

Selection and the Roy Model in the Neolithic Transition

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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

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

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 $\mathbf{H} = (l, r) = (\{0, 1\}^K, \{0, 1\}^K)$
- mutation, recombination, **selection**

► Process on haplotype pairs

- $z(g)$ is a polygenic score

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

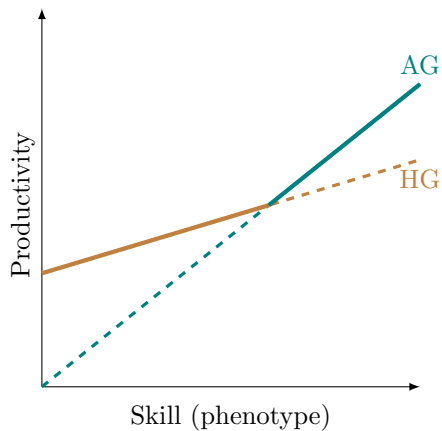
- two technologies: HG - foraging and AG - farming
- technology-specific fitness function

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

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

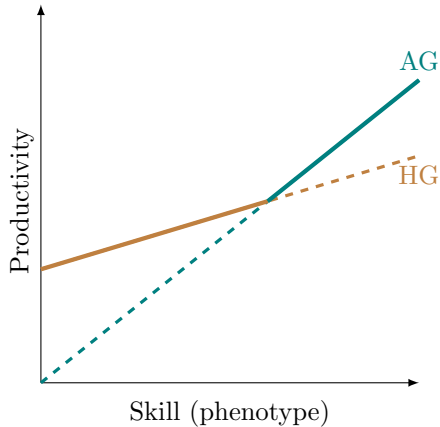
Technology choice

Roy model

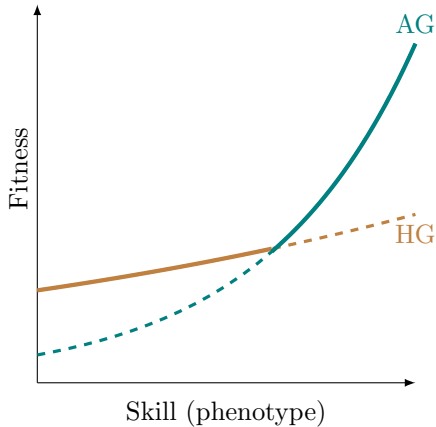


Technology choice

Roy model



Adapted to fitness



Genotypes

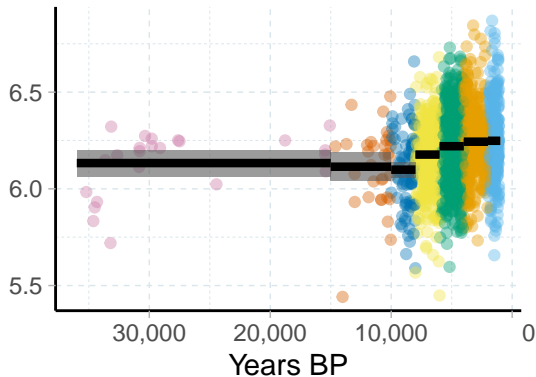
- Ancient DNA (David Reich Lab 2021)
 - 2,328 unrelated ancient individuals from Western Eurasia
 - Allele frequencies in Western hunter-gatherer (WHG) population [▶ ADMIXTURE](#)
- 1000 Genome Project
 - 503 individuals from EUR populations

GWAS estimates

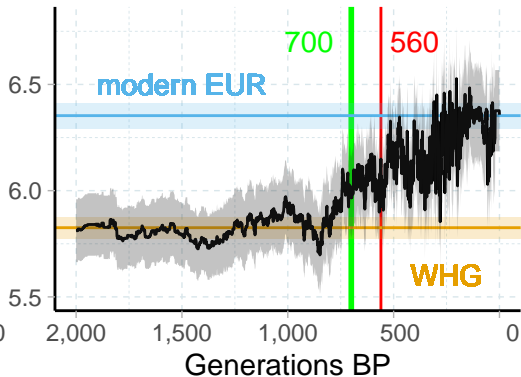
- Educational attainment (Lee et al. 2018)

Descriptive evidence

Education PGS in aDNA



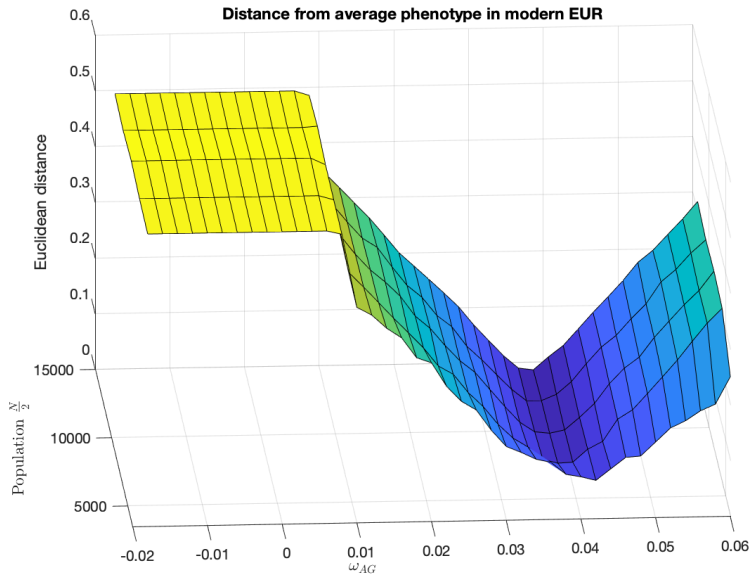
Edge and Coop (2019) Waiting-time estimator



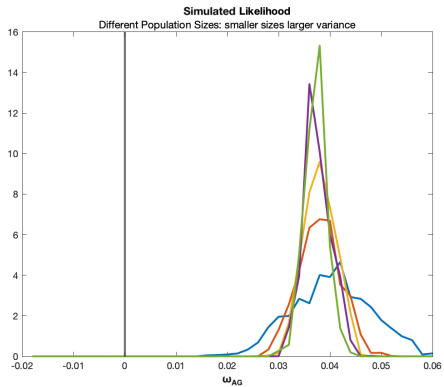
Parameter of interest: technology-specific selection gradient ω_{τ}

- 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

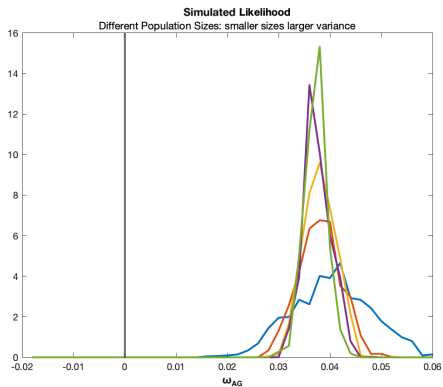
Results



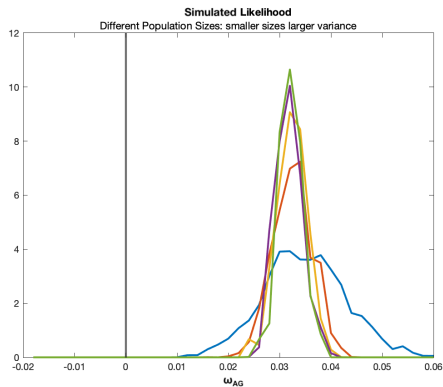
Full sample



Full sample



Truncated sample



- 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

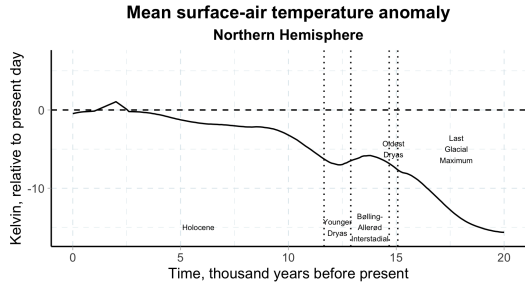
Current choices depend on actions of past generations

Future extensions:

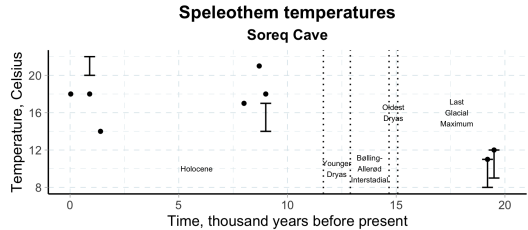
- Migration
- Estimation with path

Appendix

Climate (temperature)



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

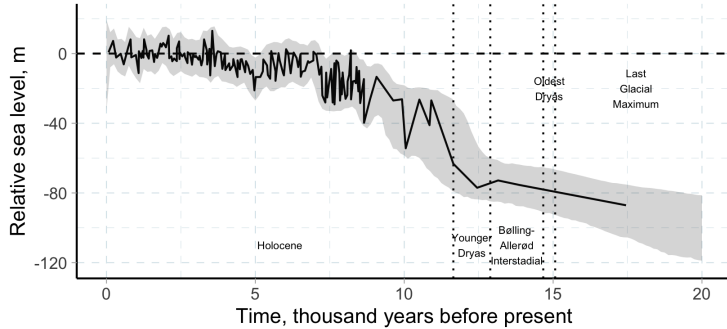


— Fluid inclusion δD temperatures

• Corrected Δ_{47} temperatures

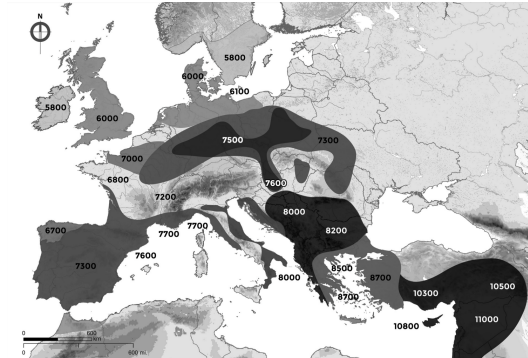
Source: Affek et al. (2008)

Red Sea level



Source: Grant et al. (2012)

Spread of farming

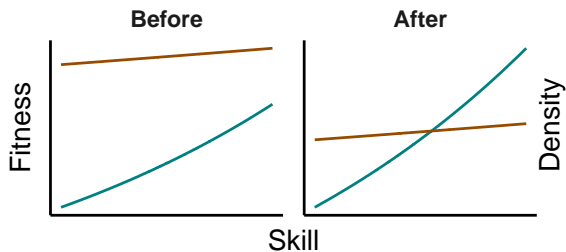


Reprinted Fig 1.1 from Shennan (2018). Dates are shown in years before present.

Process on haplotype pairs

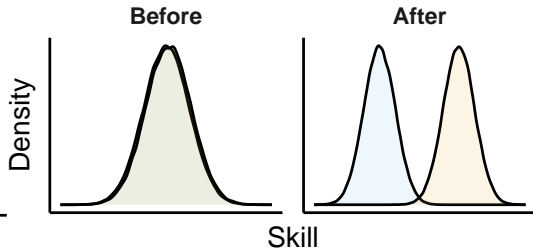
1. (**Initial condition**) Haplotype pairs $h(t)$ at time t
2. (**Mutation**) Random mutation, independent across alleles, loci and individuals.
3. (**Cross-over recombination**) Non-homogeneous Poisson distribution
4. (**Random mating**)
5. (**Reproduction**) One haplotype from each parent, independently 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

Climate shift and fitness



Technology — AG — HG

(a) Fitness functions



Initial After 10K years

(a) Population distribution

Supervised ADMIXTURE

