Variance among groups increases across generations (Buri 1956)

Drift inflates variance among populations

Gene flow (migration) reduces population differences

PC map of European genetic distances

Genetic and geographic distance
Long shared segments ⇒ recent common ancestry

Sharing with French-speaking Swiss and UK

Sharing with Irish and Germans

Geographic decay of recent relatedness

Genetic map of Britain

Colors indicate genetically similar groups.
Variance among groups increases across generations (Buri 1956)

Wahlund principle: subdivision reduces heterozygosity

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<td>Hardy-Weinberg</td>
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Amount of reduction: 2/16

\[
p_i - \bar{p} \quad (p_i - \bar{p})^2
\]

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Variance: 1/16

\[ H_S = H_T - 2V \quad (\text{Wahlund 1928}) \]

- Wahlund showed that heterozygosity is reduced by group differences in allele frequencies.
- Buri’s experiment illustrates that
  - Drift reduces heterozygosity
  - Drift increases group differences
- We need a theory to connect these facts.
- Let us build one on top of what we have already.
What we already know about heterozygosity

$$E[H_t|p_t] = 2p_tq_t \text{ (Hardy-Weinberg)}$$

$$E[H_t|p_0] = 2p_0q_0 (1 - \frac{1}{2N})^t \text{ (Ch. 2)}$$

How can these both be true?

It must be true that

$$E[p_tq_t|p_0] = p_0q_0$$

On the other hand, it is also true that

$$E[p_tq_t|p_0] = p_0q_0 - V_t \text{ (Wahlund)}$$

where $V_t$ is the variance of $p_t$ about $p_0$.

Rearranging gives the variance among groups

$$V = p_0q_0 \left[ 1 - \left( 1 - \frac{1}{2N} \right)^t \right]$$

We usually normalize this expression by dividing both sides by $p_0q_0$. The result is called $F_{ST}$:

$$F_{ST} = \frac{V}{p_0q_0} = 1 - \left( 1 - \frac{1}{2N} \right)^t$$

In data analysis, we take $p_0 \approx \bar{p}$, the current population mean.

Application to differences among human races

Theory assumes no migration. Seems unlikely, but let's see where it leads.

For major human populations, $F_{ST} \approx 0.1$.

Two major hypotheses about the age human races.

- Replacement model: about 50,000 years (2000 generations)
- Multiregional model: at least 1,000,000 years (40,000 generations)

Plug these into

$$F_{ST} = 1 - \left( 1 - \frac{1}{2N_e} \right)^t$$

and solve for $N_e$.

What do these imply about $N_e$ of major continental populations?

- Replacement: $N_e \approx 10,000$
- Multiregional: $N_e \approx 200,000$

The first figure is more plausible: agrees with genetic diversity within populations.

If human races had been separated for a million years without gene flow, race differences should be larger.

But what about gene flow?
The role of migration

- Drift increases group differences.
- Migration (m) reduces them.
- Eventually, an equilibrium is reached.

\[ F_{ST} = \frac{1}{4N_em + 1} \]

Depends only on \( N_em \). Small if \( N_em > 1 \).
Human value (\( \approx 1/9 \)) implies \( N_em \approx 2 \).

Summary

- Drift increases variance among groups and reduces that within them.
- Wahlund’s principle: \( H_S = H_T - 2V \)
- \( F_{ST} \) measures between-group variance relative to total variance.
- By distinguishing between long and short IBD blocks, we can examine geographic population structure on different time scales.