Selection and the Roy Model in the Neolithic Transition

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Introduction

Technological and climate shift

- direct effect: incentives and decisions
- **indirect effect**: population distribution

This paper

- Climate shift and adoption of agriculture over the past 14,000 years
- Link selection to economic activity choice (farming vs foraging)
- Evolution in population distribution
- **Impact**: current choices depend on actions of past generations

Contributions

Polygenic selection: Berg and Coop (2014); Racimo, Berg, and Pickrell (2018); Guo, Yang, and Visscher (2018); Cox et al. (2019); S. Mathieson and Mathieson (2018); Uricchio (2020); I. Mathieson (2021); Song et al. (2021); Stern et al. (2021); Yair and Coop (2022)

Link to economic model of activity choice

Economics of farming spread: Bowles (2011); Bowles and Choi (2013); Robson (2010); Rowthorn (2011); Rowthorn and Seabright (2010)

Emphasise the role of genotype distribution

Climate and agriculture

Holocene ($\approx$ 11,000 years ago - present)

- warmer temperatures ▸ Figures
- increased precipitation ▸ Figure
- more stable climate (Feynman and Ruzmaikin 2007)

Agriculture

- begins to spread $\approx$ 11,000 years ago ▸ Figure
- higher marginal productivity thanks to climate change
- evolutionary advantages: higher fertility, lower mortality (Shennan 2018)

Selection of farming-friendly genotypes

Model of genotype evolution

Based on Wright-Fisher model

- finite, constant population N
- K causal loci
- unit of analysis - haplotype pairs $\mathbf{H} = (l, r) = \left(\{0,1\}^K, \{0,1\}^K\right)$
- mutation, recombination, **selection**

▸ Process on haplotype pairs

Selection and technology

- $z(g)$ is a polygenic score

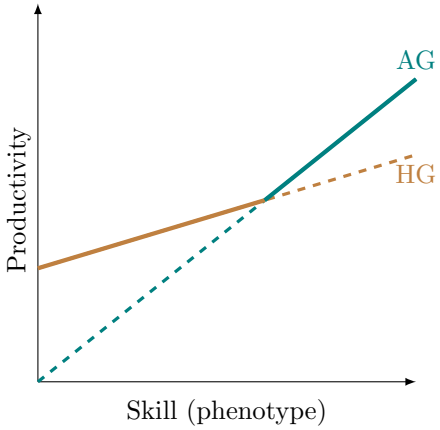
$$z(g) = \sum_{k=1}^{K} \beta(k) g(k)$$

- two technologies: HG - foraging and AG - farming
- technology-specific fitness function

$$f(z, \tau) = R_\tau \exp\left(\omega_\tau z\right), \forall \tau \in \{HG, AG\}$$

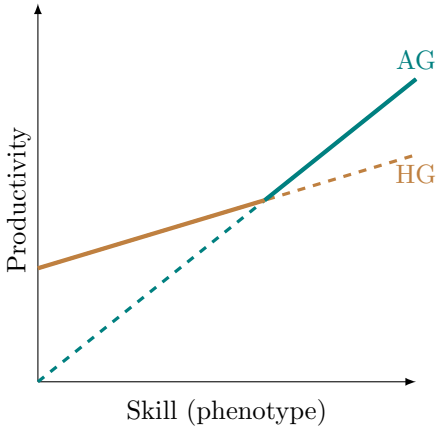
- **fitness-maximising technology choice**: $\hat{f}(z) \equiv \max_\tau f(z, \tau)$

Roy model

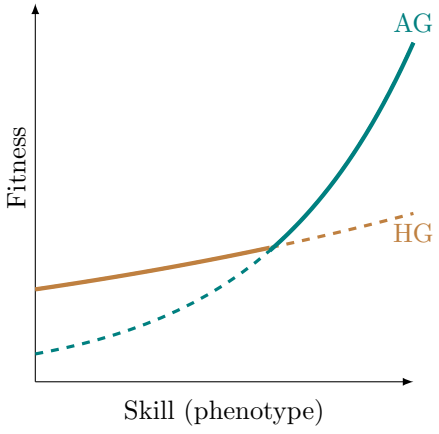


Technology choice

Roy model



Adapted to fitness



▸ Climate shift and fitness

Data

Genotypes

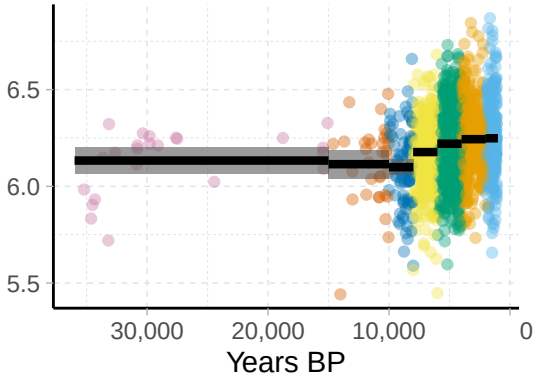
- Ancient DNA (David Reich Lab 2021)
  - 2,328 unrelated ancient individuals from Western Eurasia
  - Allele frequencies in Western hunter-gatherer (WHG) population ▸ ADMIXTURE
- 1000 Genome Project
  - 503 individuals from EUR populations

GWAS estimates

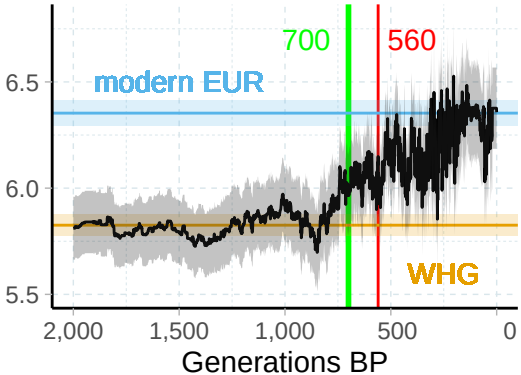
- Educational attainment (Lee et al. 2018)

Descriptive evidence

Education PGS in aDNA



Edge and Coop (2019) Waiting-time estimator

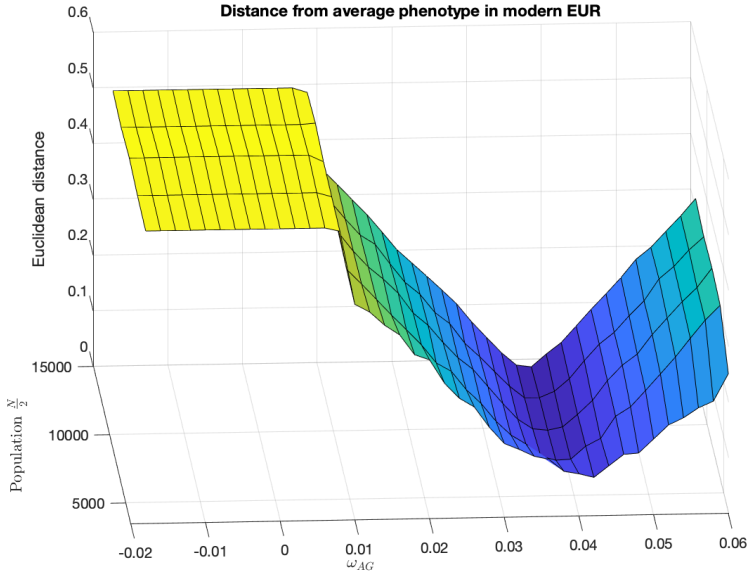


Estimation

Parameter of interest: technology-specific selection gradient ω_τ

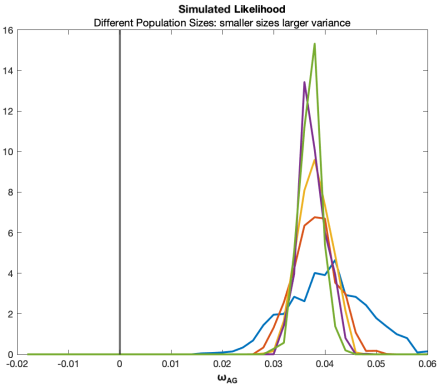
- Assume distribution before climate shift is at steady state: $\omega_{HG} = 0$
- Estimate ω_{AG} by maximising simulated likelihood
  - Draw initial haplotype matrix consistent with allele frequencies in WHG
  - Simulate independent histories from the model over T generations
  - Compute simulated likelihood of phenotypes in modern EUR

Results


Distance from average phenotype in modern EUR
Euclidean distance
0.6
0.5
0.4
0.3
0.2
0.1
0
Population $\frac{N}{2}$
15000
10000
5000
-0.02
-0.01
0
0.01
0.02
0.03
0.04
0.05
0.06
ω_{AG}

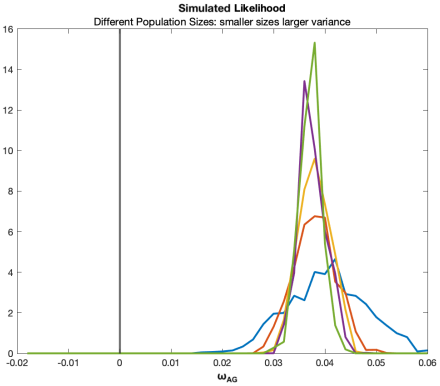
Results

Full sample

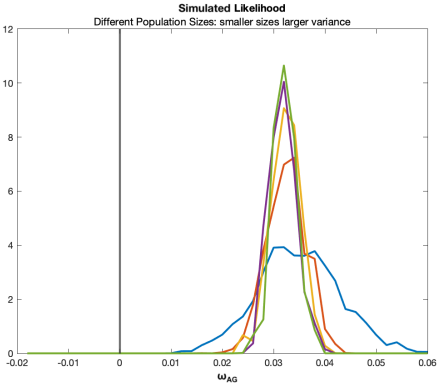


Results

Full sample



Truncated sample



Conclusion

- Study genetic evolution in European populations over the last 14,000 years
- Extend Wright-Fisher model with activity choice in the spirit of Roy model
- Estimate using ancient and modern genotypes

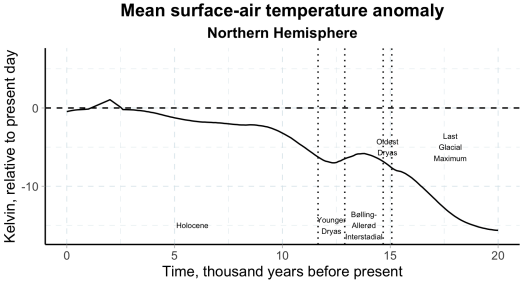
Current choices depend on actions of past generations

Future extensions:

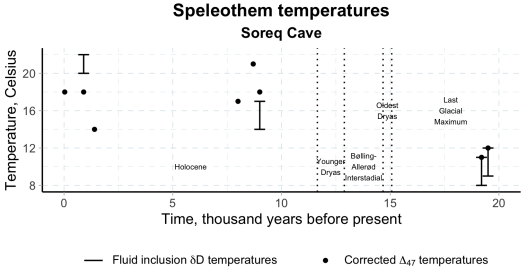
- Migration
- Estimation with path

Appendix

Climate (temperature)



Source: de Boer, Lourens, and van de Wal (2014)



Source: Affek et al. (2008)

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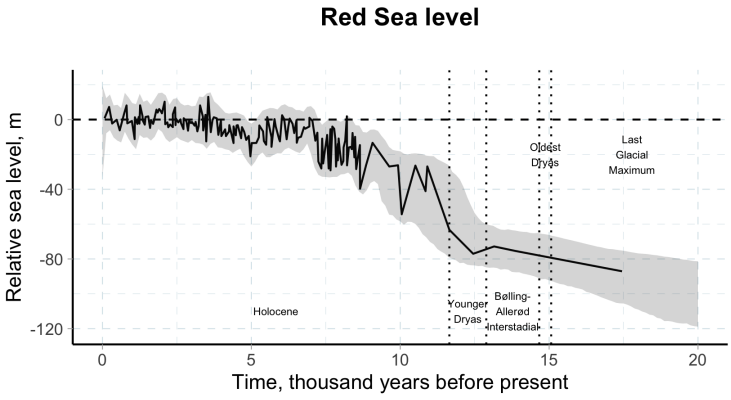
Climate (precipitation)



Source: Grant et al. (2012)

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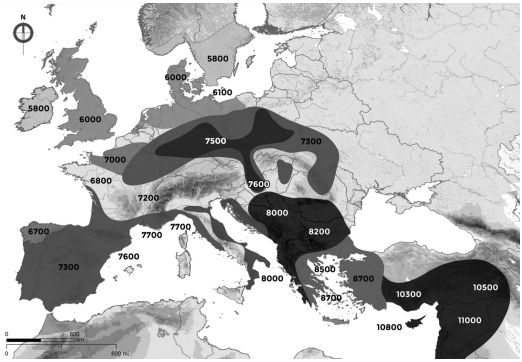
Spread of farming



Reprinted Fig 1.1 from Shennan (2018). Dates are shown in years before present.

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Process on haplotype pairs

1. (**Initial condition**) Haplotype pairs $h(t)$ at time t
2. (**Mutation**) Random mutation, independent across alleles, loci and individuals.
3. (**Cross-over recombination**) Non-homogeneous Poisson distribution
4. (**Random mating**)
5. (**Reproduction**) One haplotype from each parent, independently across children and chromosomes
6. (**Selection**) *Relative* fitness of every child reaching the reproductive age
7. (**Next generation**) Random draw from multinomial distribution over the haplotypes of size N and probabilities adjusted by the relative fitness

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Climate shift and fitness

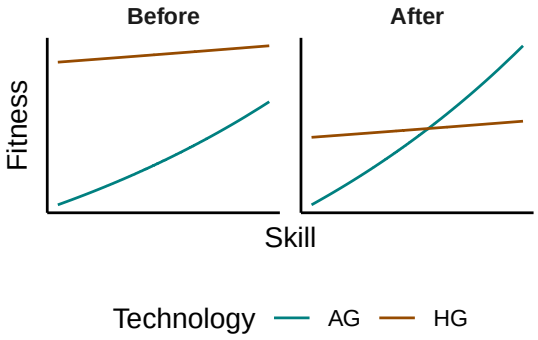

Figure 1: Fitness functions

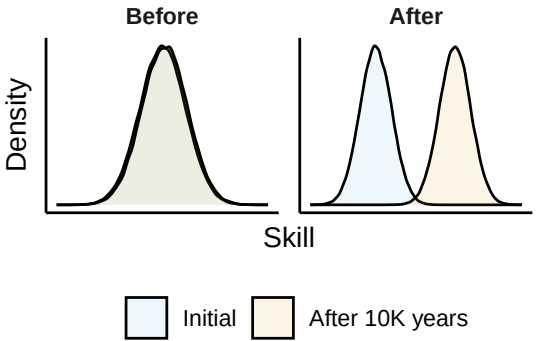

Figure 2: Population distribution

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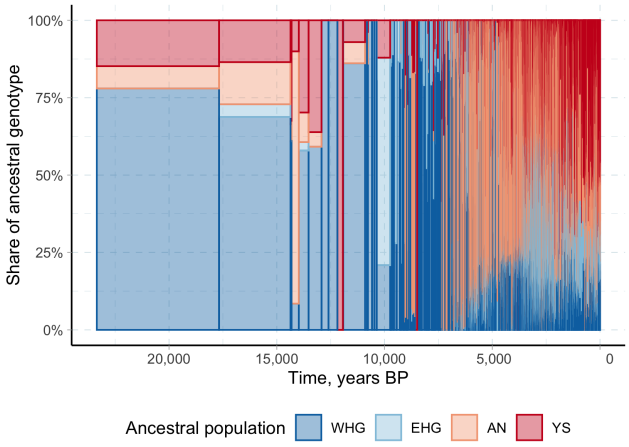
Supervised ADMIXTURE



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