

$$Purifying\ selection \Rightarrow D < 0$$

$$Positive\ selection \Rightarrow D > 0$$

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- Sequence evolution models make significant idealizations about the evolutionary process (rates, rate heterogeneity, demographics)

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- This is done using a sequence evolution model that incorporates randomly occurring adaptive mutations: *the PRF model* (Sawyer and Hartl 1992)

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  - Involves problematic idealizations about the nature and rate of evolutionary processes
- Or, we can select the model and parameter values based on molecular data
  - Relies on model selection statistics (now the standard strategy)

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  - Demographic fluctuations affect the whole genome whereas selection targets specific genes
  - Functional information about the genes under consideration can help constrain the sequence evolution model

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  - Social intelligence hypotheses: e.g., the demands of larger social groups or the Machiavellian arms race between cheating and detection
  - Recent emphasis on cooperation and collaboration (Sterelny 2012; Tomasello et al 2012)

Cooperation as the key?

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  - Sterelny: information pooling facilitates the productivity of cooperation, leads to adaptations for “high-fidelity cultural learning”
- Once cooperation becomes entrenched punishment and partner choice help enforce it

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Convergence on a key result:

- Correlated interaction of behaviors is the key to the evolution of cooperation (Hamilton 1964; Skyrms 1996; Fletcher and Doebeli 2009)

Lurking danger:

- Mechanisms can generate negatively correlated interactions that facilitate the evolution of spite (Hamilton 1970; Price 1970)

Generating correlations

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- Conditional behavior
  - Greenbeards (West and Gardner 2010)
  - Direct and indirect reciprocity (Trivers 1971; Nowak and Sigmund 2005)
  - Partner choice (Eshel and Cavalli-Sforza 1982; Baumard et al. 2013)

Generating correlations

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- Many others: signaling; spatial or population structure; ***small population or group size***

Help versus Harm

Consider two games: Help and Harm

Conditional behavior can enable the evolution of costly social behavior:

1. Help: altruism conditional on pairing with another altruist

2. Harm: spite conditional on pairing with an egoist

Help (Prisoner's Dilemma)

	altruism	egoism
altruism	b-c	-c
egoism	b	0

Harm (Prisoner's Delight)

	egoism	spite
egoism	0	-h
spite	-c	-h-c

b = benefit from altruism
h = harm from spite
c = cost to help or harm

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  - For example: Lehmann et al (2009) examine coevolution of neutral markers and marker-based conditional behavior
- Our approach: model coevolution of conditional strategies and a continuous recognition parameter
  - Recognition ability or “conditionality” of behavior

Help versus Harm

Consider two populations:

1. All conditional altruism in Help
2. All conditional spite in Harm

Suppose we let recognition evolve in these populations

1. Recognition selected against in Help
2. Recognition is selected for in Harm

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- Four strategies:

E : egoism in both

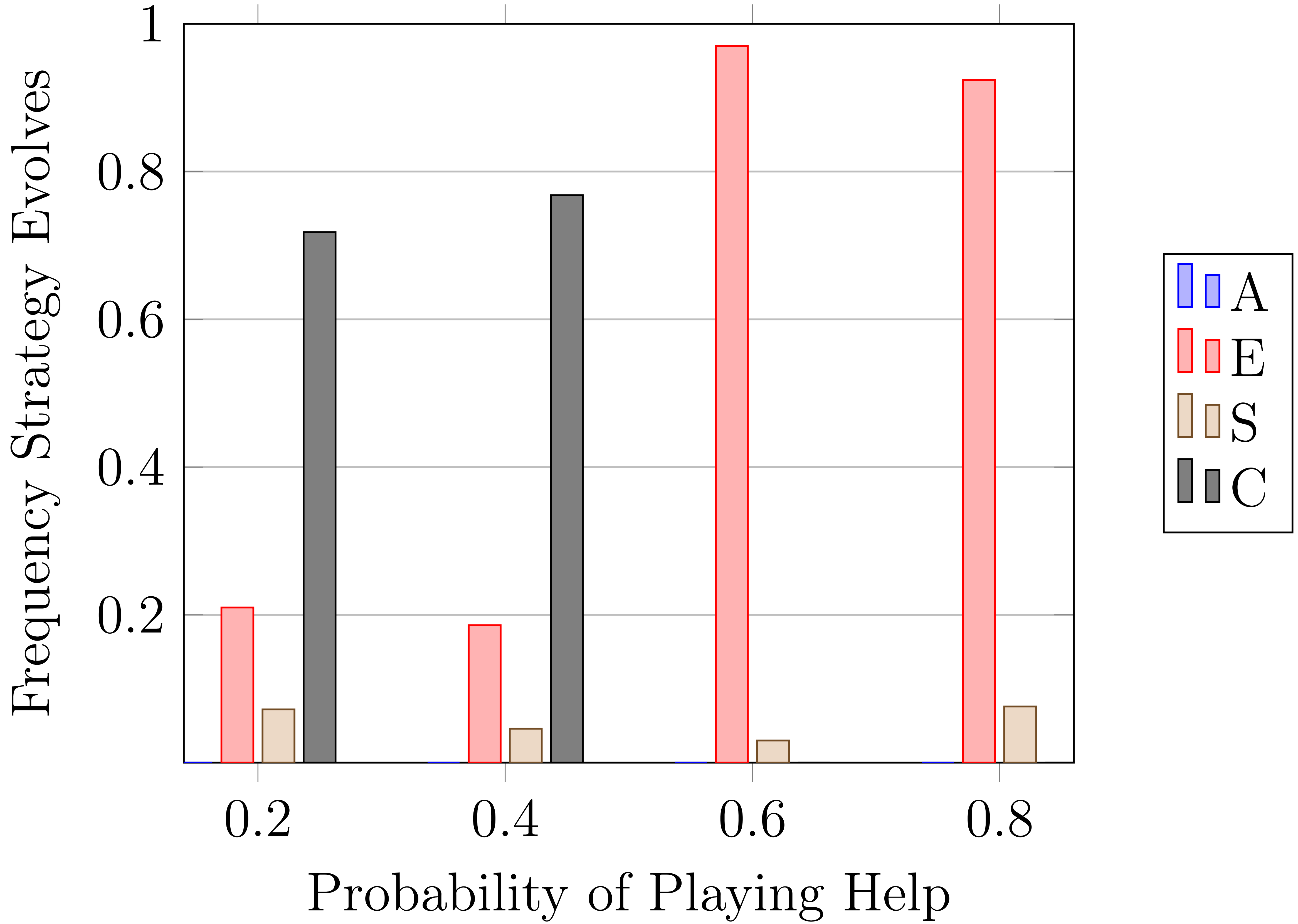
A : conditional altruism in Help

S : conditional spite in Harm

C : conditional altruism in Help and conditional spite in Harm

Coevolution

- Populations are represented by two vectors: one for type frequencies, one for recognition ability
- Recognition ability can range from 0 and 1
- Individuals meet at random
- Evolution occurs according to the replicator dynamics acting on both type frequencies and recognition ability simultaneously



1
0.8
0.6
0.4
0.2
Frequency Strategy Evolves
0.2
0.4
0.6
0.8
Probability of Playing Help
A
E
S
C

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- The standard story: cooperation evolves first in favorable conditions followed by punishment to enforce it
  - Punishment interpreted as altruism and poses a second-order free rider problem
- We have an alternative to the standard story about the evolution of punishment
  - Conditional spite may evolve first, stabilize recognition, allow cooperation to evolve later
  - Conditional spite may coevolve with conditional altruism

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- This scenario reverses the order of evolution
    - Conditional harming may have evolved first
    - And it may be crucial for maintaining the very mechanisms that enable cooperation
- There is a persistent challenge: the evolution of social behavior is a complicated affair and more formal work needs to be done to provide any help to paleobiological research

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- What should our attitude be towards the usefulness of evolutionary modeling for paleobiology?

1. On molecular tests for selection: optimistic, especially when augmented with information on gene function

2. On cooperation and cognitive complexity: less optimistic, especially given the potential evolutionary role of spite

The coincidence

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- Disparate instances of evolutionary modeling: molecular sequence evolution versus evolution of social behavior
- Yet both are missing the same crucial component: ***demographic information on population size and structure***

The end. Thanks.

Citations and papers available upon request

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The evolution of spite and recognition is part of a collaborative project undertaken with Rory Smead at Northeastern University