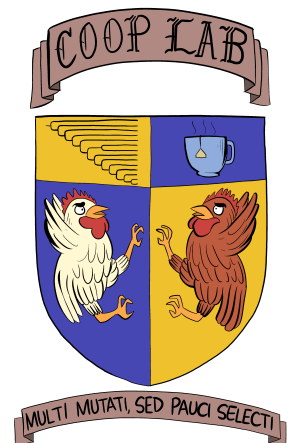


Distinguishing modes of convergent adaptation

Kristin Lee, Jeremy Berg, Graham Coop
University of California, Davis



Convergent adaptation

Adaptation across similar environments

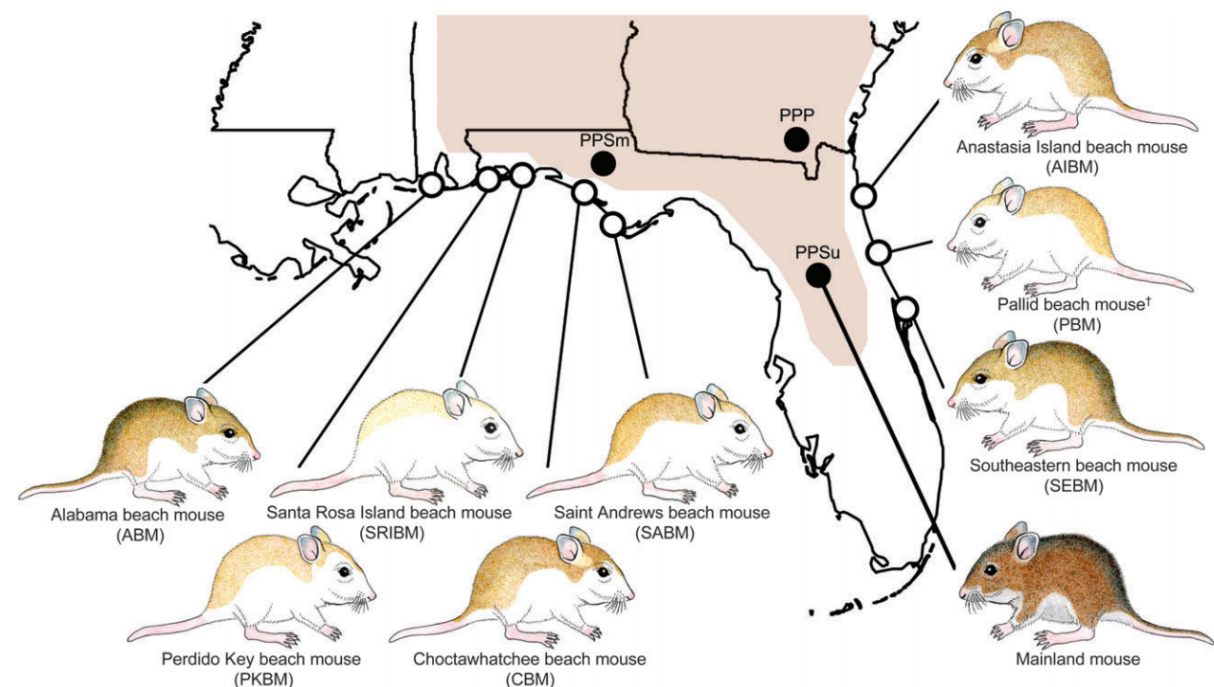
Many levels of convergent adaptation:

Phenotypic level across
species

Phenotypic level
within species



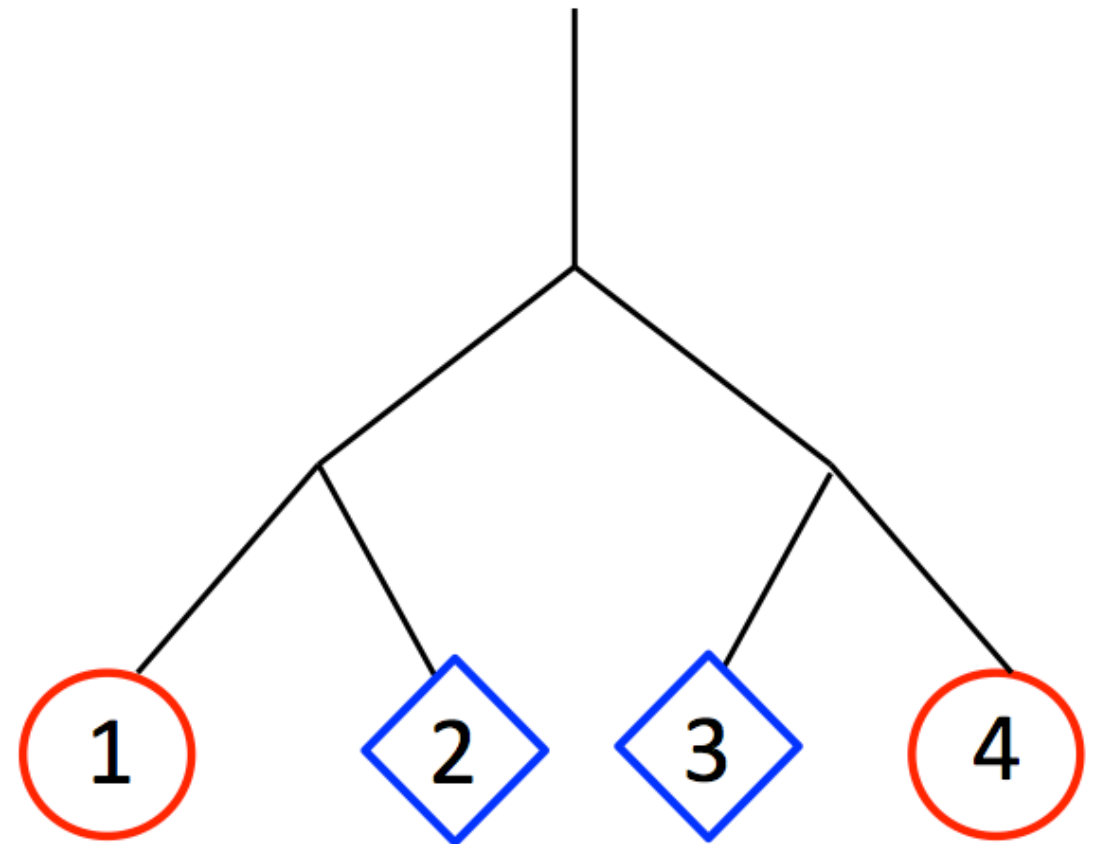
<http://webecoist.momtastic.com/2012/09/10/arctic-animals-37-photos-of-snow-white-wildlife/>



Steiner et al., *MBE* (2009)

Modes of genotypic convergent adaptation

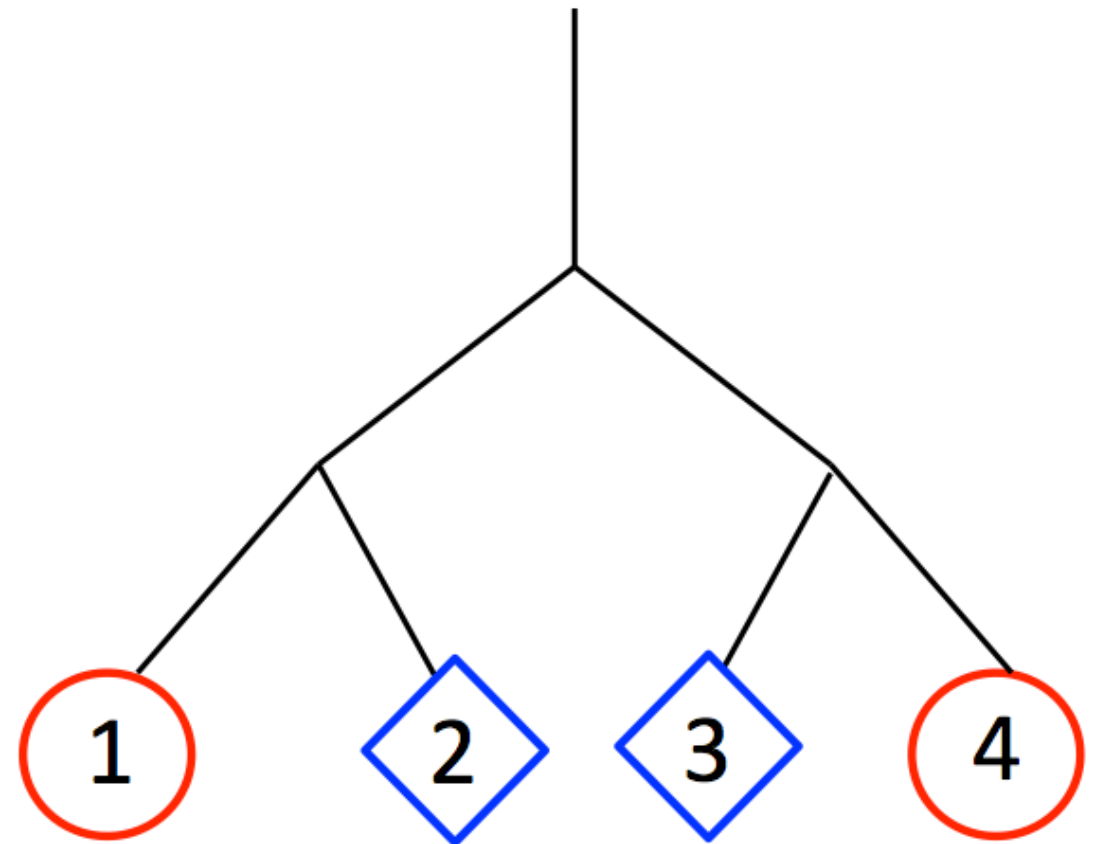
Multiple populations respond to similar environmental pressure using same genes



Modes of genotypic convergent adaptation

Multiple populations respond to similar environmental pressure using same genes

What is the basis of this adaptation?

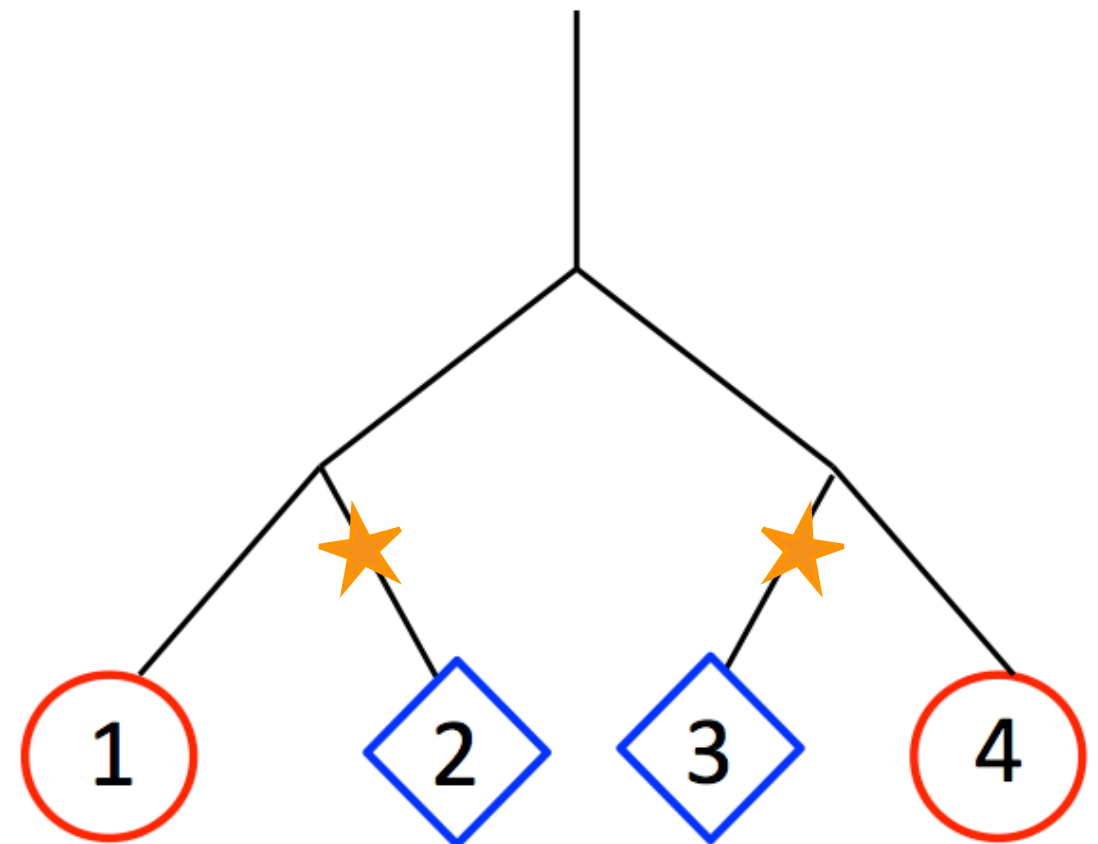


Modes of genotypic convergent adaptation

Multiple populations respond to similar environmental pressure using same genes

What is the basis of this adaptation?

1. Independent mutations in isolated populations

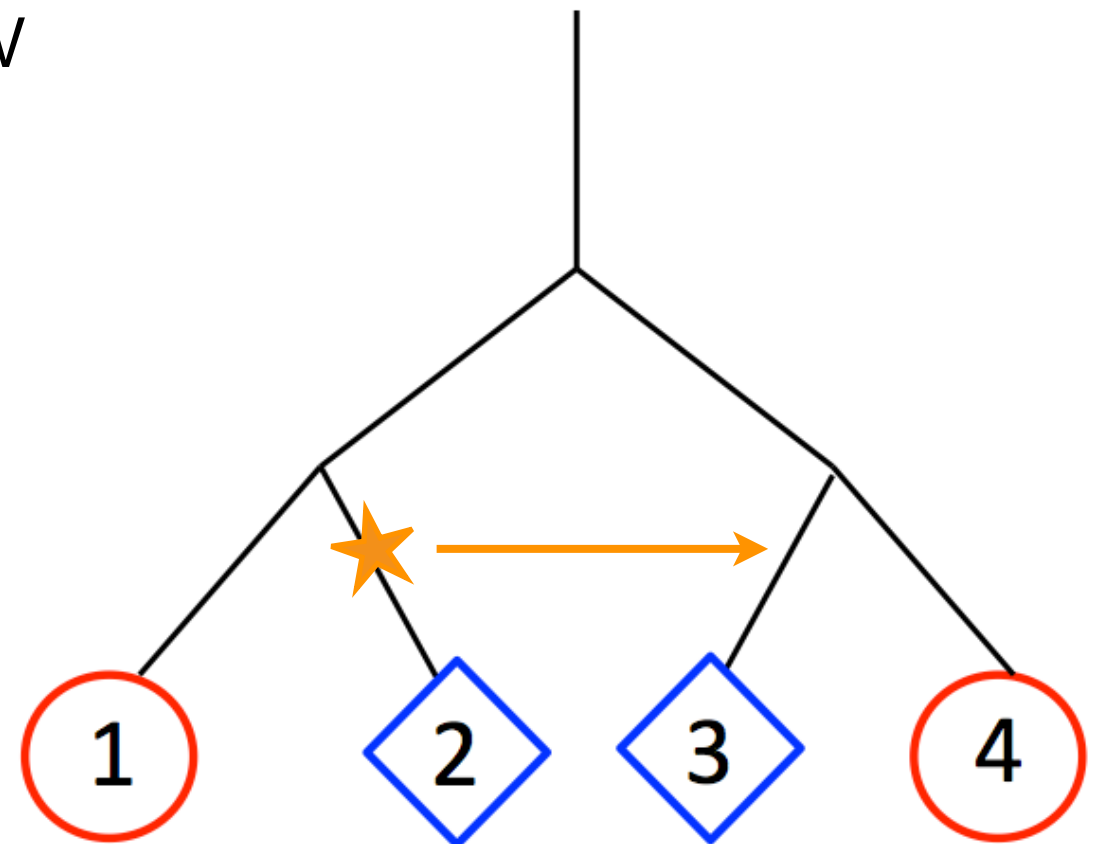


Modes of genotypic convergent adaptation

Multiple populations respond to similar environmental pressure using same genes

What is the basis of this adaptation?

1. Independent mutations in isolated populations
2. Single origin with gene flow

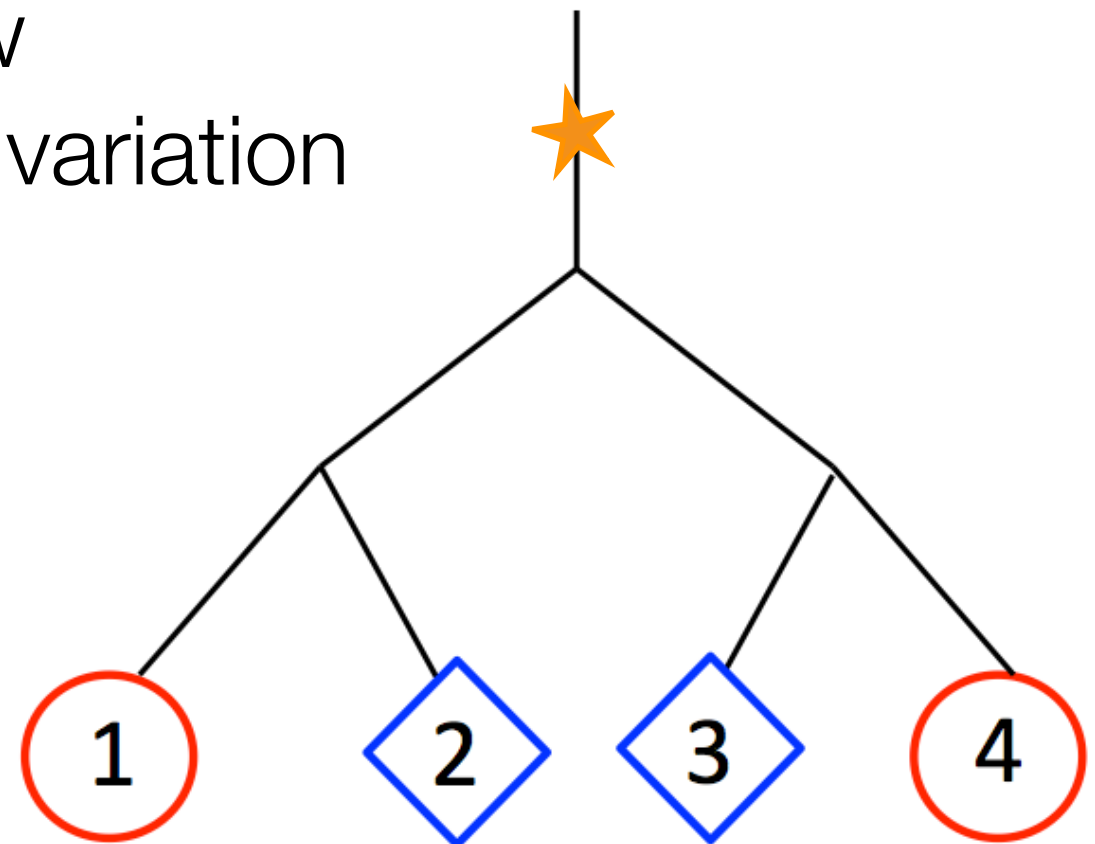


Modes of genotypic convergent adaptation

Multiple populations respond to similar environmental pressure using same genes

What is the basis of this adaptation?

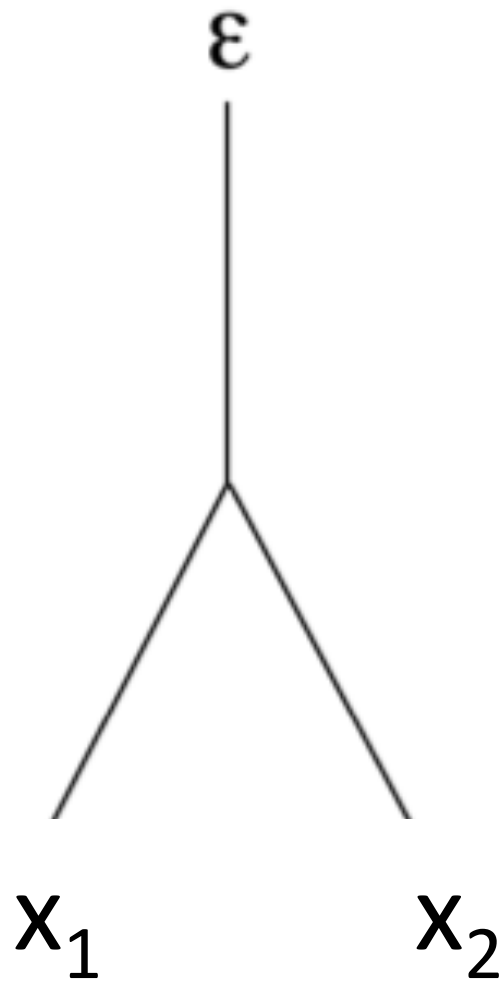
1. Independent mutations in isolated populations
2. Single origin with gene flow
3. Shared ancestral standing variation



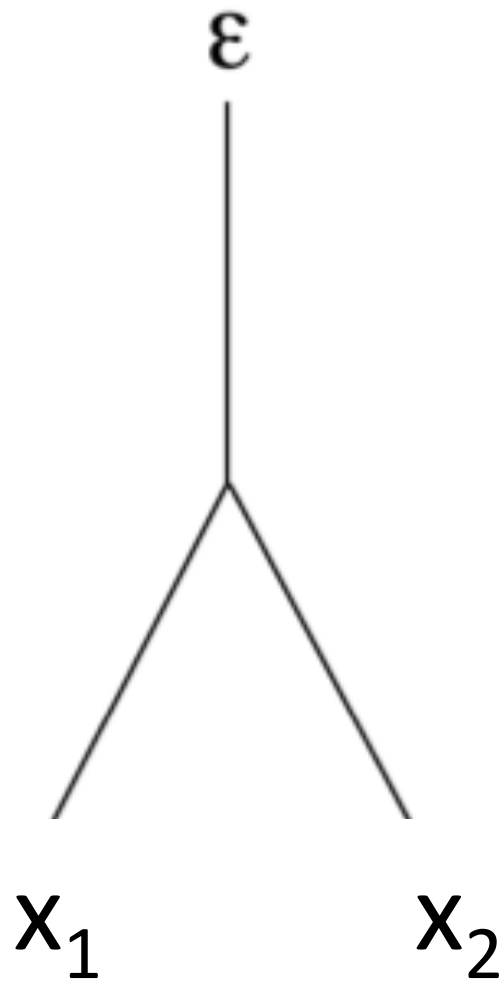
How can we distinguish modes of convergent adaptation using population genomic data?

1. Model allele frequencies around selected site
 - Null model
 - Variance within populations experiencing selection
 - Covariance between selected populations
2. Composite-likelihood approach to distinguish between these models

Effect of drift on population allele frequencies

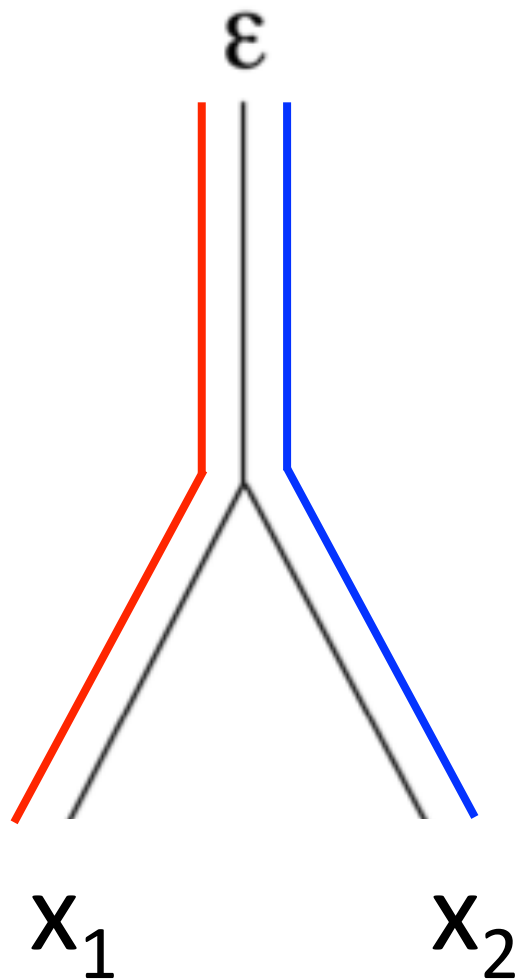


Effect of drift on population allele frequencies



$$\mathbb{E}[\Delta x_1] = \mathbb{E}[\Delta x_2] = 0$$

Effect of drift on population allele frequencies

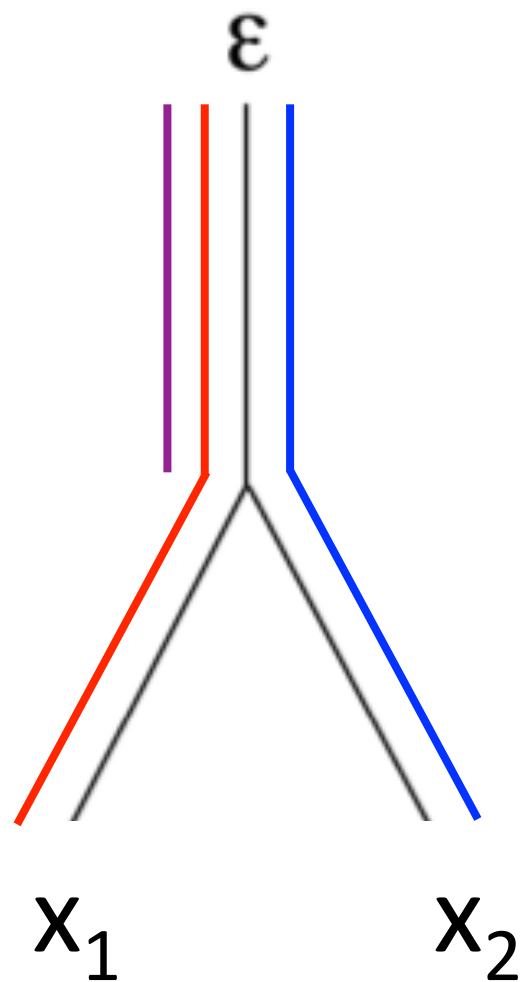


$$\mathbb{E}[\Delta x_1] = \mathbb{E}[\Delta x_2] = 0$$

$$\text{Var}[\Delta x_1] = \epsilon(1 - \epsilon)f_{11}$$

$$\text{Var}[\Delta x_1] = \epsilon(1 - \epsilon)f_{22}$$

Effect of drift on population allele frequencies



$$\mathbb{E}[\Delta x_1] = \mathbb{E}[\Delta x_2] = 0$$

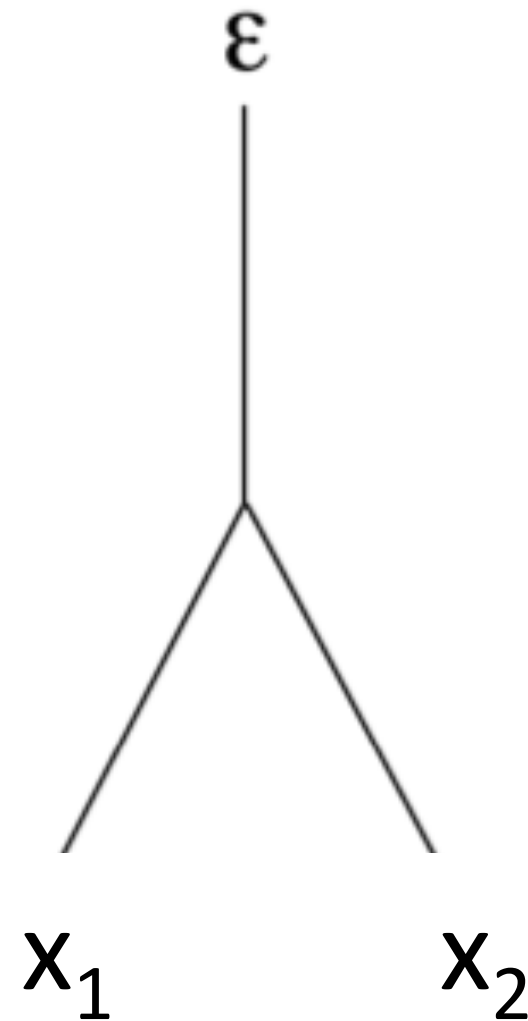
$$\text{Var}[\Delta x_1] = \epsilon(1 - \epsilon)f_{11}$$

$$\text{Var}[\Delta x_1] = \epsilon(1 - \epsilon)f_{22}$$

$$\text{Cov}[\Delta x_1] = \epsilon(1 - \epsilon)f_{12}$$

Coancestry coefficients

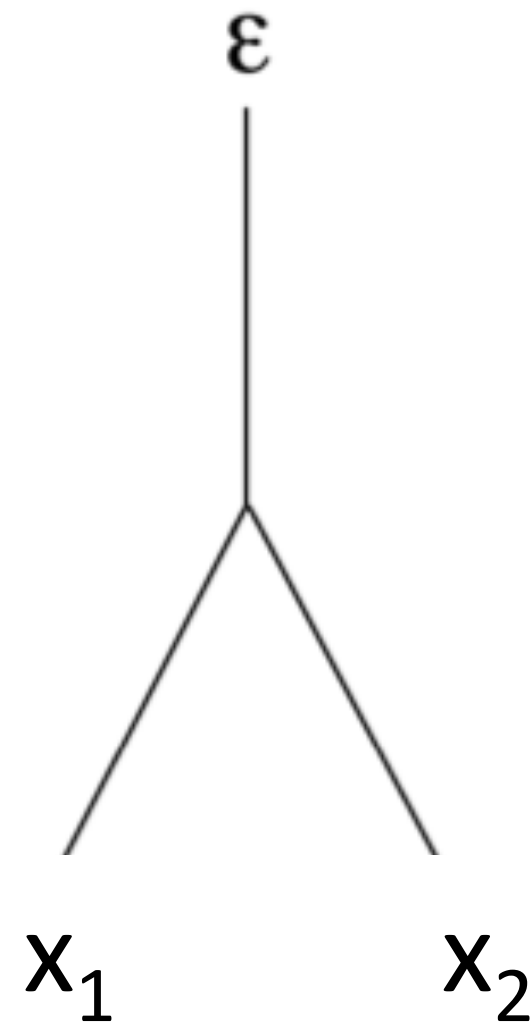
$$f_{ii} = \frac{\text{Var}[x_i]}{\epsilon(1 - \epsilon)}$$



Coancestry coefficients

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Probability a pair of lineages coalesce before reaching the ancestral population



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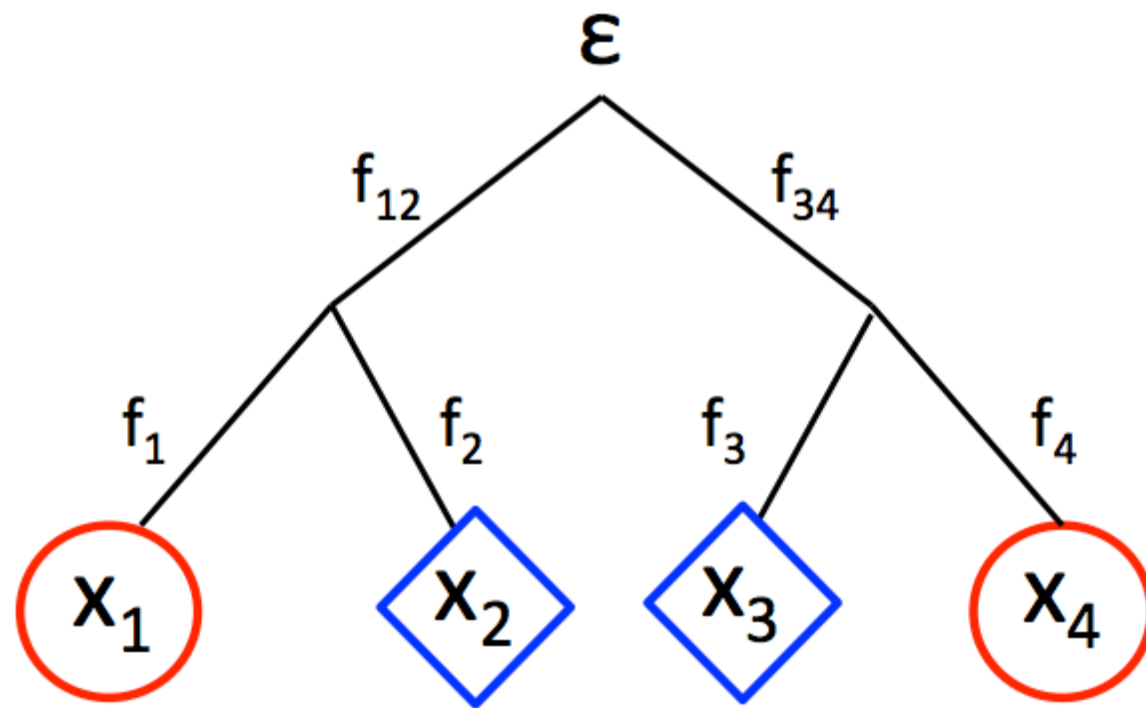
Coancestry coefficients

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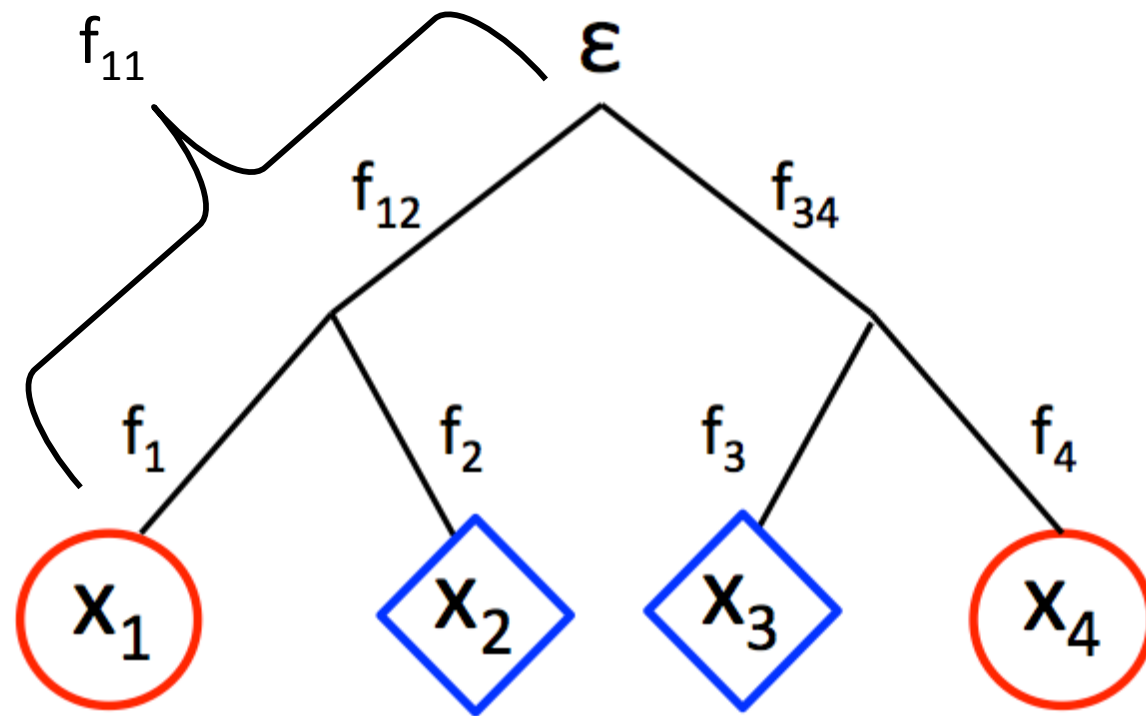
Probability a pair of lineages coalesce before reaching the ancestral population



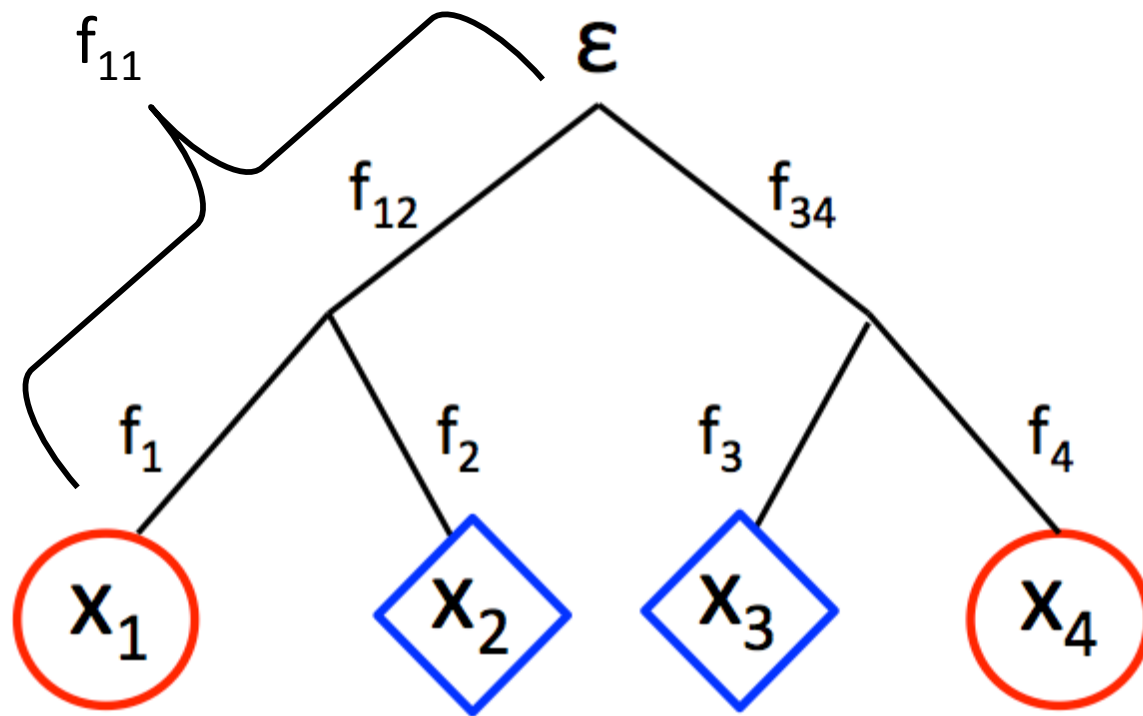
Four population model



Four population model

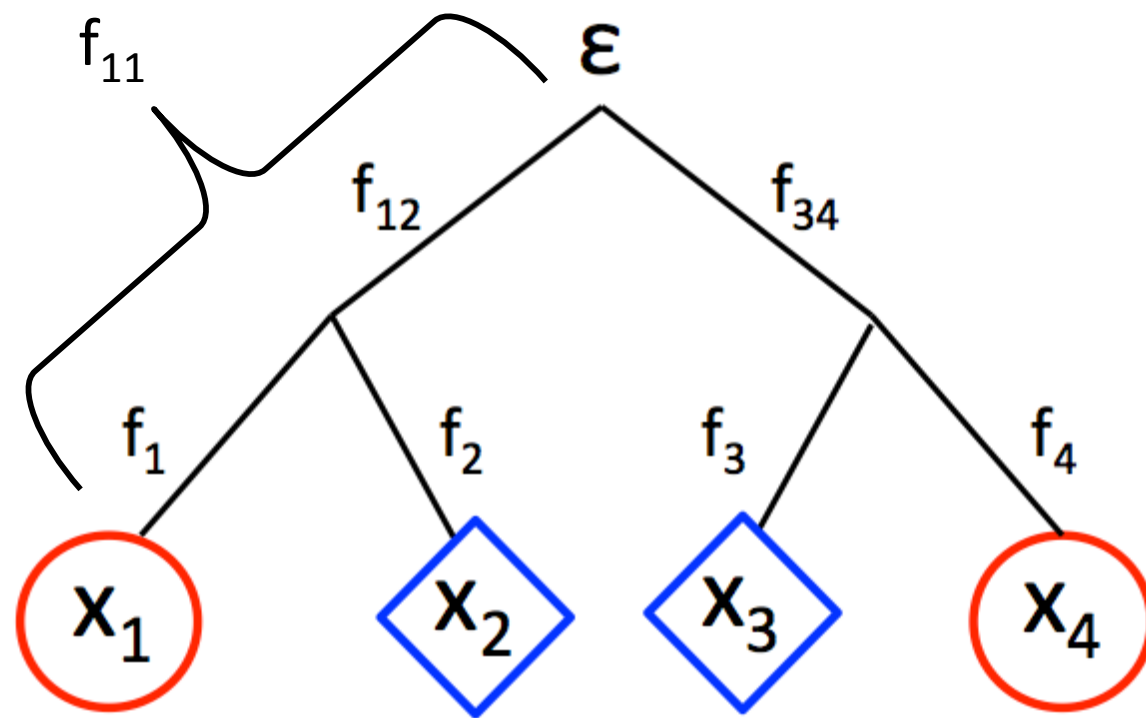


Four population model



$$\mathbf{F} = \begin{bmatrix} f_{11} & f_{12} & 0 & 0 \\ f_{12} & f_{22} & 0 & 0 \\ 0 & 0 & f_{33} & f_{34} \\ 0 & 0 & f_{34} & f_{44} \end{bmatrix}$$

Four population model



$$\mathbf{F} = \begin{bmatrix} f_{11} & f_{12} & 0 & 0 \\ f_{12} & f_{22} & 0 & 0 \\ 0 & 0 & f_{33} & f_{34} \\ 0 & 0 & f_{34} & f_{44} \end{bmatrix}$$

We can model population allele frequencies as multivariate normal

$$\vec{x} \sim \mathcal{N}(\epsilon \vec{1}, \epsilon(1 - \epsilon)\mathbf{F})$$

Effect of hitchhiking

Selection impacts linked neutral allele frequencies

$$\mathbb{E}[\Delta x_1] = 0$$

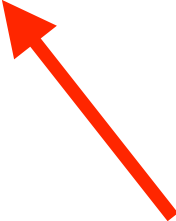
$$\text{Var}[\Delta x_1] = \epsilon(1 - \epsilon)y^2$$

Effect of hitchhiking

Selection impacts linked neutral allele frequencies

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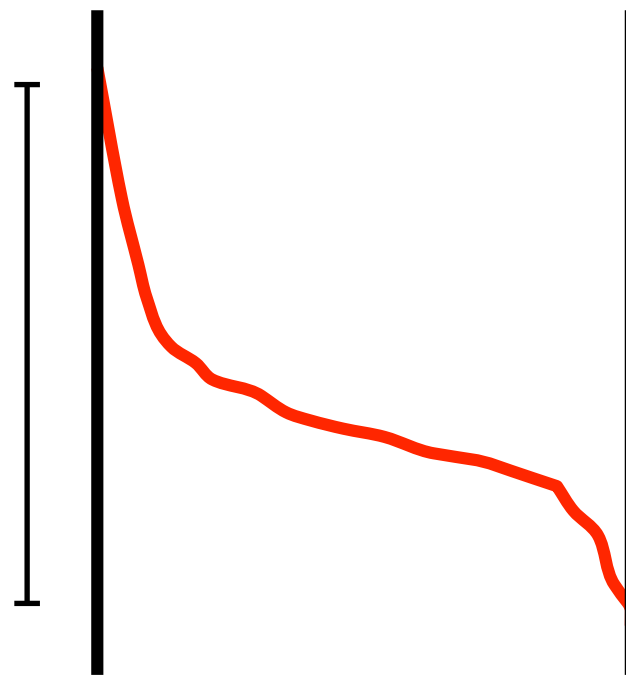


Probability a pair of lineages coalesce during the selective sweep

Selective sweeps increase probability of coalescing

y^2 = probability two lineages coalesce during the sweep =
probability neither recombine off of the beneficial background

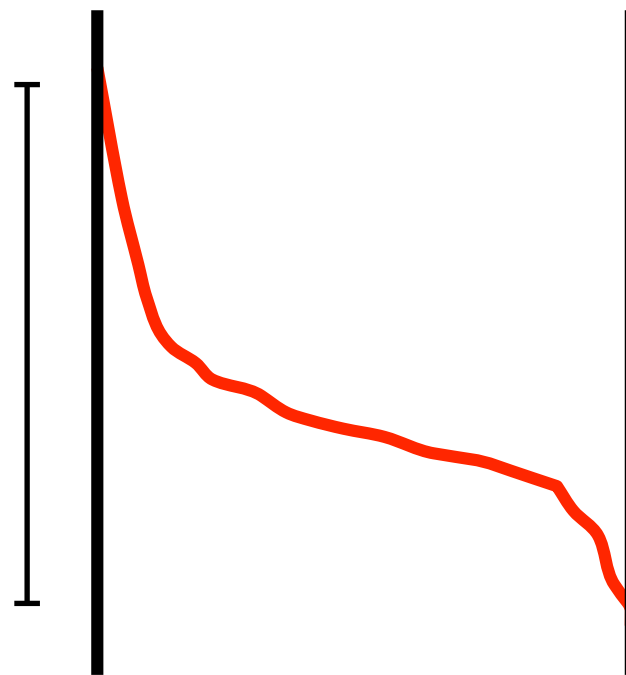
$$t_s \approx \frac{2\log(2N_e)}{s}$$



Selective sweeps increase probability of coalescing

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$$t_s \approx \frac{2\log(2N_e)}{s}$$



$$y^2 \approx e^{-rt_s}$$

Selective sweeps increase probability of coalescing

y^2 = probability two lineages coalesce during the sweep =
probability neither recombine off of the beneficial background



$$\text{Var}[\Delta x_i] \approx \epsilon(1 - \epsilon) (y^2 + (1 - y^2)f_{ii})$$

Selective sweeps increase probability of coalescing

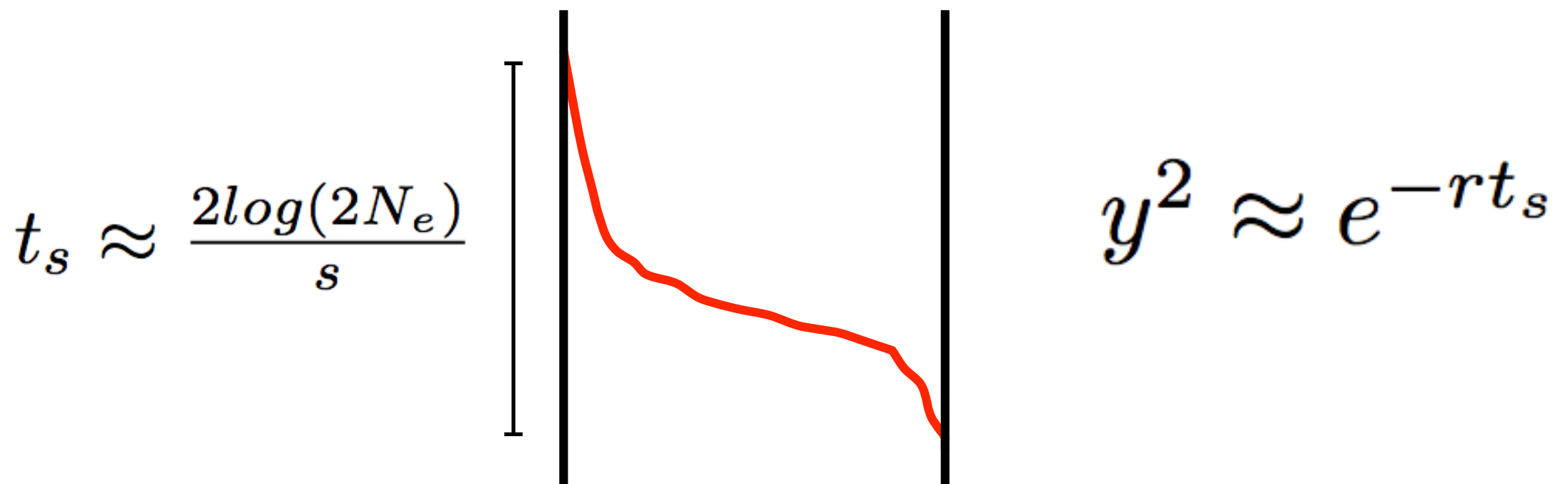
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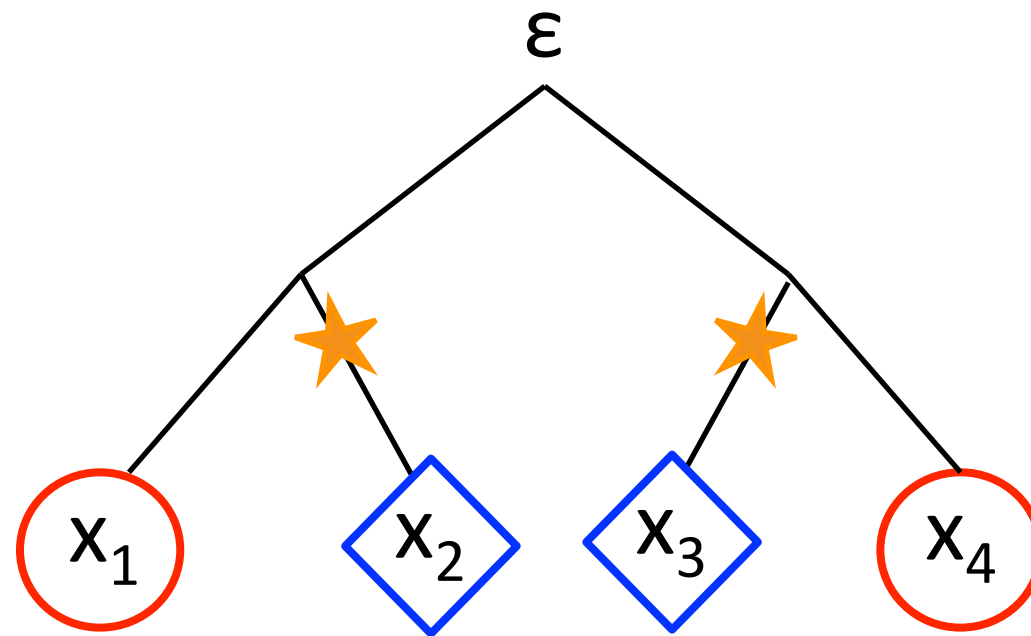
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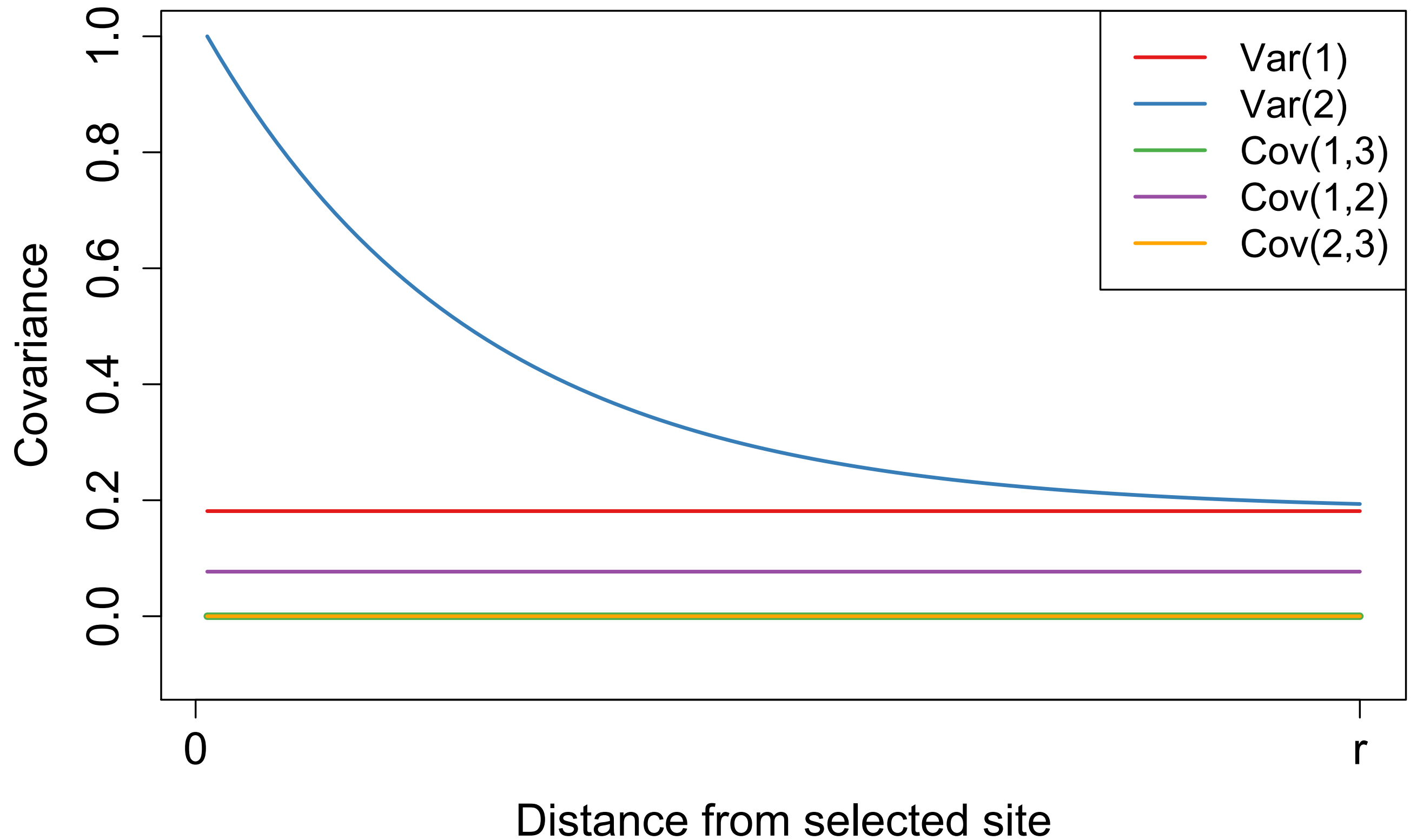
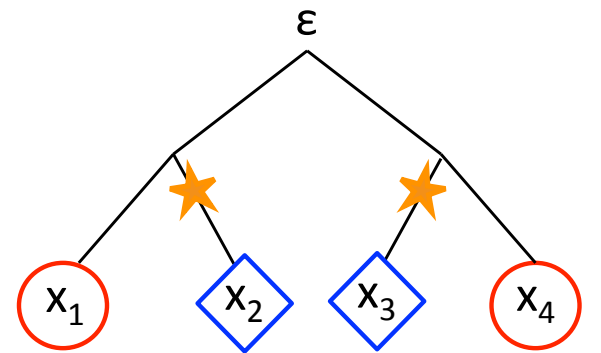
$$\text{Var}[\Delta x_i] \approx \epsilon(1 - \epsilon) (y^2 + (1 - y^2) \underline{f_{ii}})$$

1. Independent sweep model

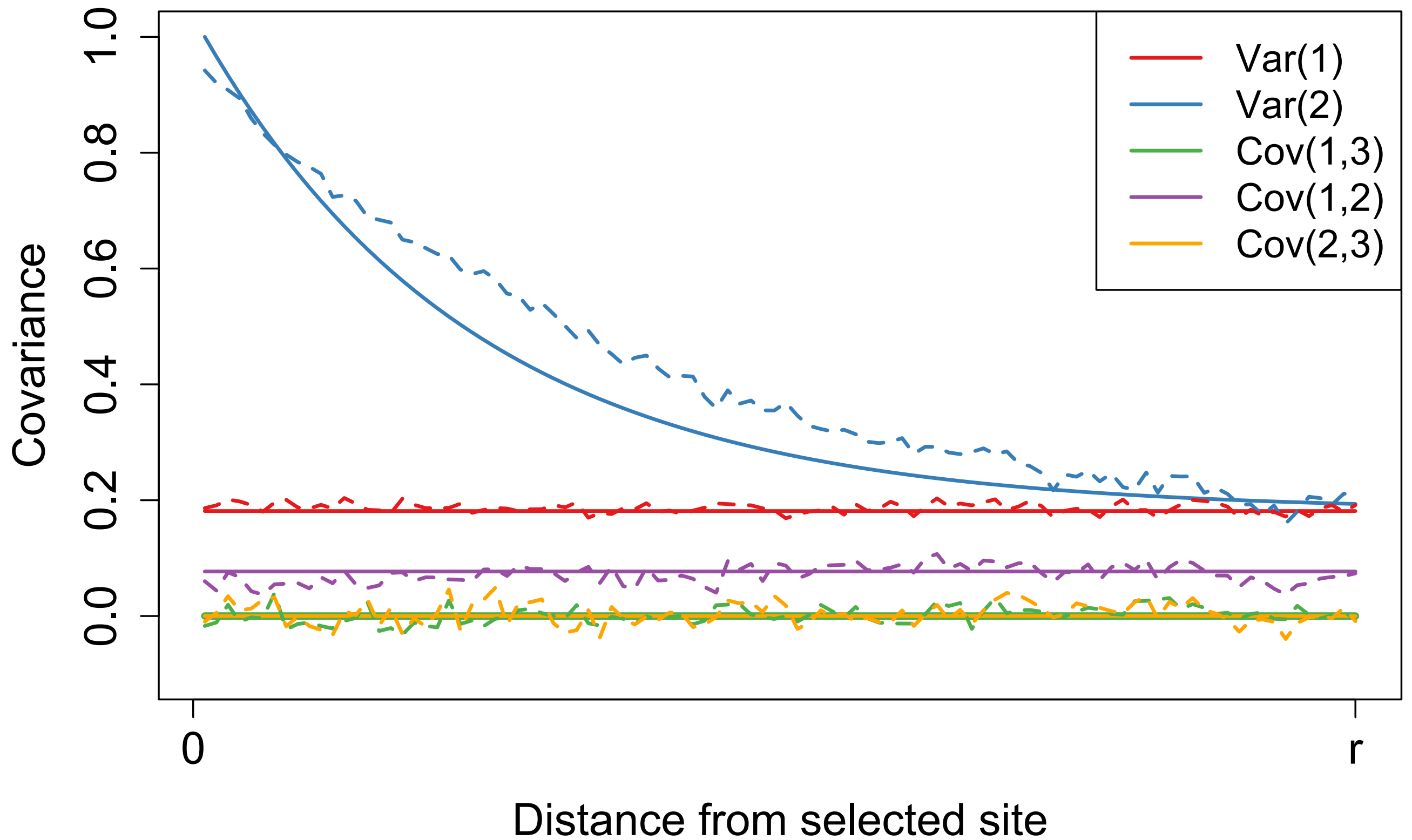
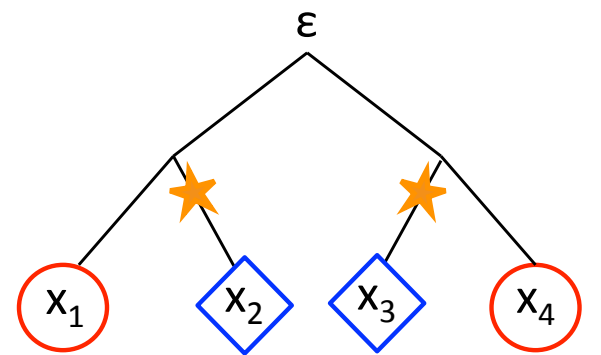


$$\mathbf{F} + \Omega = \begin{bmatrix} f_{11} & f_{12} & 0 & 0 \\ f_{12} & f_{22} + y^2(1 - f_{22}) & 0 & 0 \\ 0 & 0 & f_{33} + y^2(1 - f_{33}) & f_{34} \\ 0 & 0 & f_{34} & f_{44} \end{bmatrix}$$

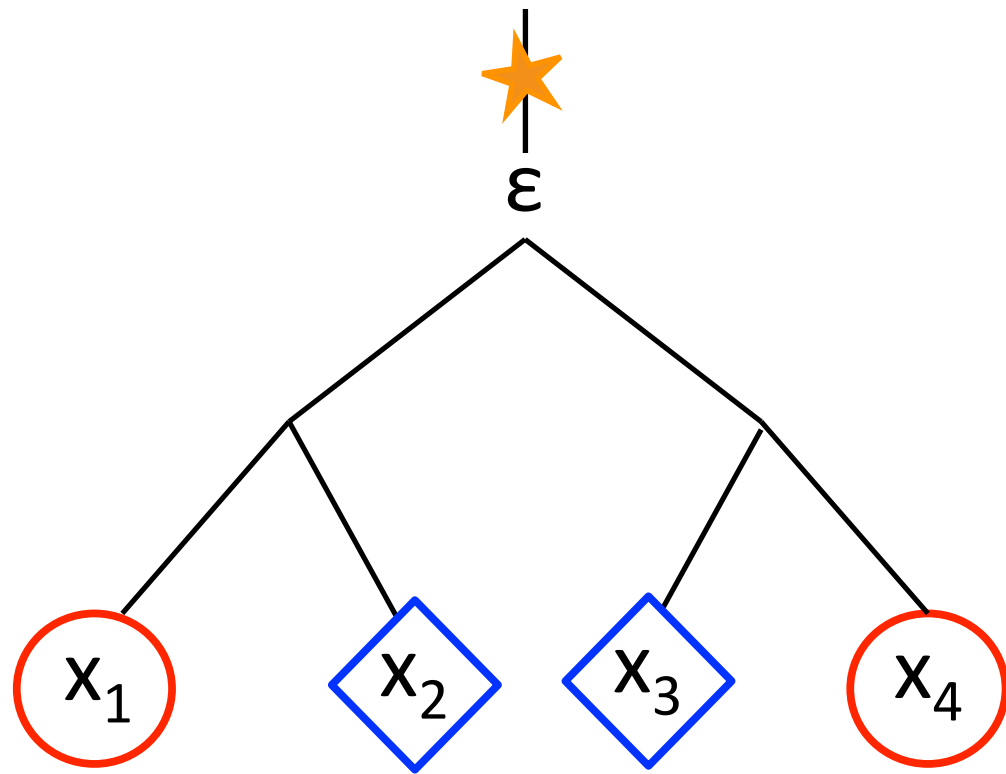
Independent mutation model variances and covariances



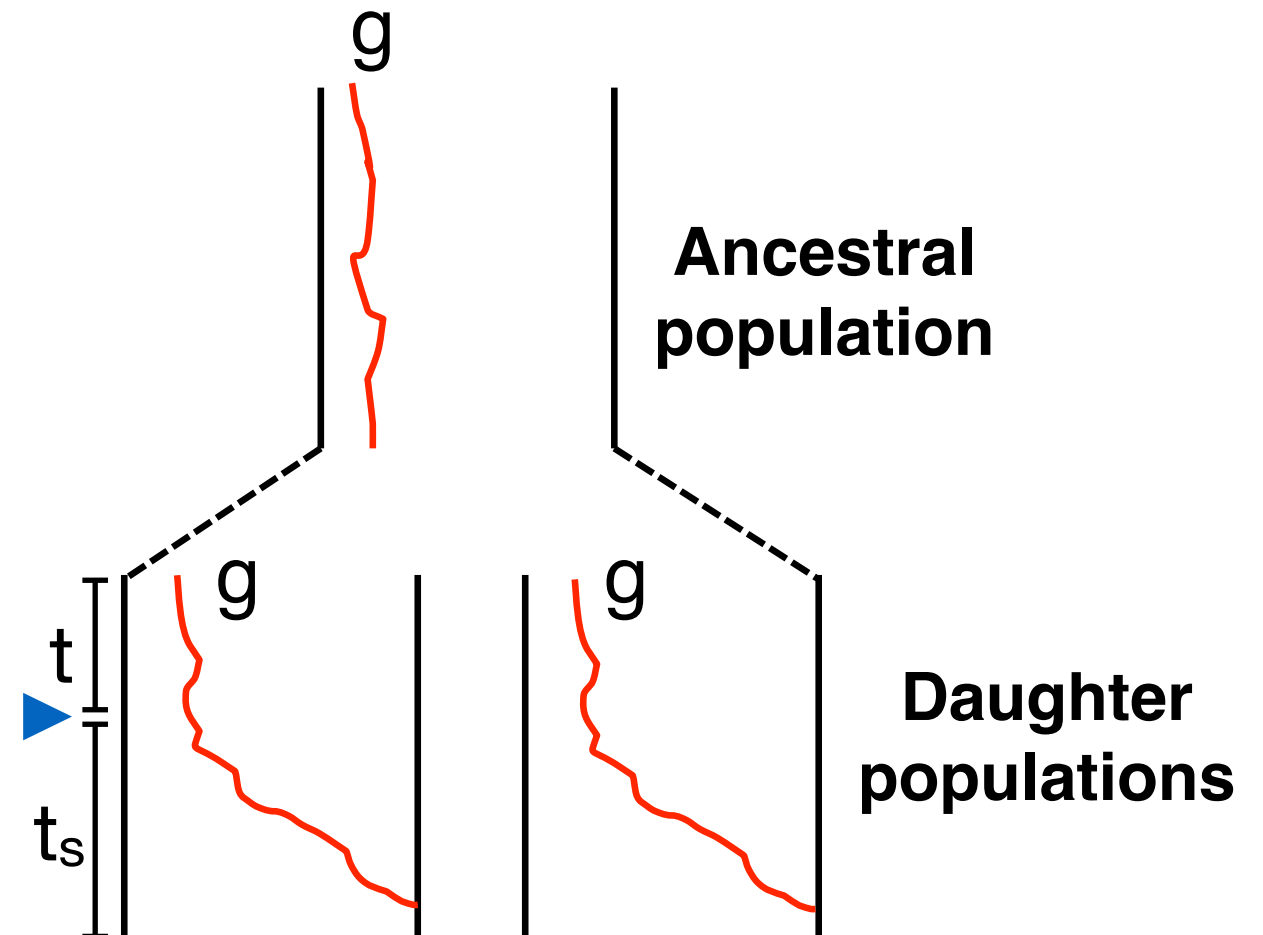
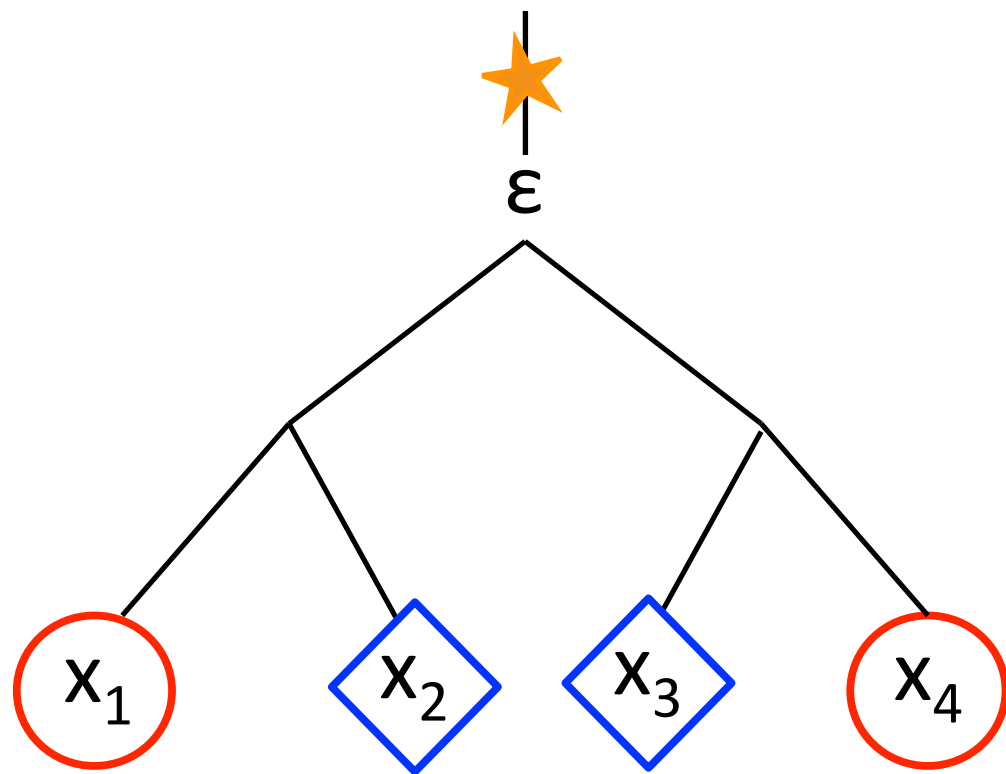
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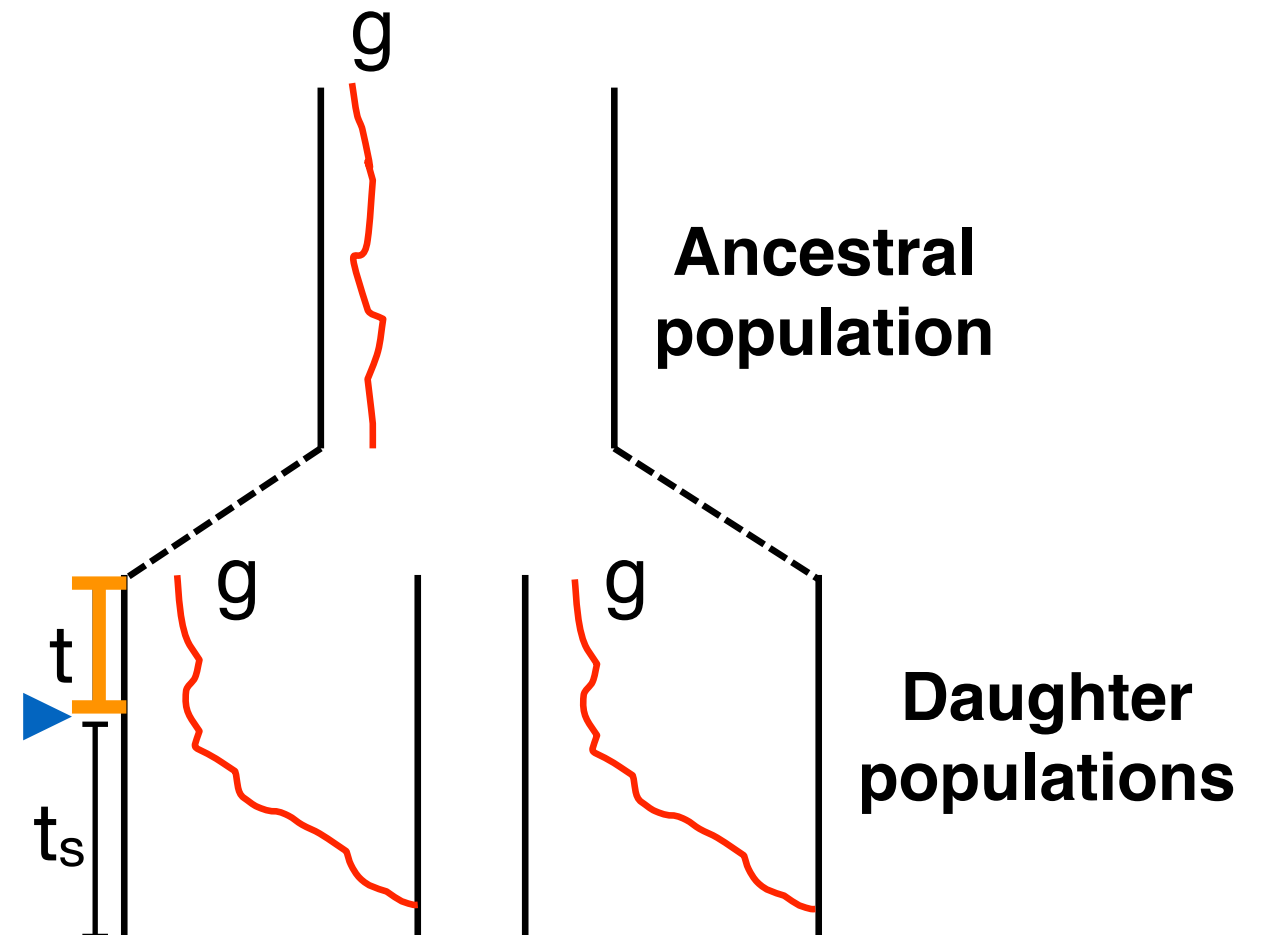
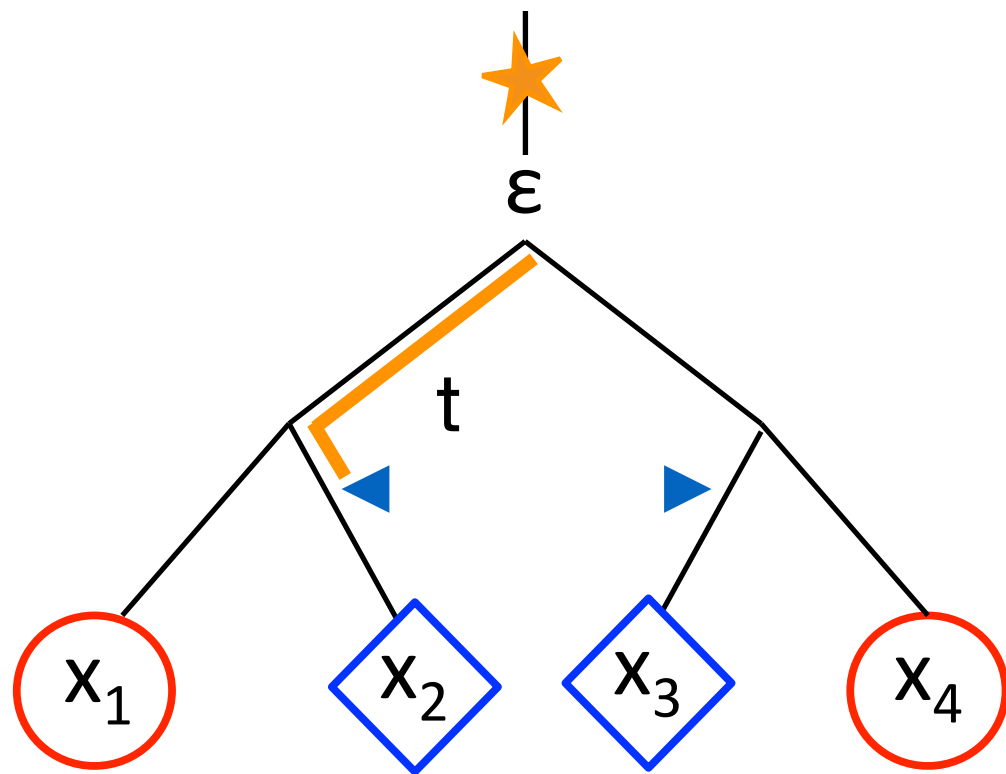
2. Shared ancestral standing variation



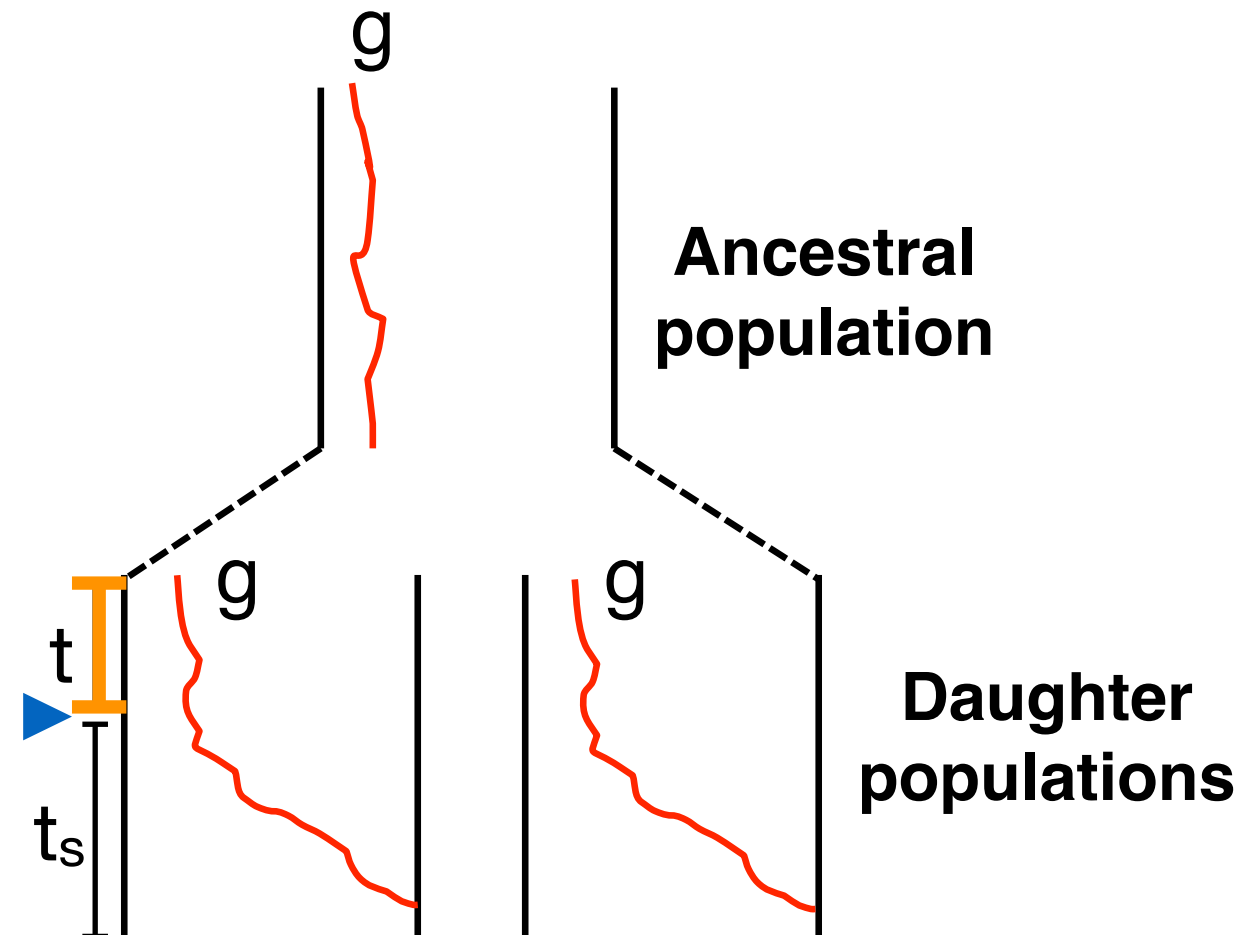
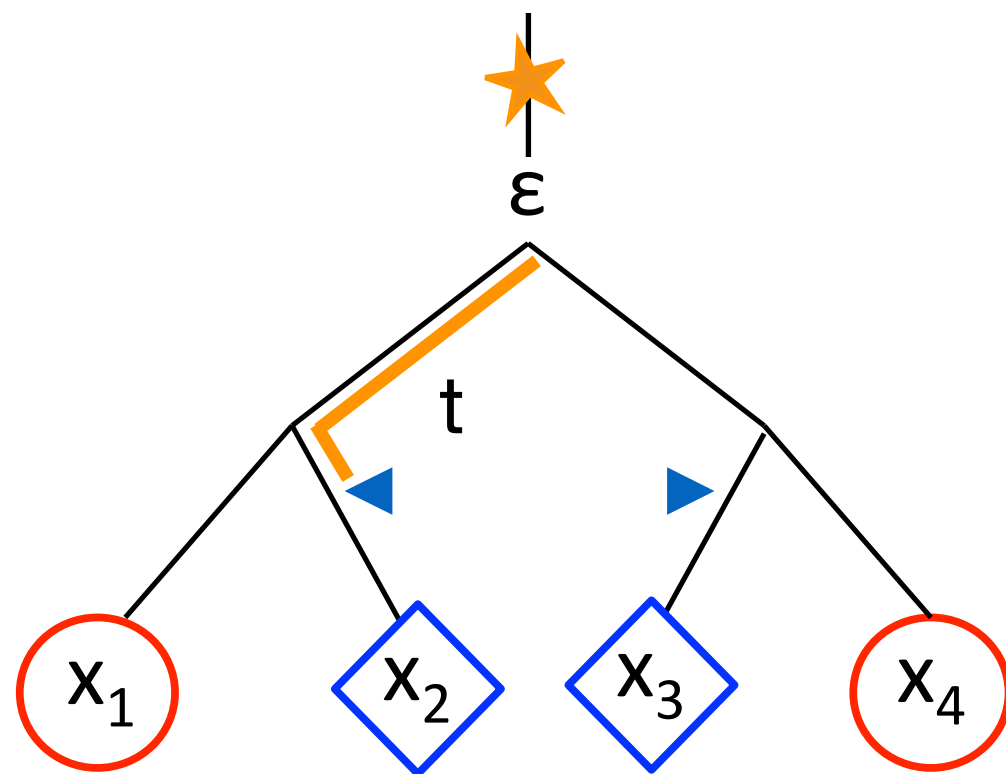
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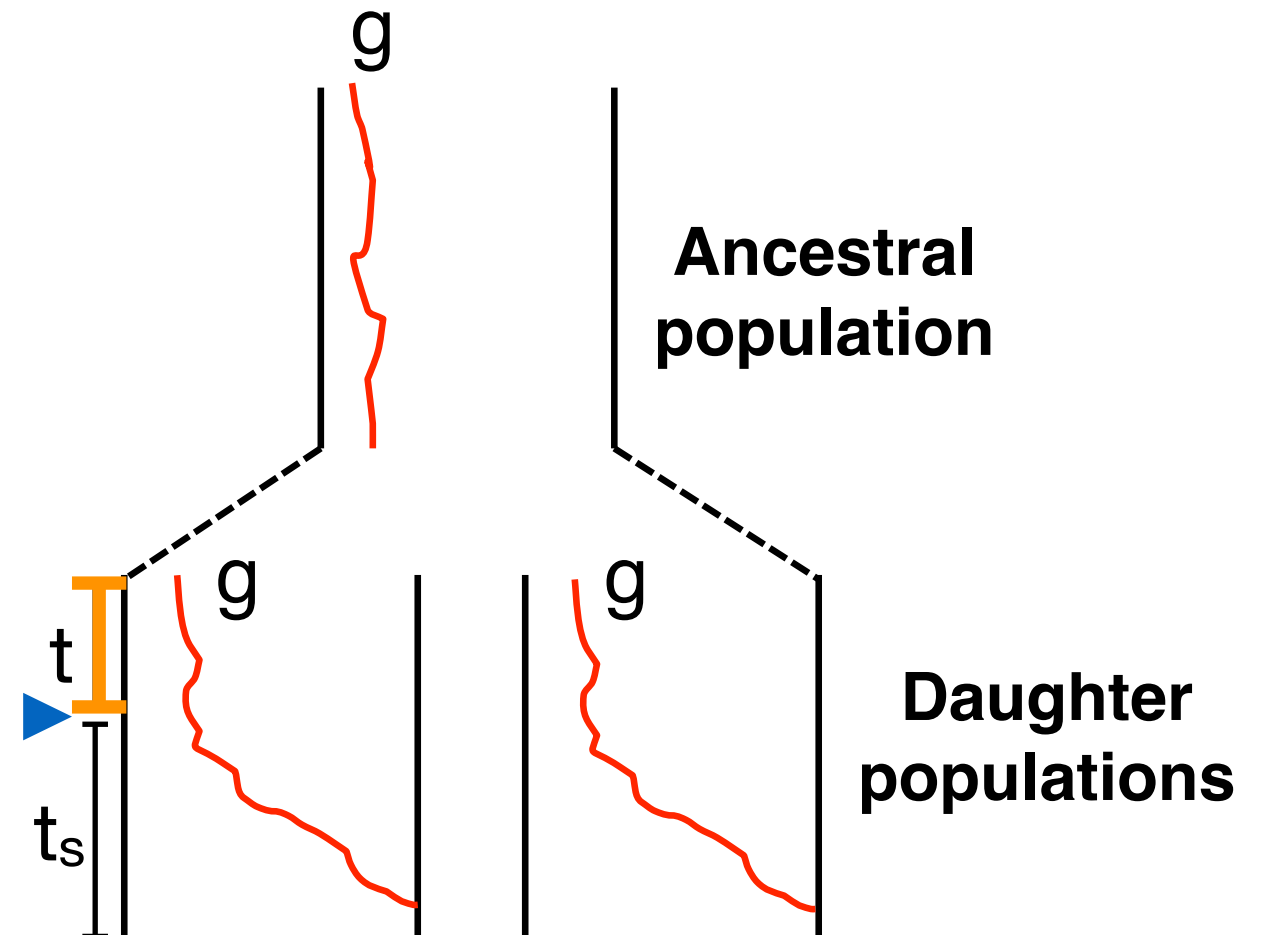
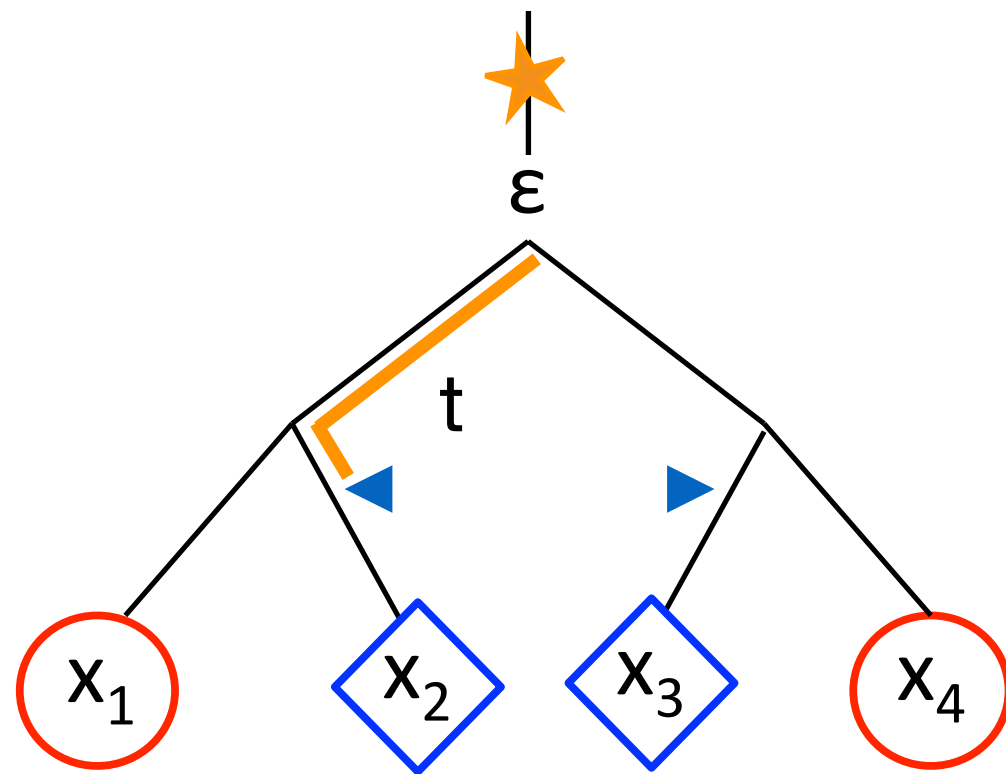


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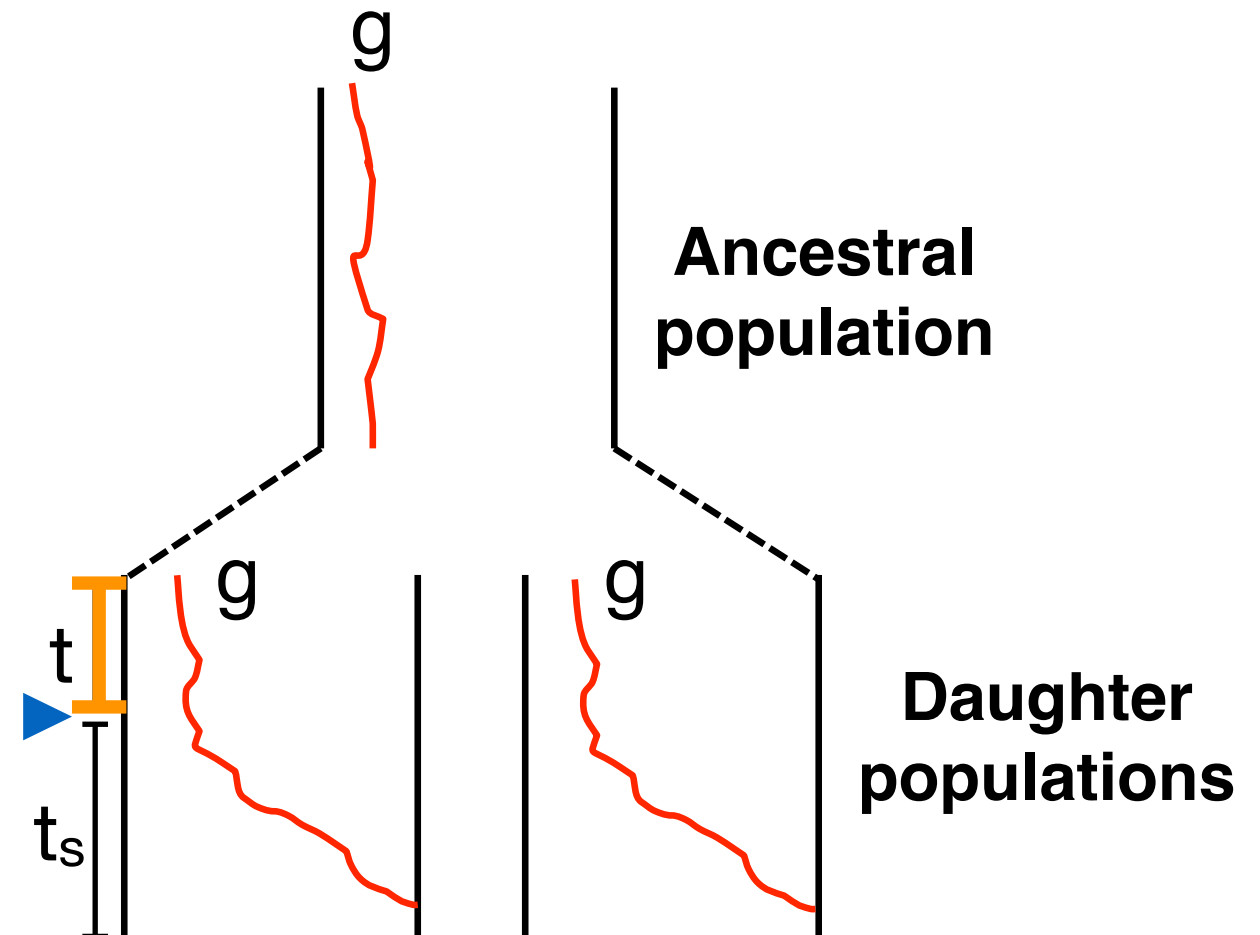
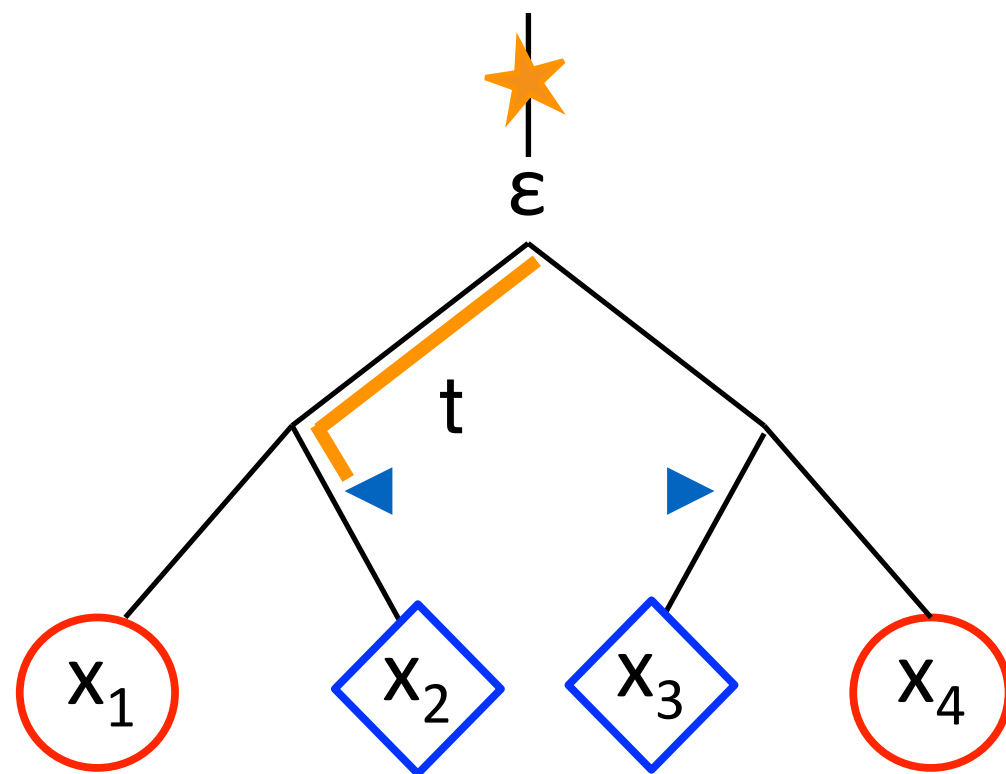
$$\text{Var}[\Delta x_i] \approx \epsilon(1 - \epsilon) \left(f_{ii} + y^2 h_1(r, g)(1 - f_{ii}) \right)$$

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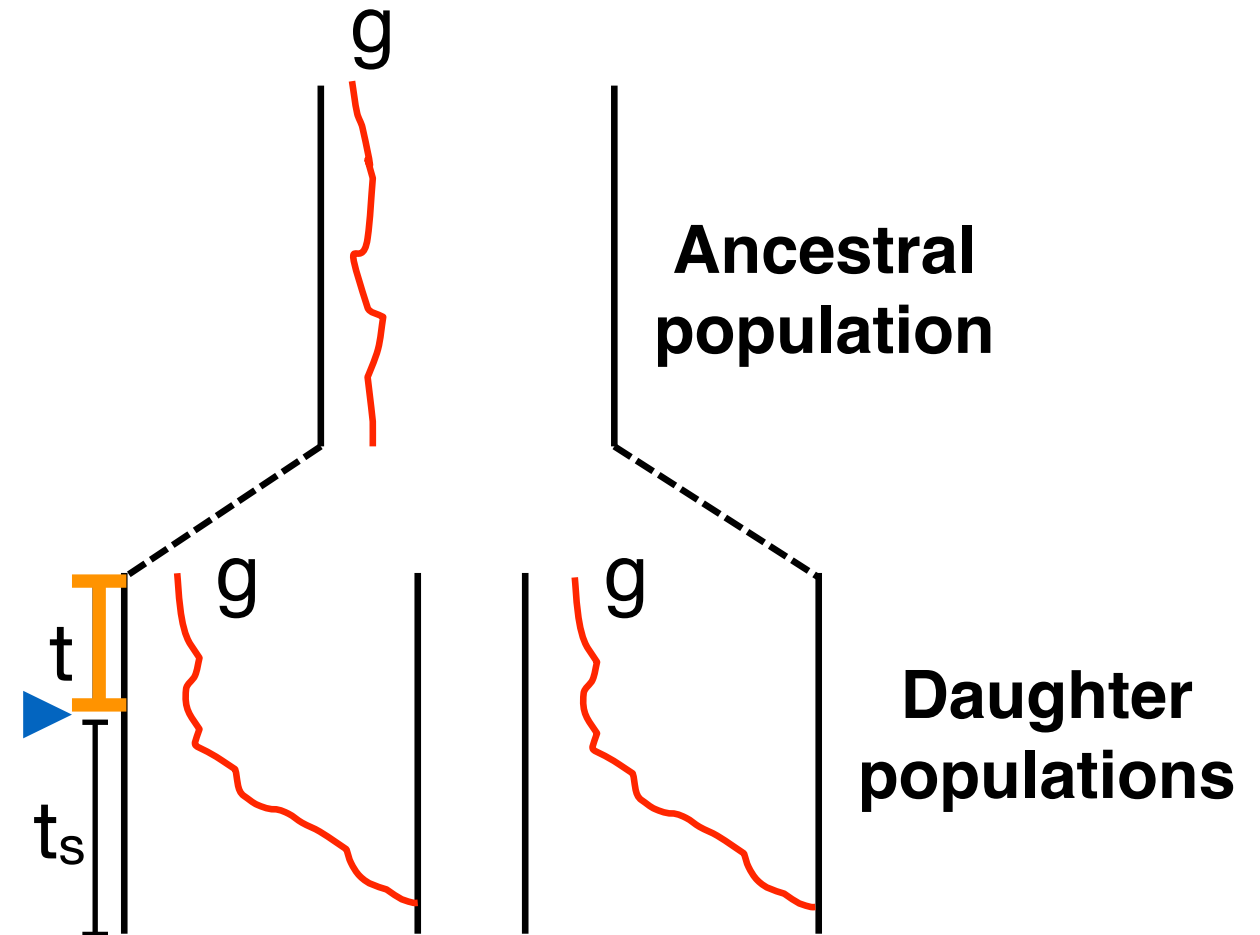
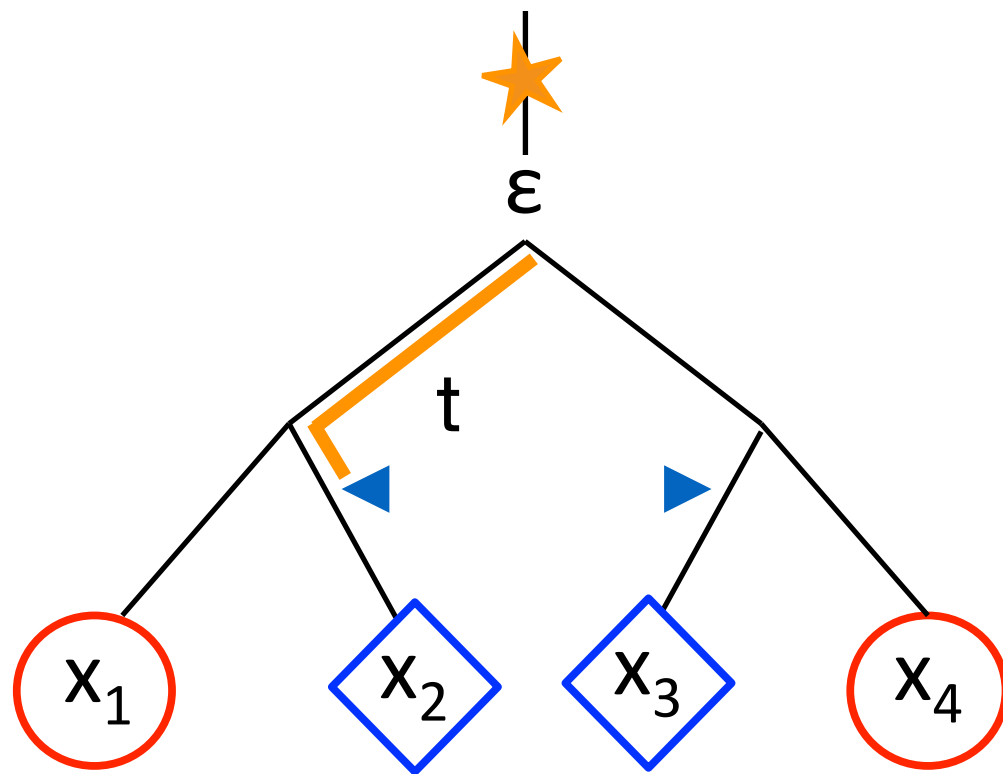
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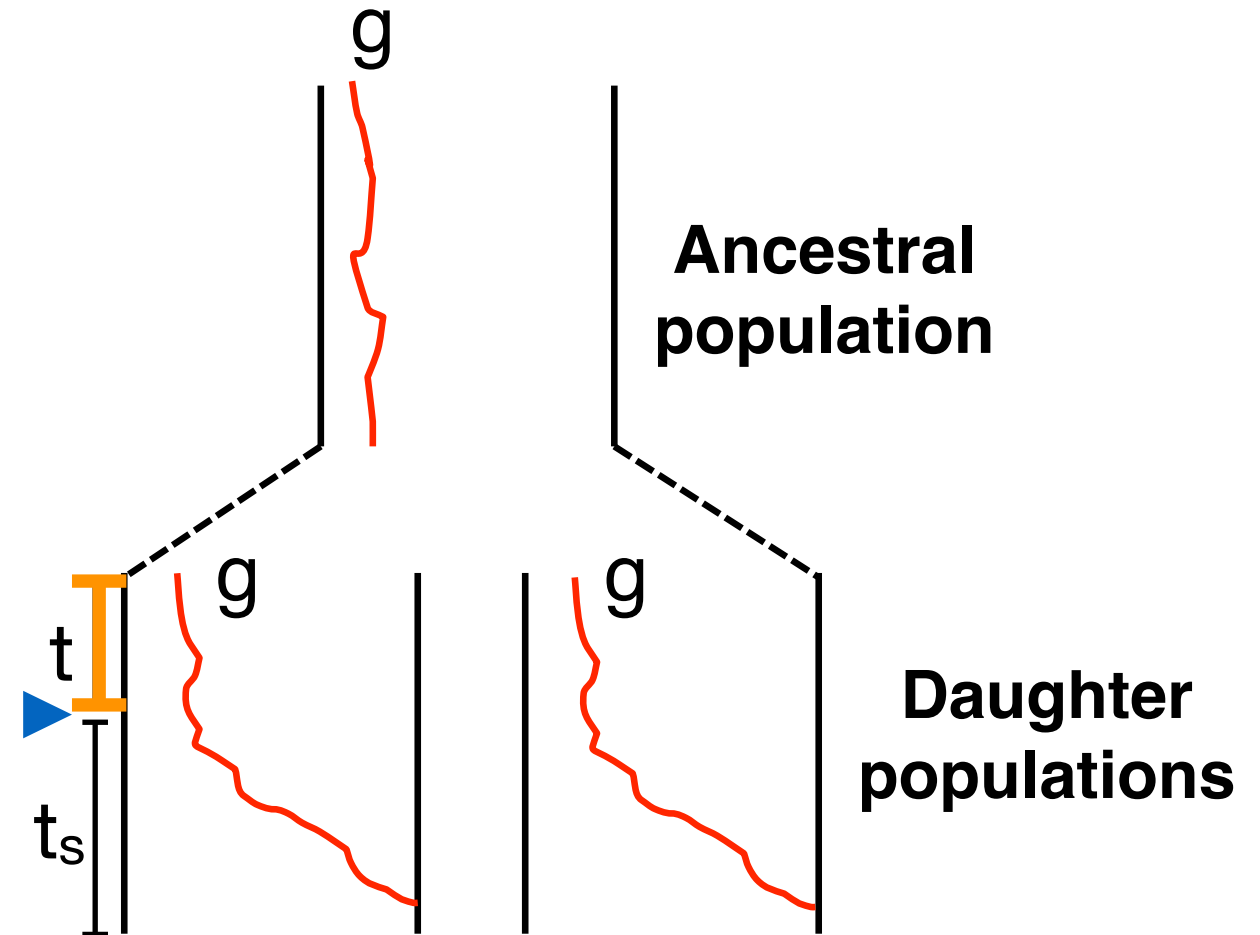
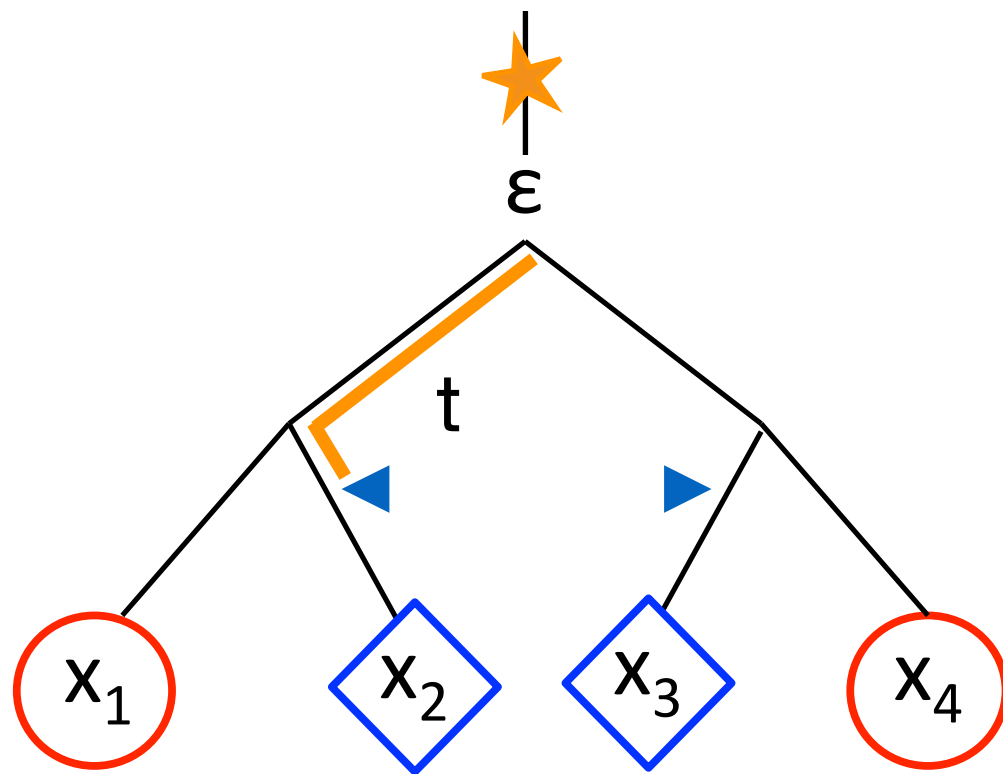
2. Shared ancestral standing variation



$$\text{Var}[\Delta x_i] \approx \epsilon(1 - \epsilon)(f_{ii} + y^2 h_1(r, g)(1 - f_{ii}))$$

$$\text{Cov}[\Delta x_2, \Delta x_3] \approx \epsilon(1 - \epsilon)(y^2 h_2(r, g, t))$$

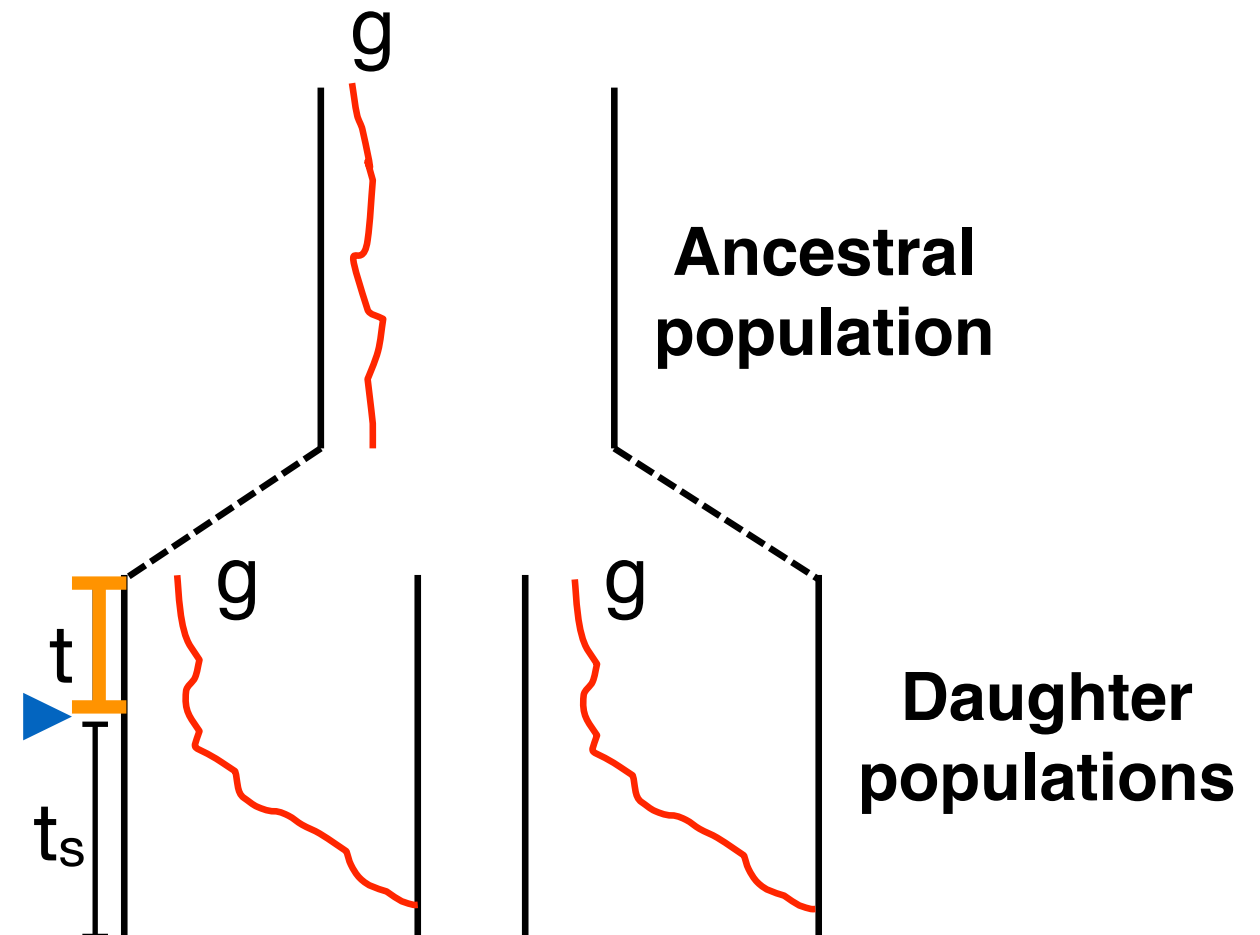
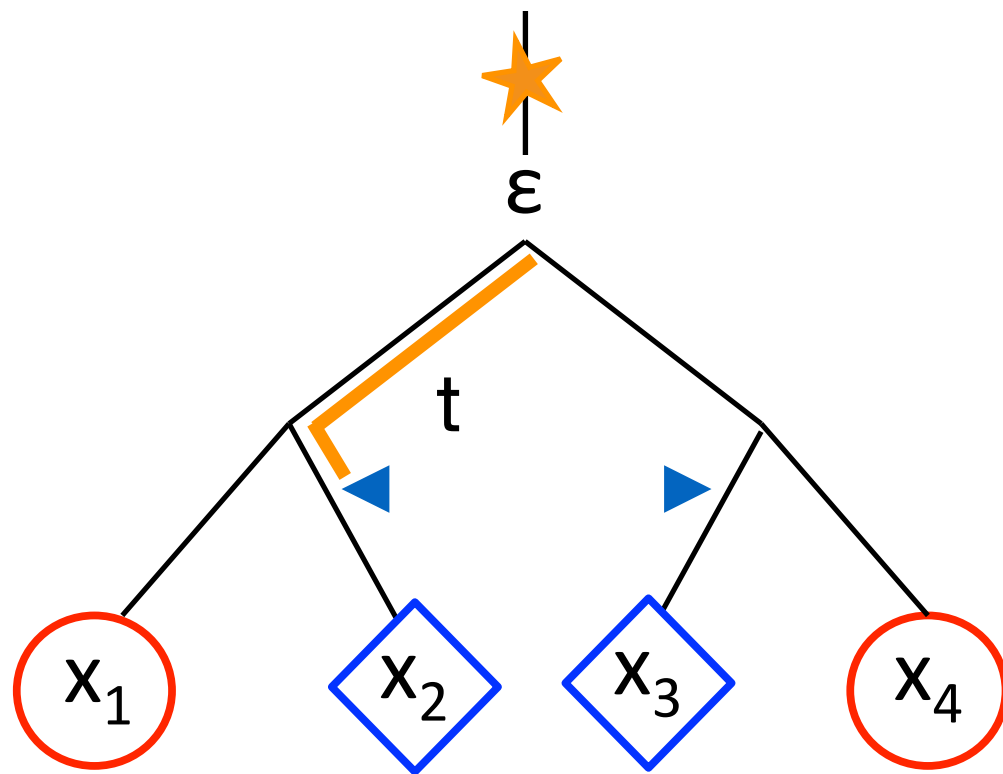
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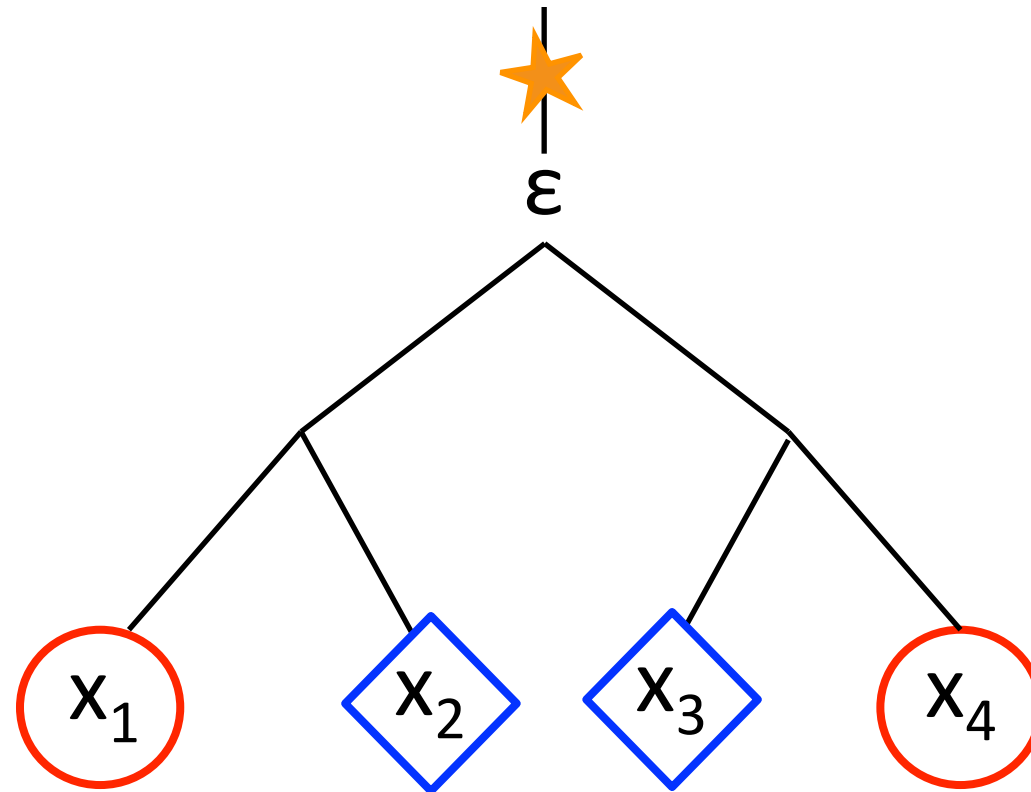
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2. Shared ancestral standing variation



$$\mathbf{F} + \Omega = \begin{bmatrix} f_{11} & f_{12} & 0 & 0 \\ f_{12} & f_{22} + y^2 h_1 (1 - f_{22}) & y^2 h_2 & 0 \\ 0 & y^2 h_2 & f_{33} + y^2 h_1 (1 - f_{33}) & f_{34} \\ 0 & 0 & f_{34} & f_{44} \end{bmatrix}$$

Inference method

Given location of selected site and model, can calculate probability of observed neutral allele frequencies a given distance from selected site.

$$P(D_l \mid r_l, \mathbf{F}, \Theta_M, M) \approx \mathcal{N}(D_l \mid \epsilon_l, \mathbf{F} + \Omega_M(r_l, \mathbf{F}, \Theta_M))$$



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$$\mathcal{L}(\Theta_M, M; D) = \left(\prod_{i=1}^{L_{left}} P(D_i \mid r_i, \mathbf{F}, \Theta_M, M) \right) \left(\prod_{j=1}^{L_{right}} P(D_j \mid r_j, \mathbf{F}, \Theta_M, M) \right)$$

Application to data:

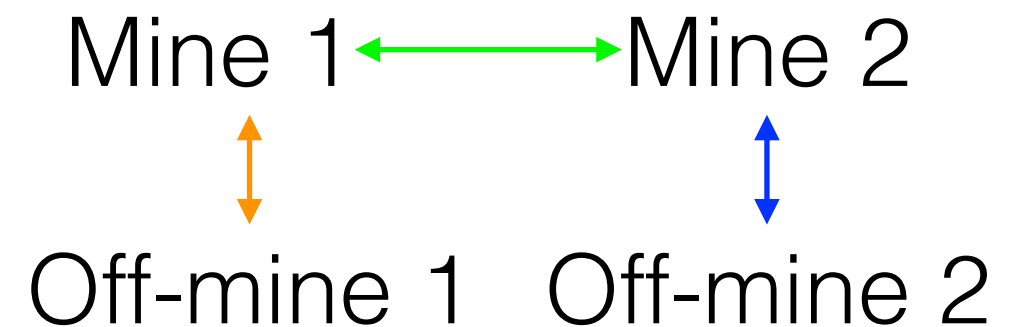
Mimulus guttatus adaptation to copper on mine tailings in California



John Willis

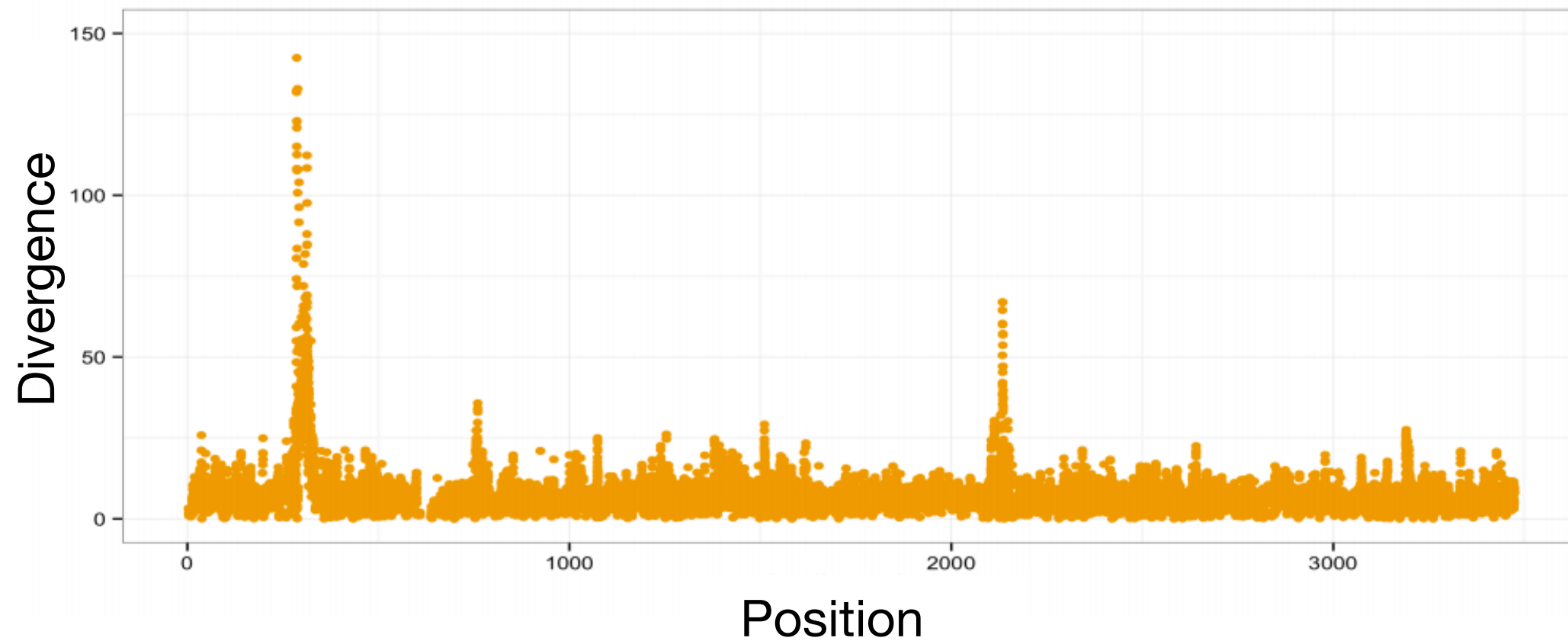


Kevin Wright



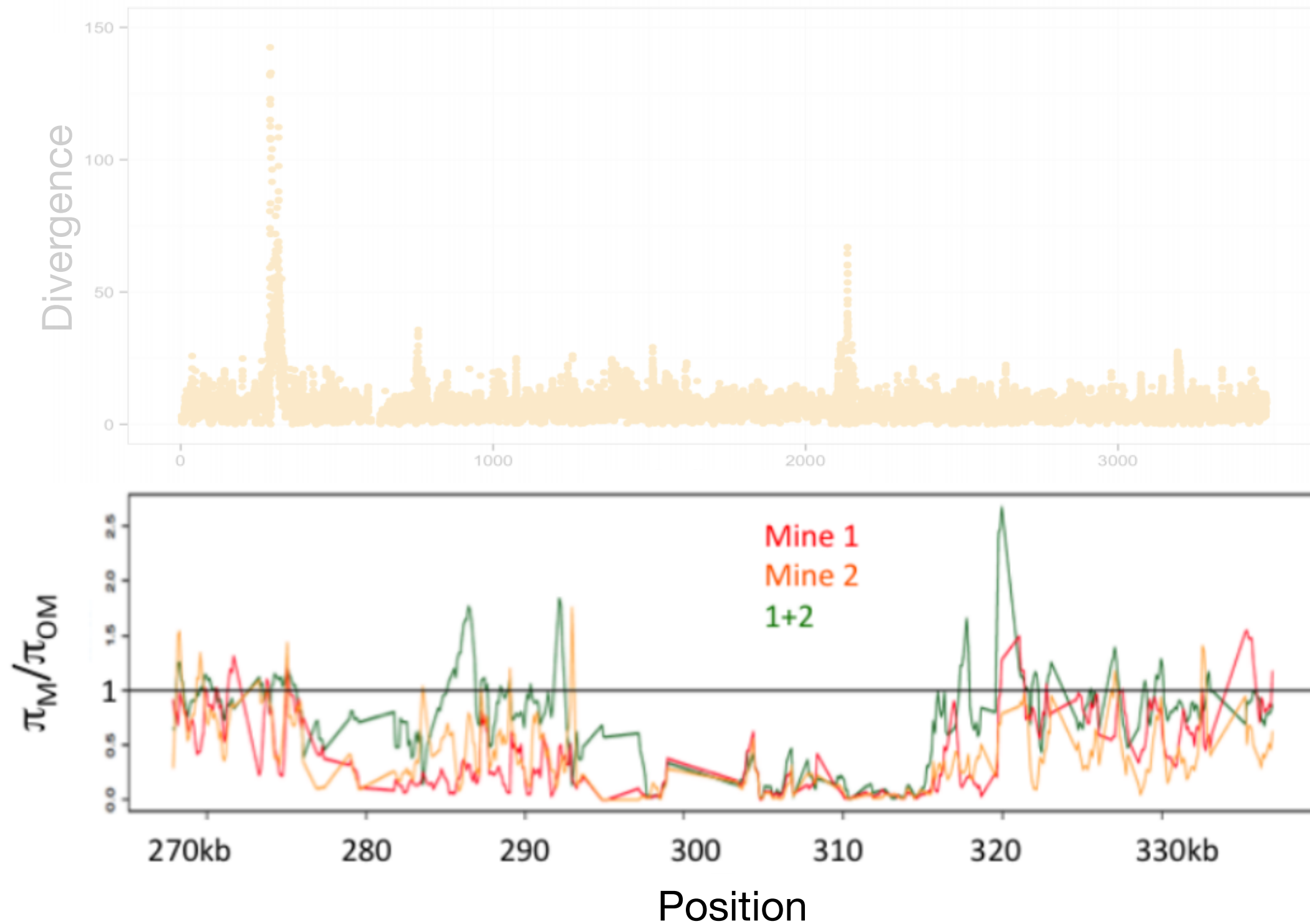
Application to data:

Mimulus guttatus adaptation to copper on mine tailings in California

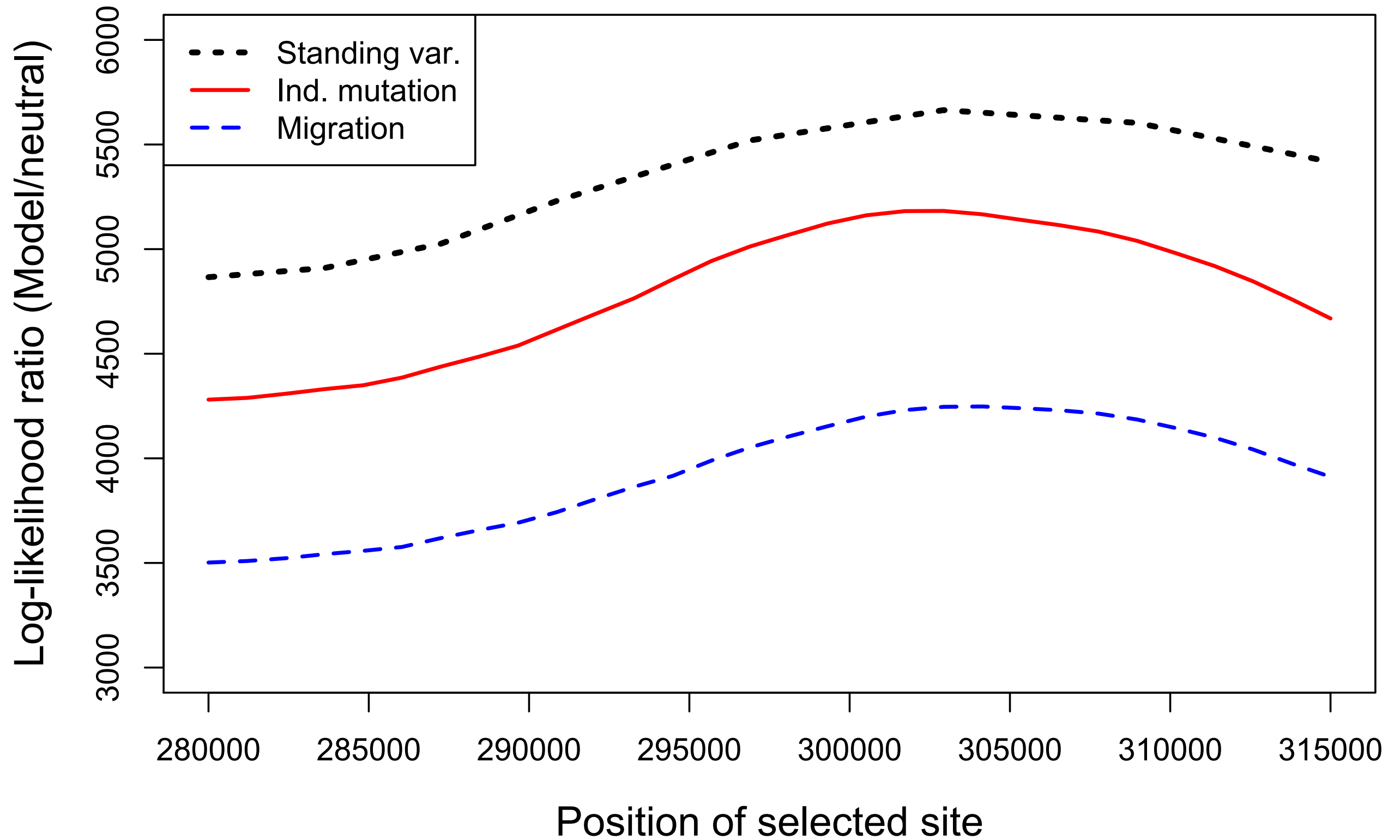


Application to data:

Mimulus guttatus adaptation to copper on mine tailings in California

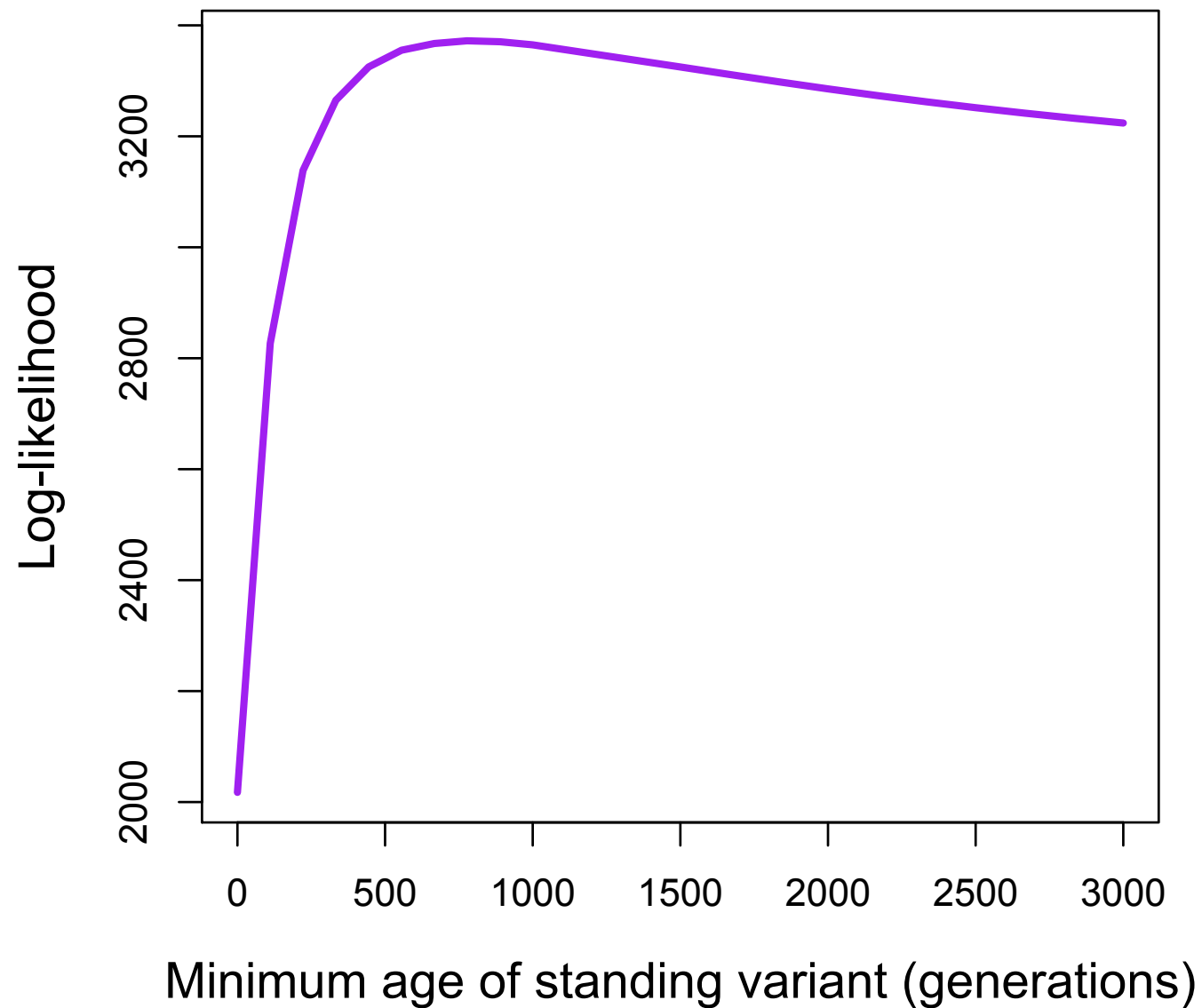


Log-likelihood ratio under different models compared to neutral model



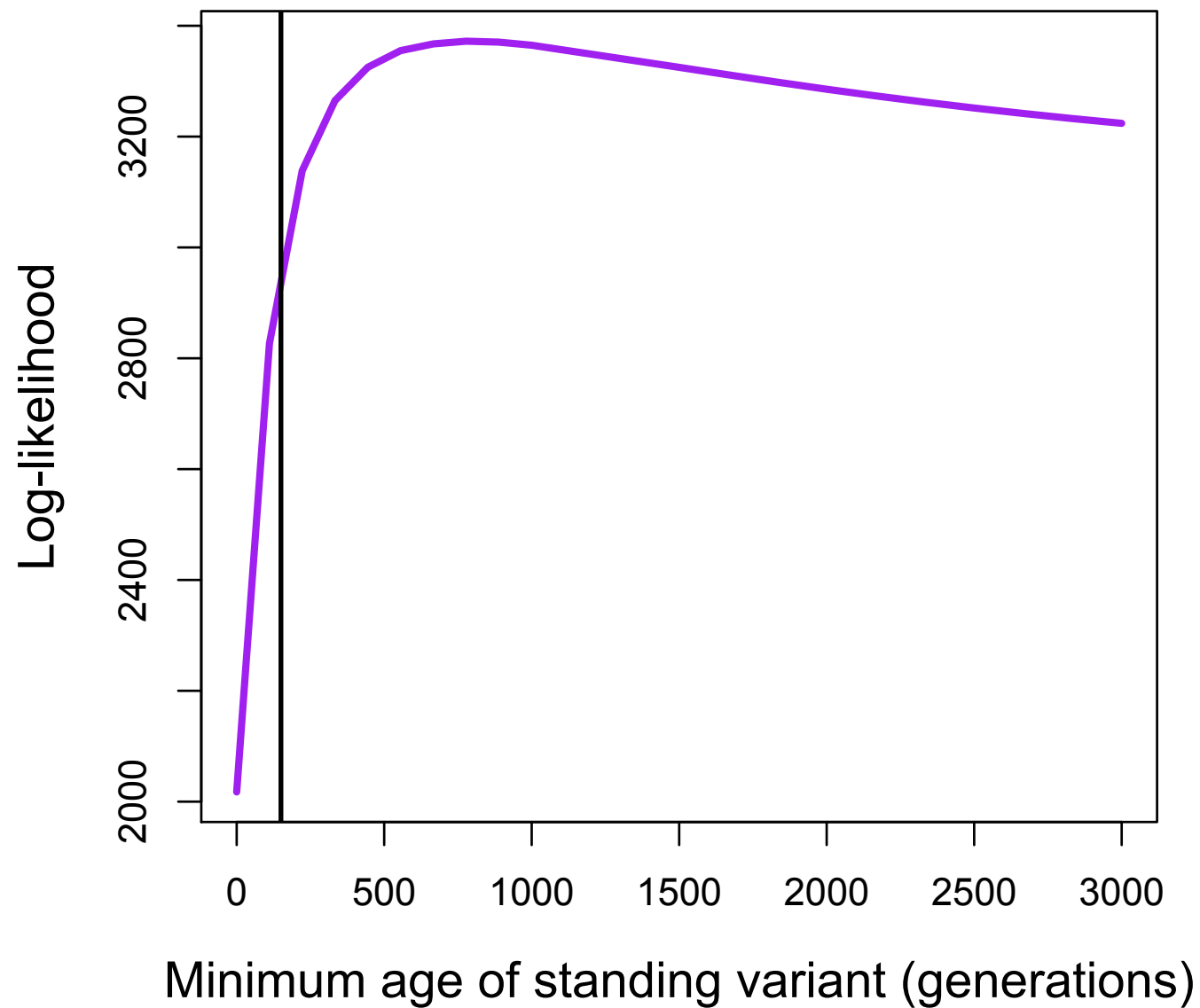
Under standing variation at most likely selected site

Profile log-likelihood surface for t



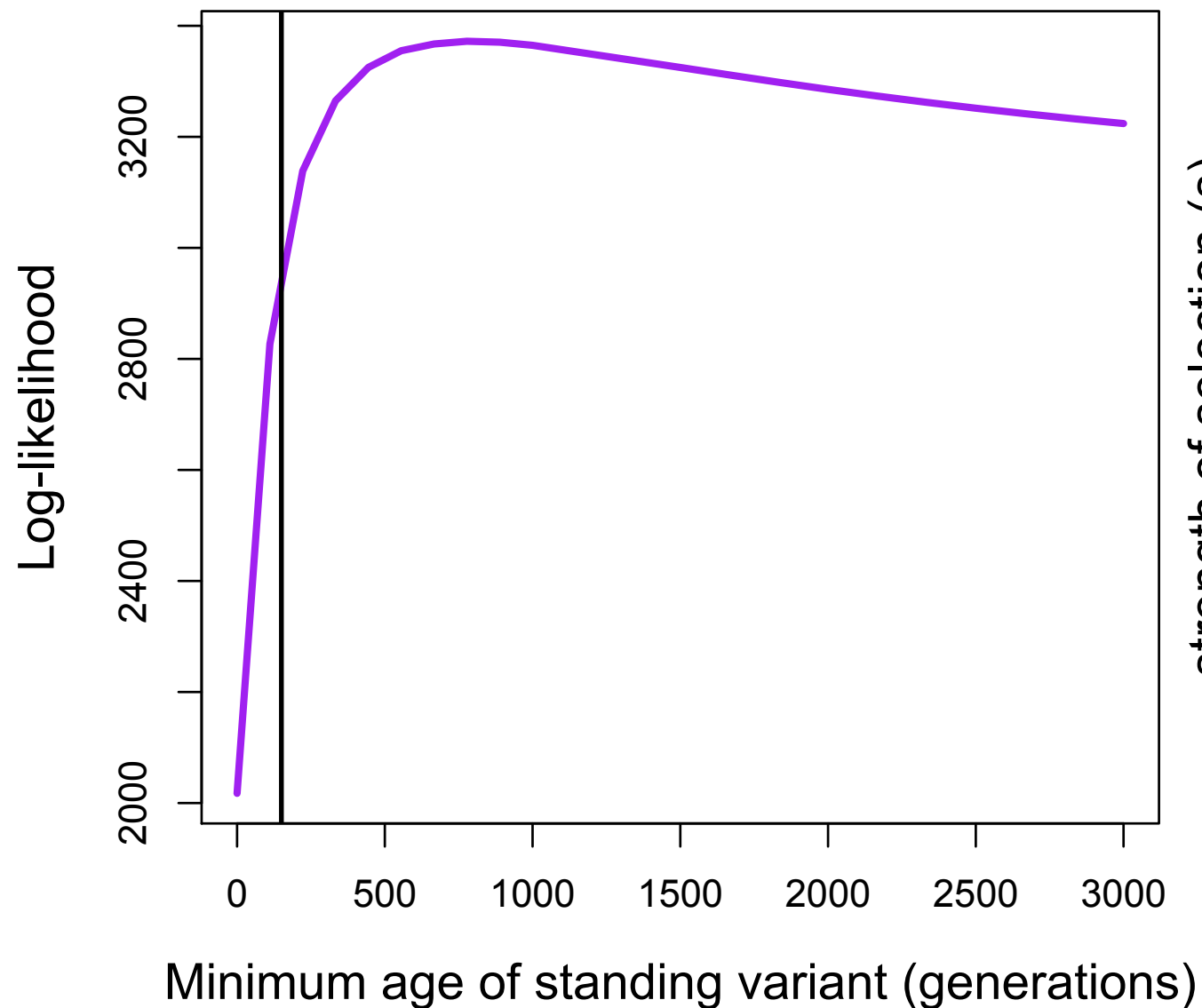
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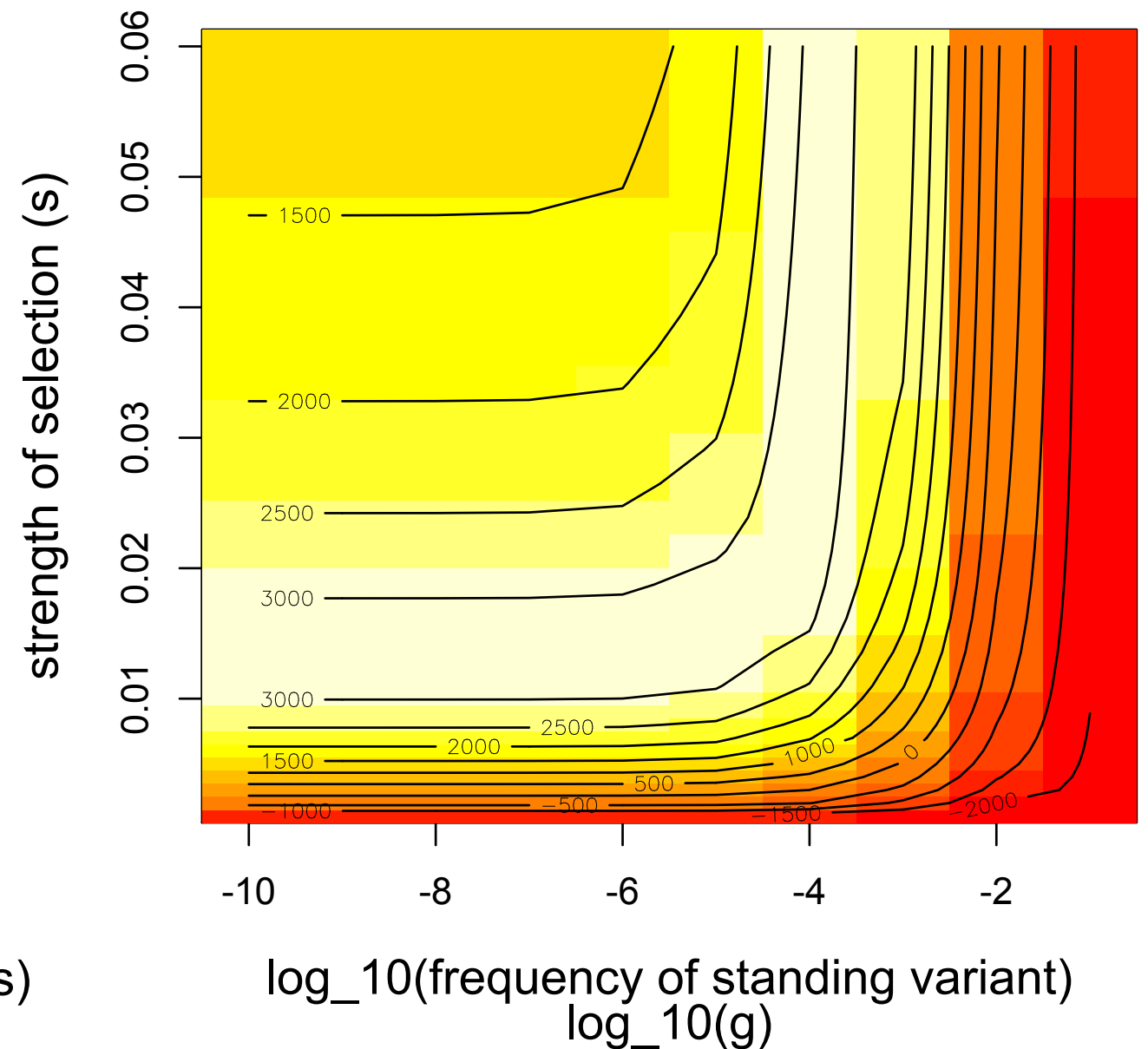


Under standing variation at most likely selected site

Profile log-likelihood surface for t



Log-likelihood surface of s and g



Conclusions

1. Can define models for modes of convergent adaptation for multiple populations with arbitrary relationships
2. Applied inference method to *Mimulus guttatus* copper tolerance data
 - Can apply to a wide range of other datasets

Thank you!



The Coop Lab

Jeremy Berg, Gideon Bradburd, Graham Coop, Alisa Sedghifar, Chenling Xu,
Ivan Juric, Simon Aeschbacher, Vince Buffalo

Application to data:

Mimulus guttatus adaptation to copper on mine tailings in California

GENETIC DIVERSITY IN TOP “SWEEP REGION”.

