

# 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

## Selection and technology

- $z(g)$  is a polygenic score

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

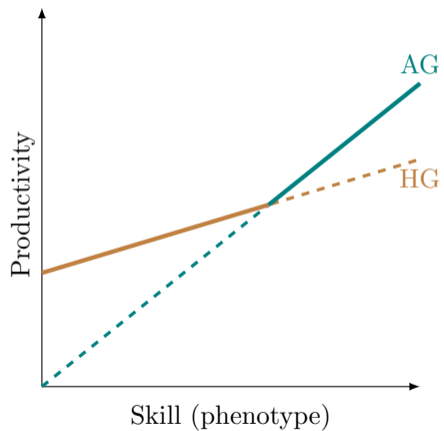
- two technologies: HG - foraging and AG - farming
- technology-specific fitness function

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

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

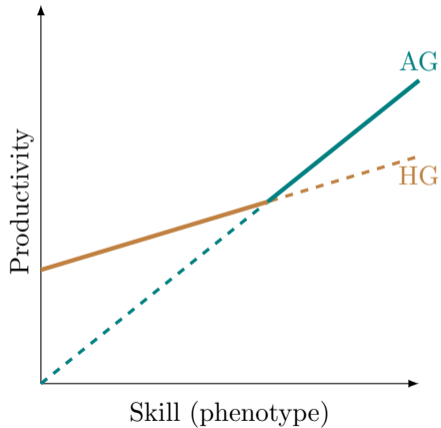
# Technology choice

## Roy model

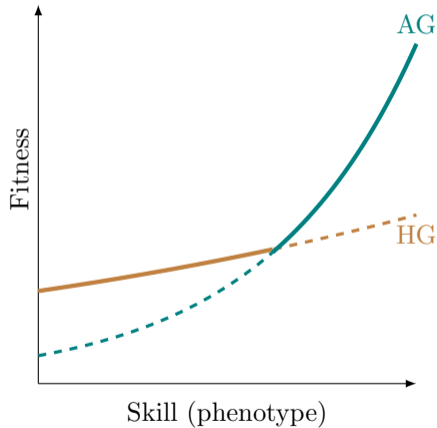


# Technology choice

Roy model



Adapted to fitness





## Genotypes

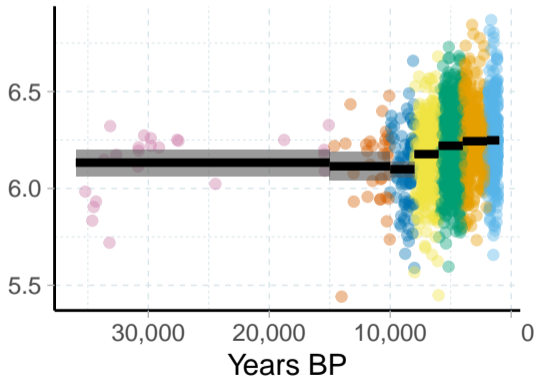
- Ancient DNA (David Reich Lab 2021)
  - 2,328 unrelated ancient individuals from Western Eurasia
  - Allele frequencies in Western hunter-gatherer (WHG) population ▶ ADMIXTURE
- 1000 Genome Project
  - 503 individuals from EUR populations

## GWAS estimates

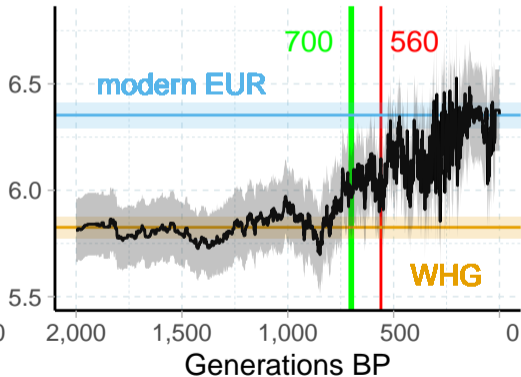
- Educational attainment (Lee et al. 2018)

# Descriptive evidence

## Education PGS in aDNA



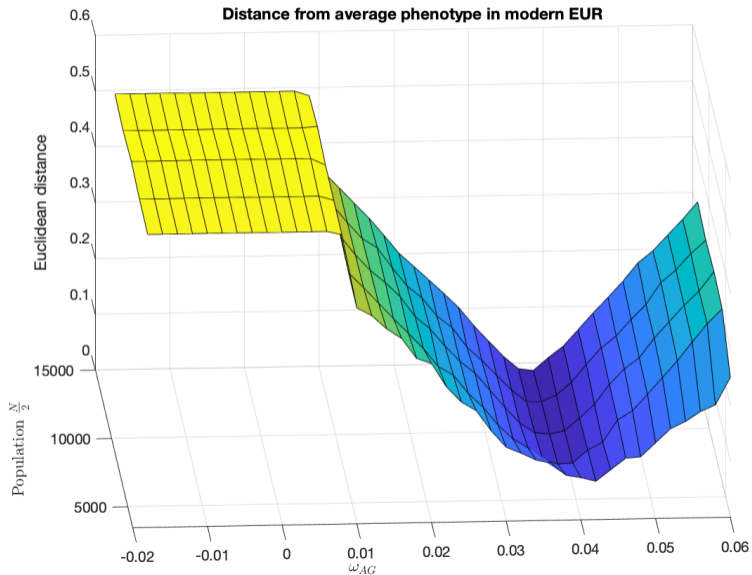
## Edge and Coop (2019) Waiting-time estimator



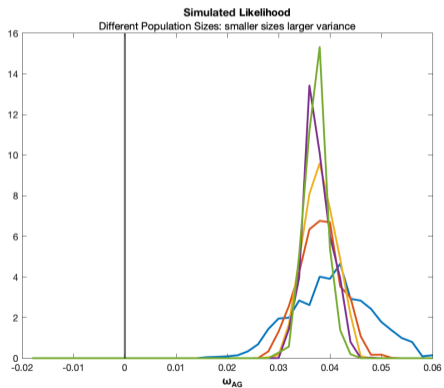
Parameter of interest: technology-specific selection gradient  $\omega_{\tau}$

- Assume distribution before climate shift is at steady state:  $\omega_{HG} = 0$
- Estimate  $\omega_{AG}$  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

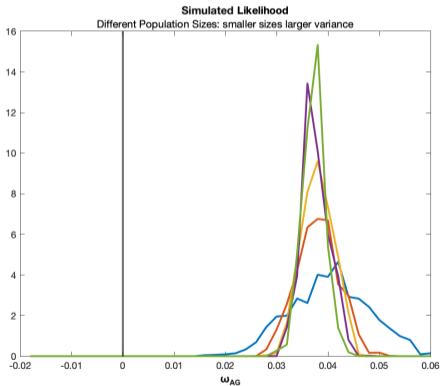
# Results



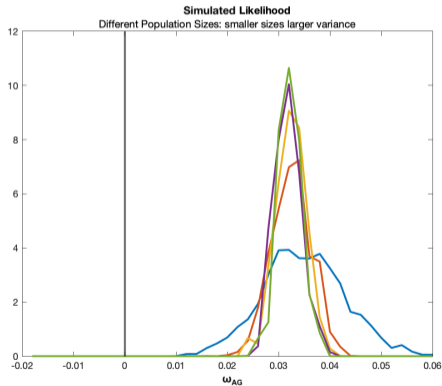
## Full sample



## 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

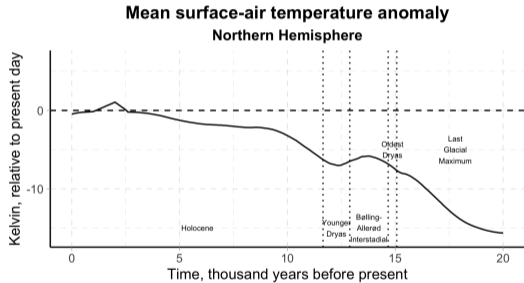
Future extensions:

- Migration
- Estimation with path

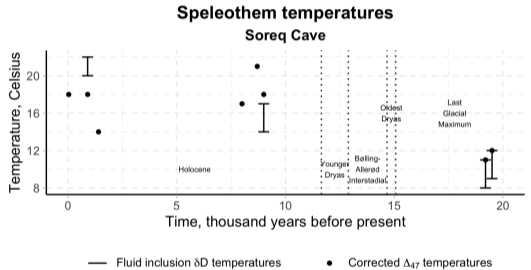
# Appendix



# Climate (temperature)



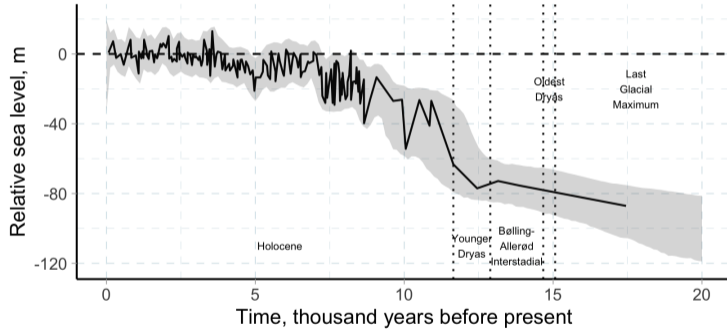
Source: de Boer, Lourens, and van de Wal (2014)



Source: Affek et al. (2008)

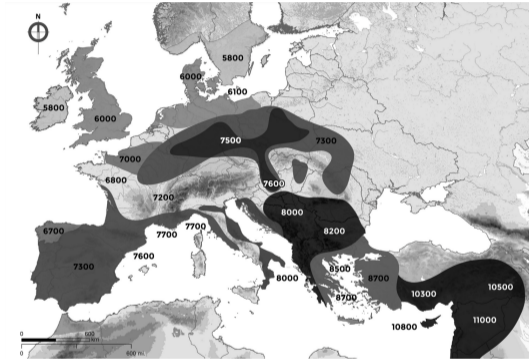
# Climate (precipitation)

## Red Sea level



Source: Grant et al. (2012)

# Spread of farming

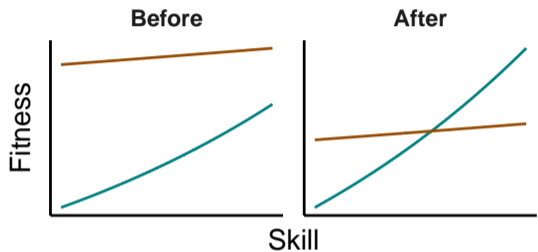


Reprinted Fig 1.1 from Shennan (2018). Dates are shown in years before present.

## Process on haplotype pairs

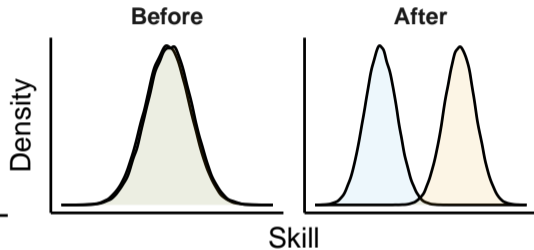
1. (**Initial condition**) Haplotype pairs  $h(t)$  at time  $t$
2. (**Mutation**) Random mutation, independent across alleles, loci and individuals.
3. (**Cross-over recombination**) Non-homogeneous Poisson distribution
4. (**Random mating**)
5. (**Reproduction**) One haplotype from each parent, independently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

(b) Population distribution

# Supervised ADMIXTURE

