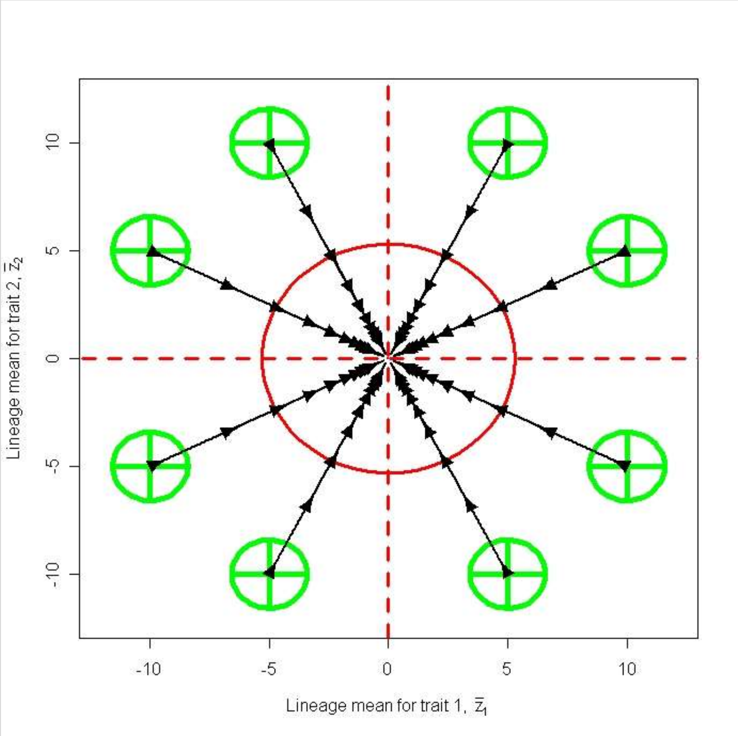
2.3 Selection and Evolution on a Surface



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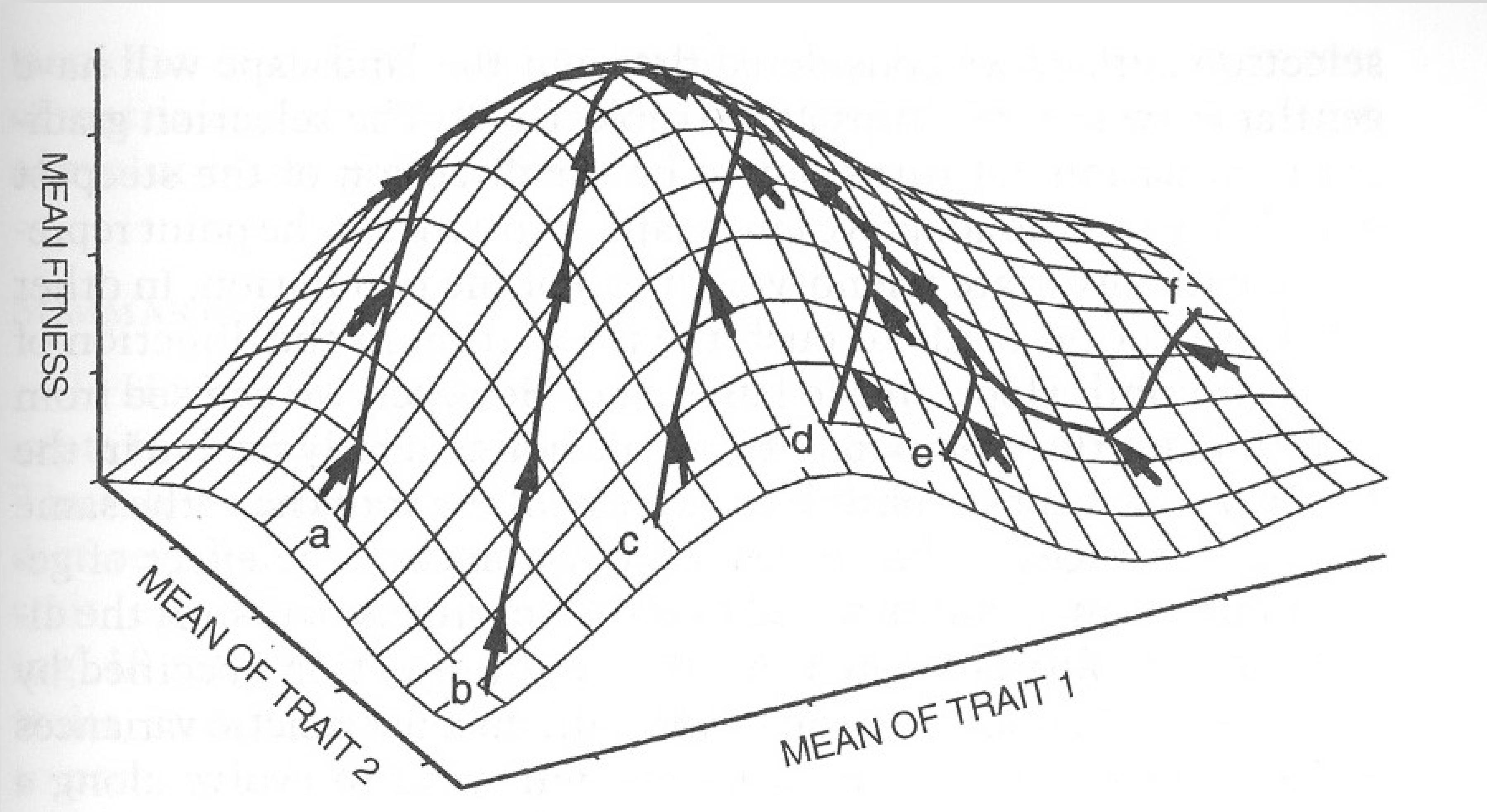
Evolution of the trait mean on an adaptive landscape: more than a metaphor



Three Parts

1. Selection on single & multiple traits
2. Selection on a surface
3. Evolution on adaptive landscapes

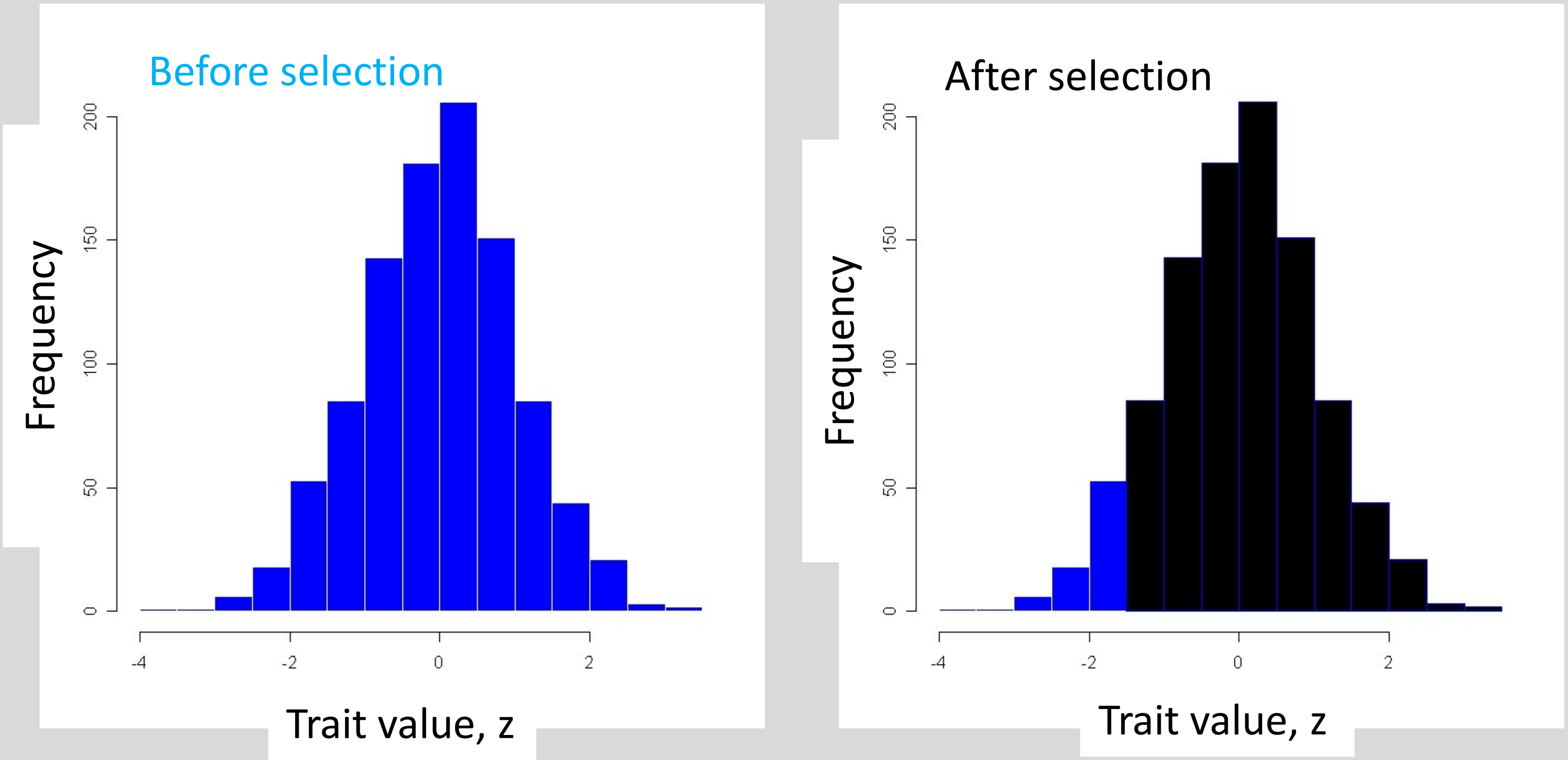
Part 1. Selection on a Single & Multiple Traits

Thesis

- Selection changes trait distributions.
- The contrast between distributions before and after selection provides a powerful description of the force of selection.
- Multivariate measures of selection can correct for the effects of correlations between traits.

1. Selection changes the univariate trait distribution

a. The contrast between distributions before and after selection is particularly revealing



2. Shift in the trait mean, the linear selection differential, s

a. A particular example

$$s = \bar{z}^* - \bar{z} = 0.16 - (-0.01) = 0.17$$

b. The general case

$$\bar{z} = \int p(z) z dz$$

where p(z) is trait frequency before selection

$$\bar{z}^* = \int p(z)^* z dz$$

where p(z)* is trait frequency after selection

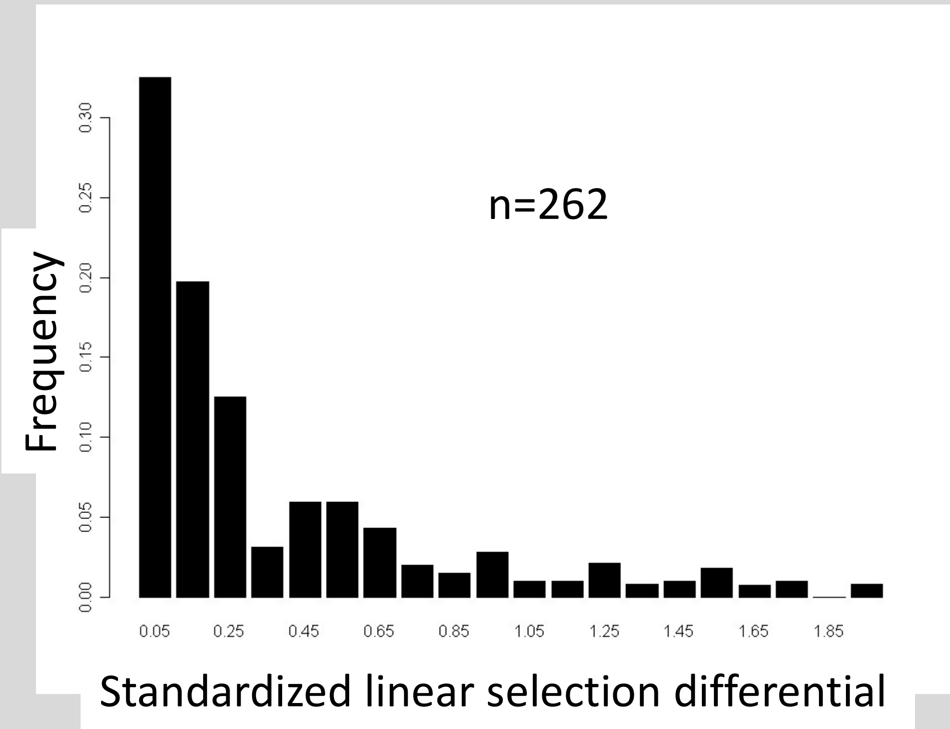
$$p(z)^* = w(z) p(z)$$

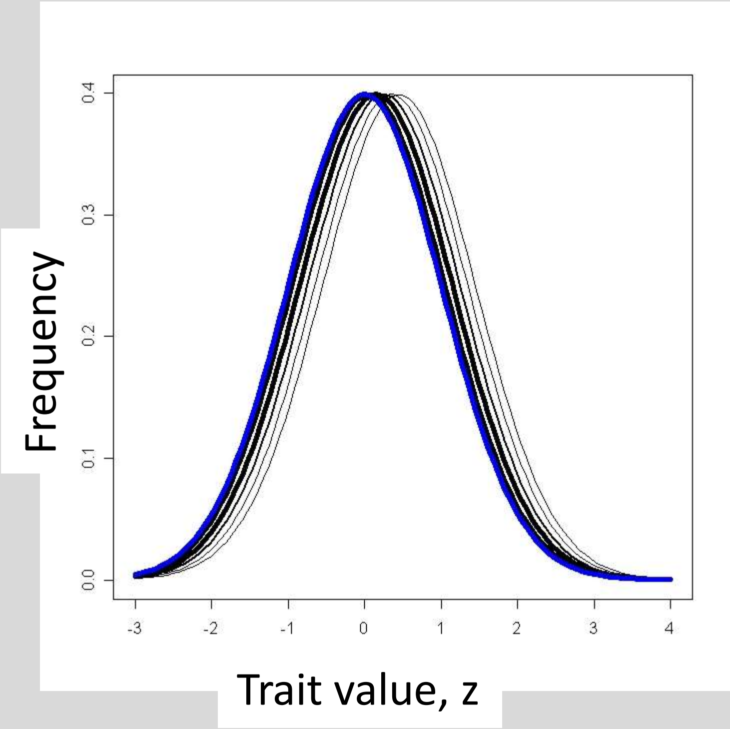
where w(z) is relative fitness of the z trait class

3. Examples and Surveys of selection differentials

a. The standardized linear selection differential, s′

$$s' = (\bar{z}^* - \bar{z})/\sqrt{P}$$

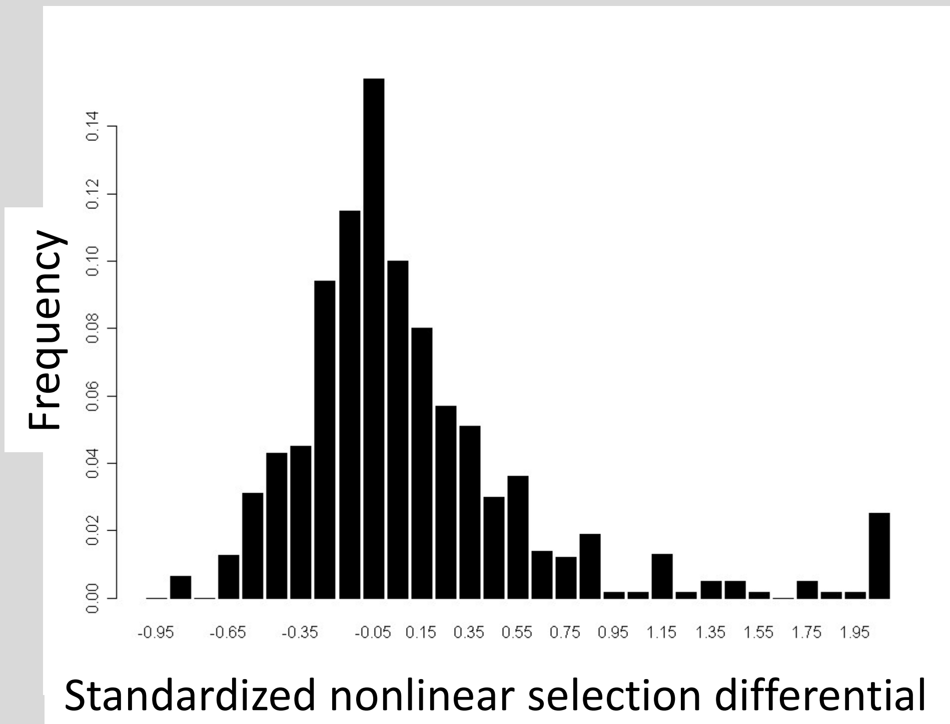


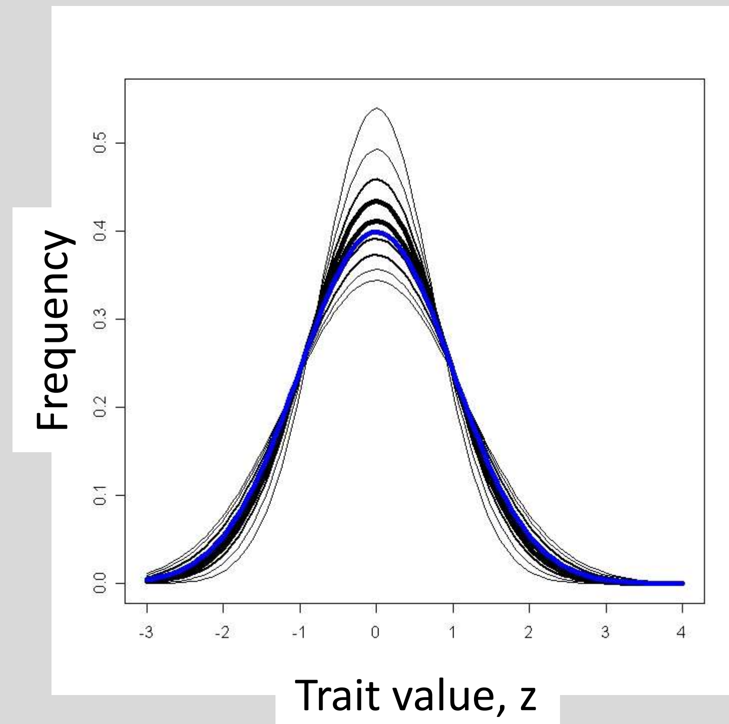


3. Examples andSurveys of selection differentials

b. The standardized nonlinear selection differential, C'

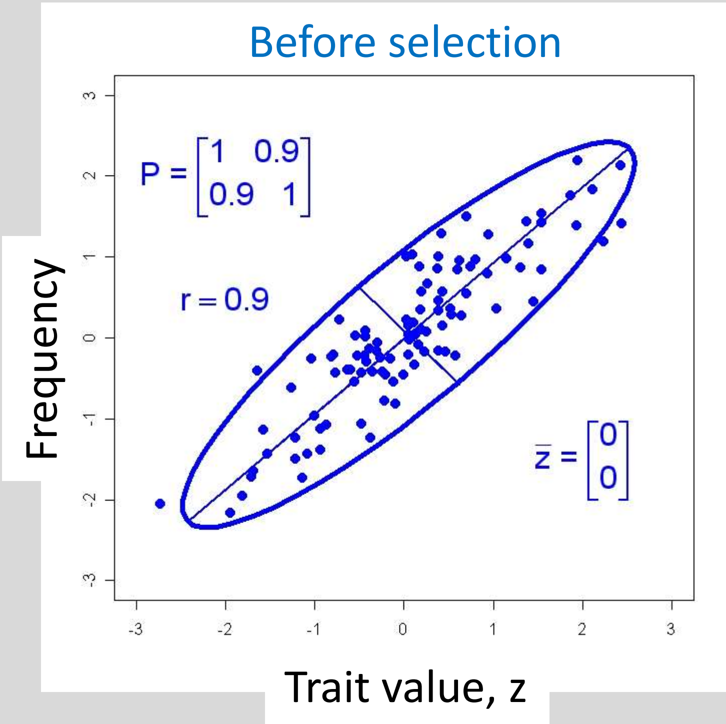
$$C' = (P^* - P + s^2)/P$$

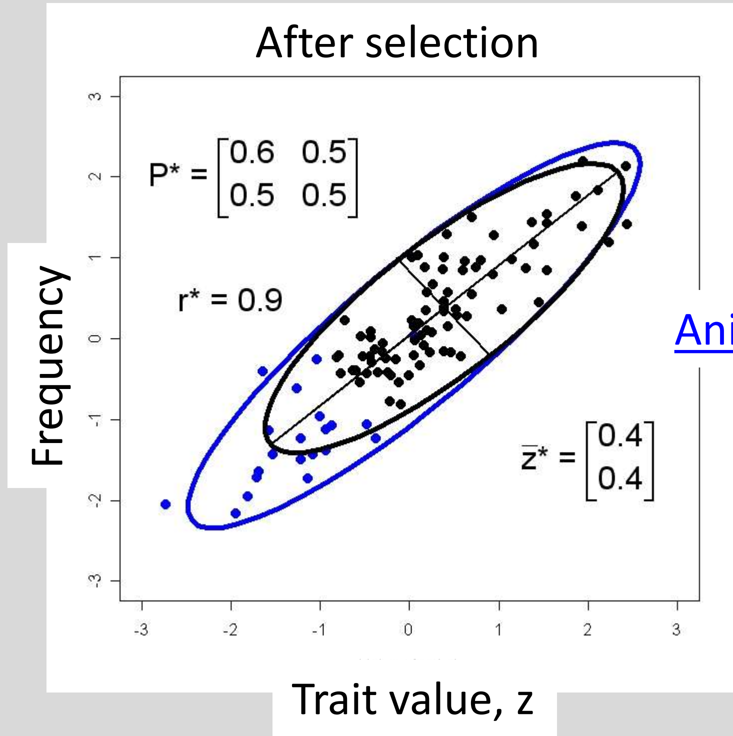




4. Selection changes the multivariate trait distribution

a. The contrast between distributions before and after selection



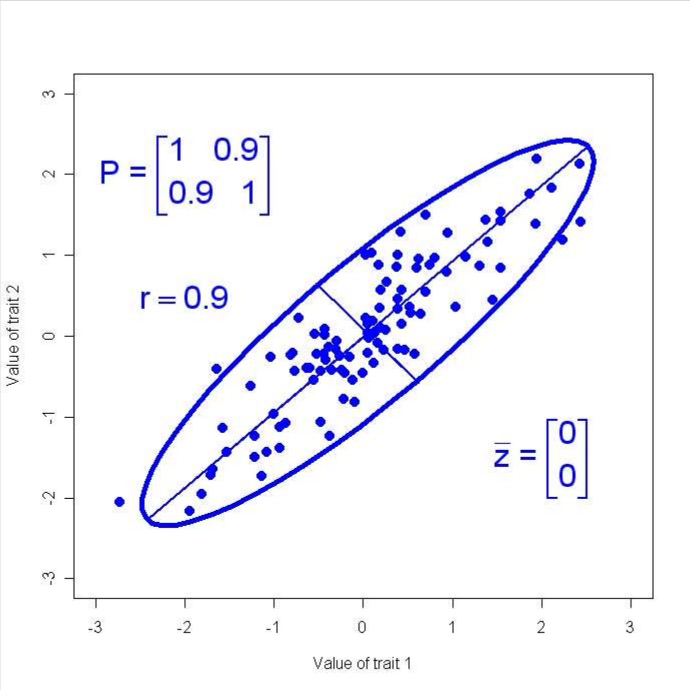


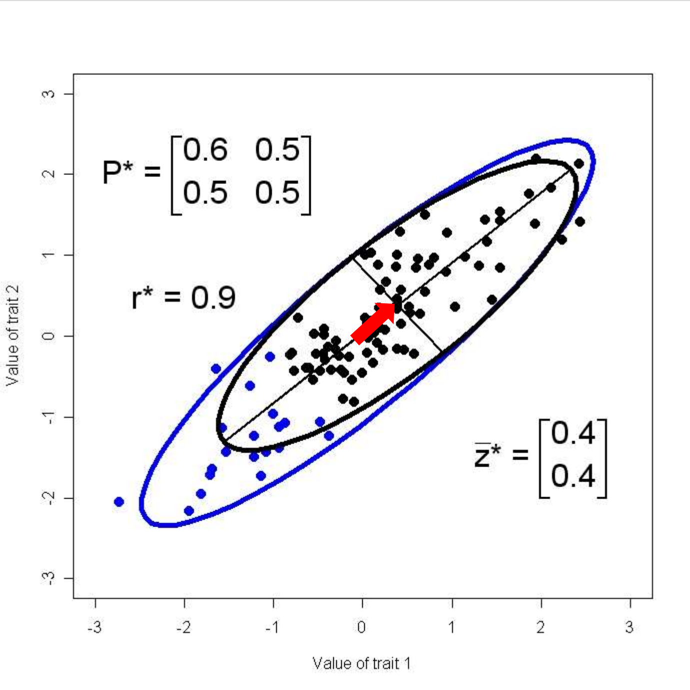
Animation2

4. Selection changes the multivariate trait distribution

b. The directional selection differential, s, is a vector

$$s = Cov(w,z) = \begin{bmatrix} Cov(w,z_1) \\ Cov(w,z_2) \end{bmatrix} = \bar{z} - \bar{z}^* = \begin{bmatrix} \bar{z}_1 - \bar{z}_1{}^* \\ \bar{z}_2 - \bar{z}_2{}^* \end{bmatrix} = \begin{bmatrix} s_1 \\ s_2 \end{bmatrix}$$

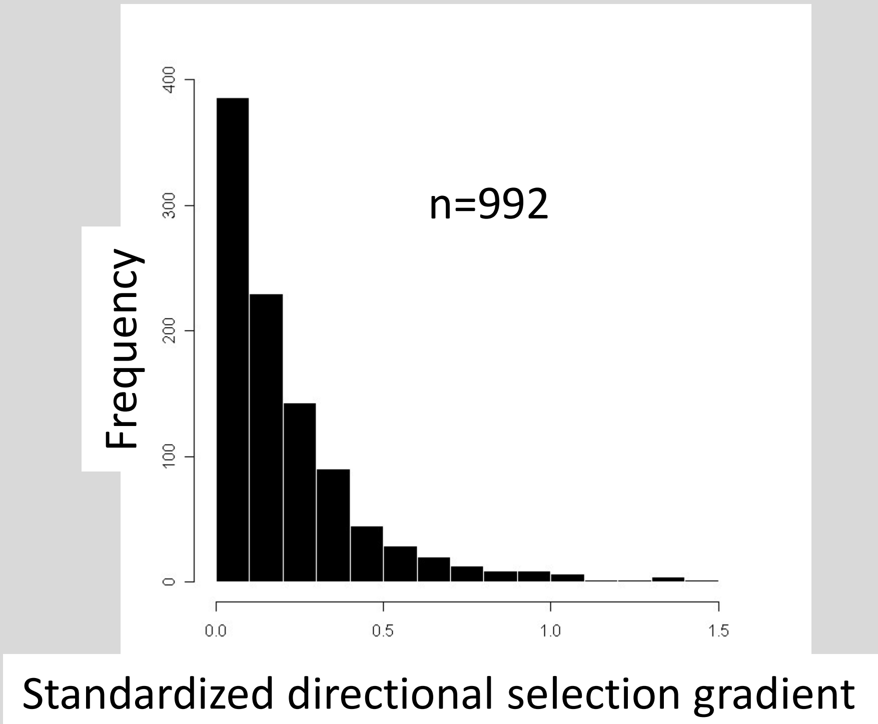


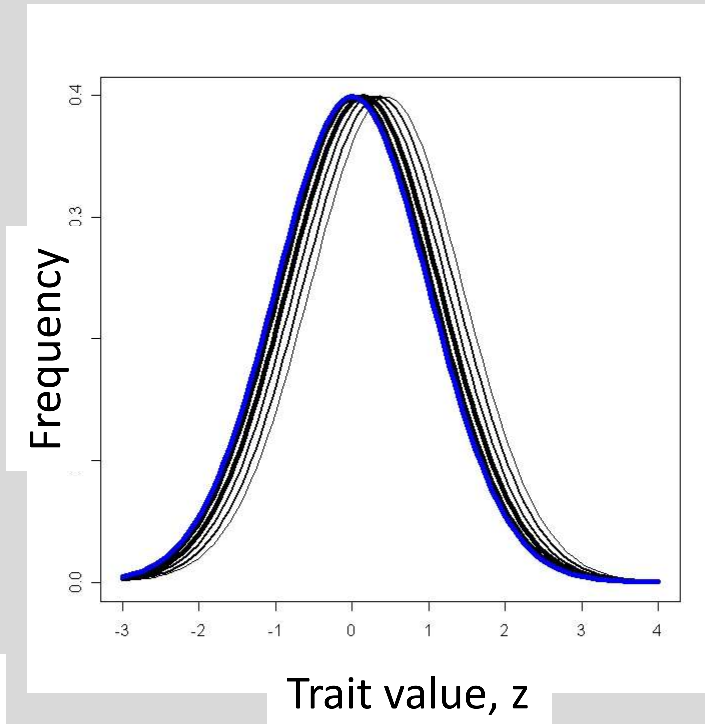


5. Survey

Standardized directional selection gradients, β

$$\beta \equiv P^{-1}s$$

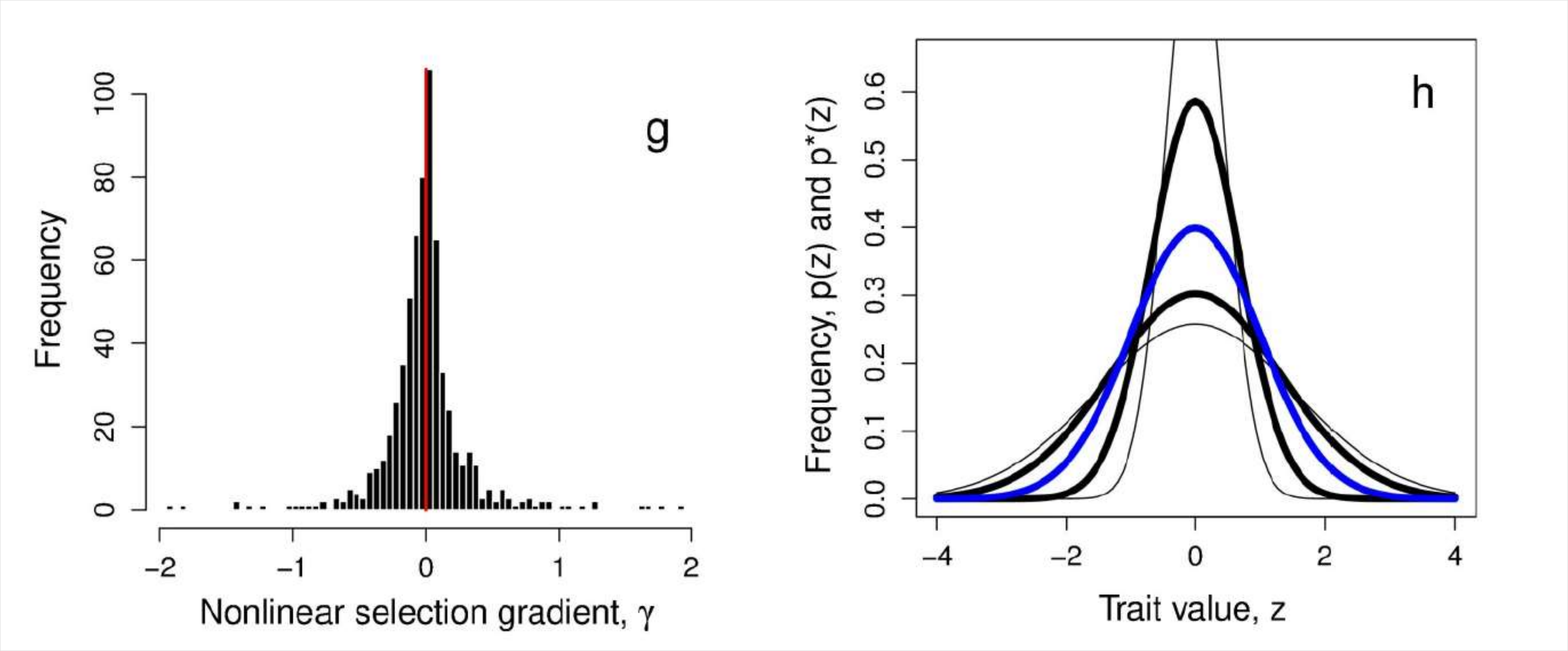




5. Survey, continued

Standardized nonlinear selection gradients, γ

$$\gamma \equiv P^{-1} C P^{-1}$$



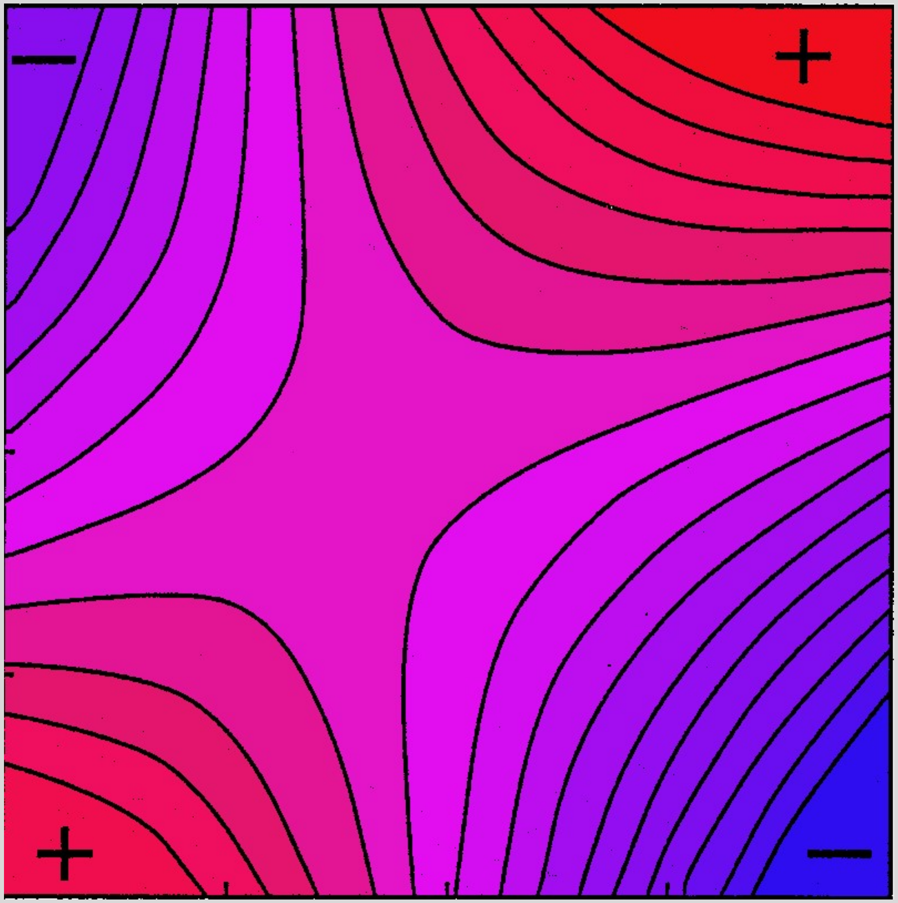
What have we learned?

1. The change in trait distributions before and after selection within a generation can be used to derive useful measures of selection.

2. Using those measures we can distinguish between the effects of directional and stabilizing selection.

3. We can also distinguish between the direct and indirect effects of selection mediated by correlations between traits.

Part 2. Selection as a Surface



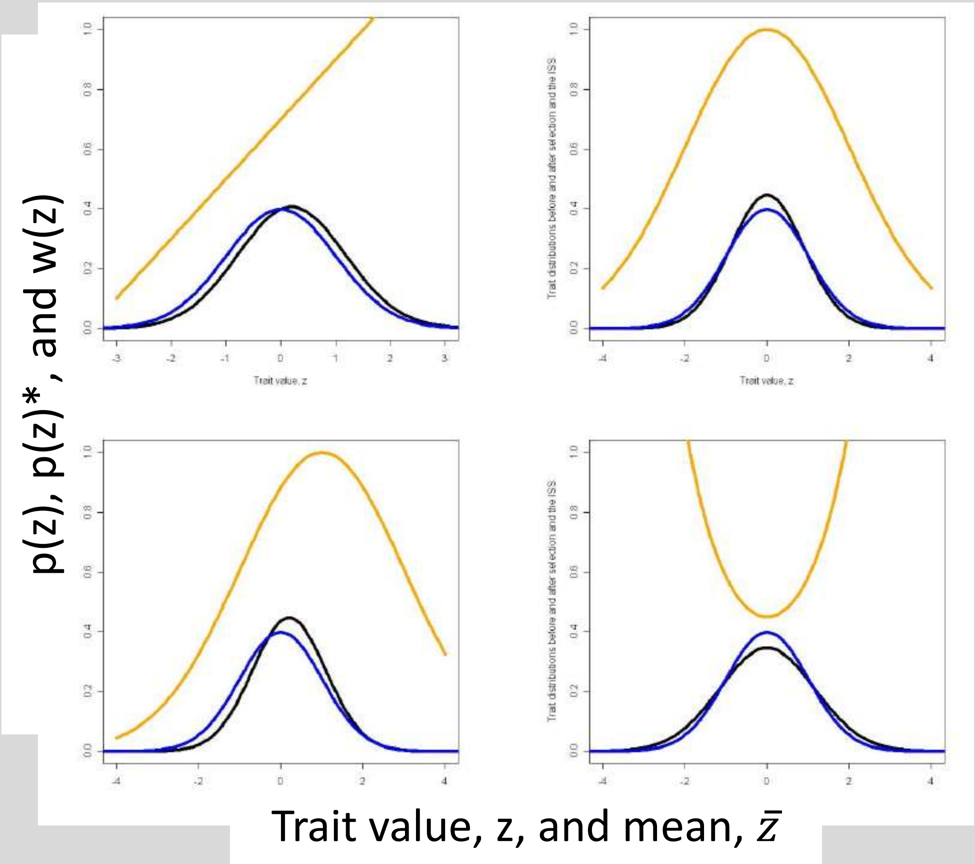
Thesis

- We can think of selection as a surface.
- Selection surfaces allow us to estimate selection parameters, as well as visualize selection.
- To visualize and estimate, we need to keep track of three kinds of surfaces:
  1. the individual selection surface
  2. our approximation of that surface
  3. the adaptive landscape.

1. The Individual Selection Surface

Expected individual fitness, $w(z)$, as a function of trait value, z

a. A model for how selection that changes trait means and variances



[Animation 0]

2. Approximations to the univariate ISS

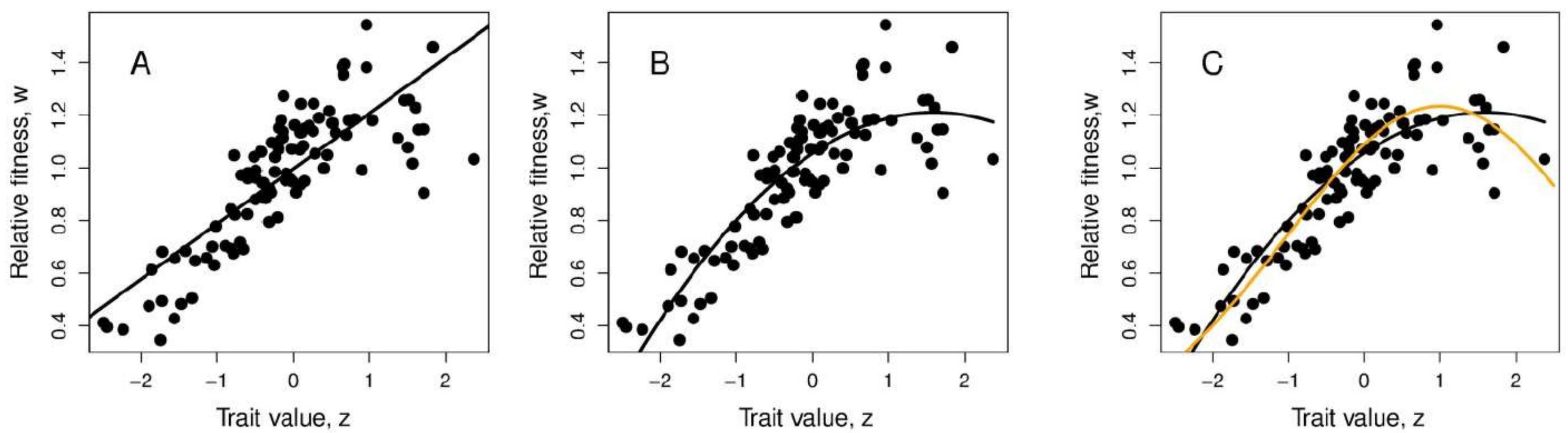
Linear & quadratric approximations:
a way to estimate β and γ

$$w(z) = \alpha + \beta z + \varepsilon$$ linear

$$w(z) = \alpha + \beta z + \frac{1}{2}\gamma z^2 + \varepsilon$$ quadratic*

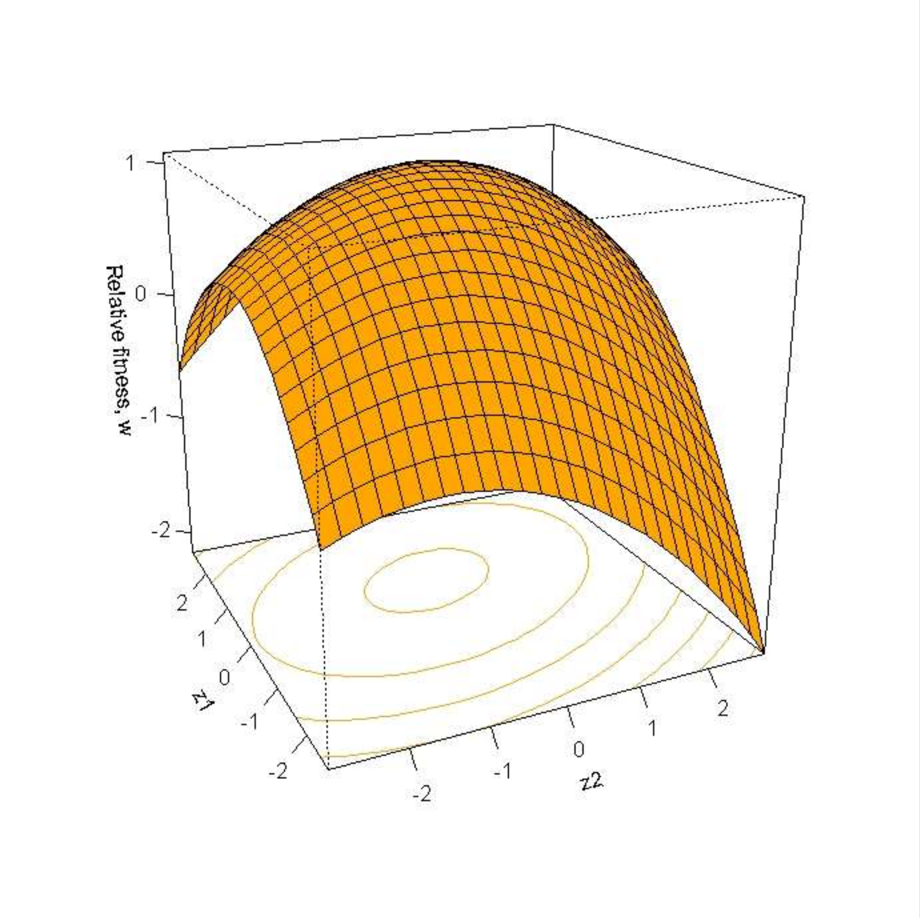
* the factor of ½ makes γ a second derivative

2. Linear and quadratic approximations to a Gaussian ISS



3. The multivariate individual selection surface, *ISS*

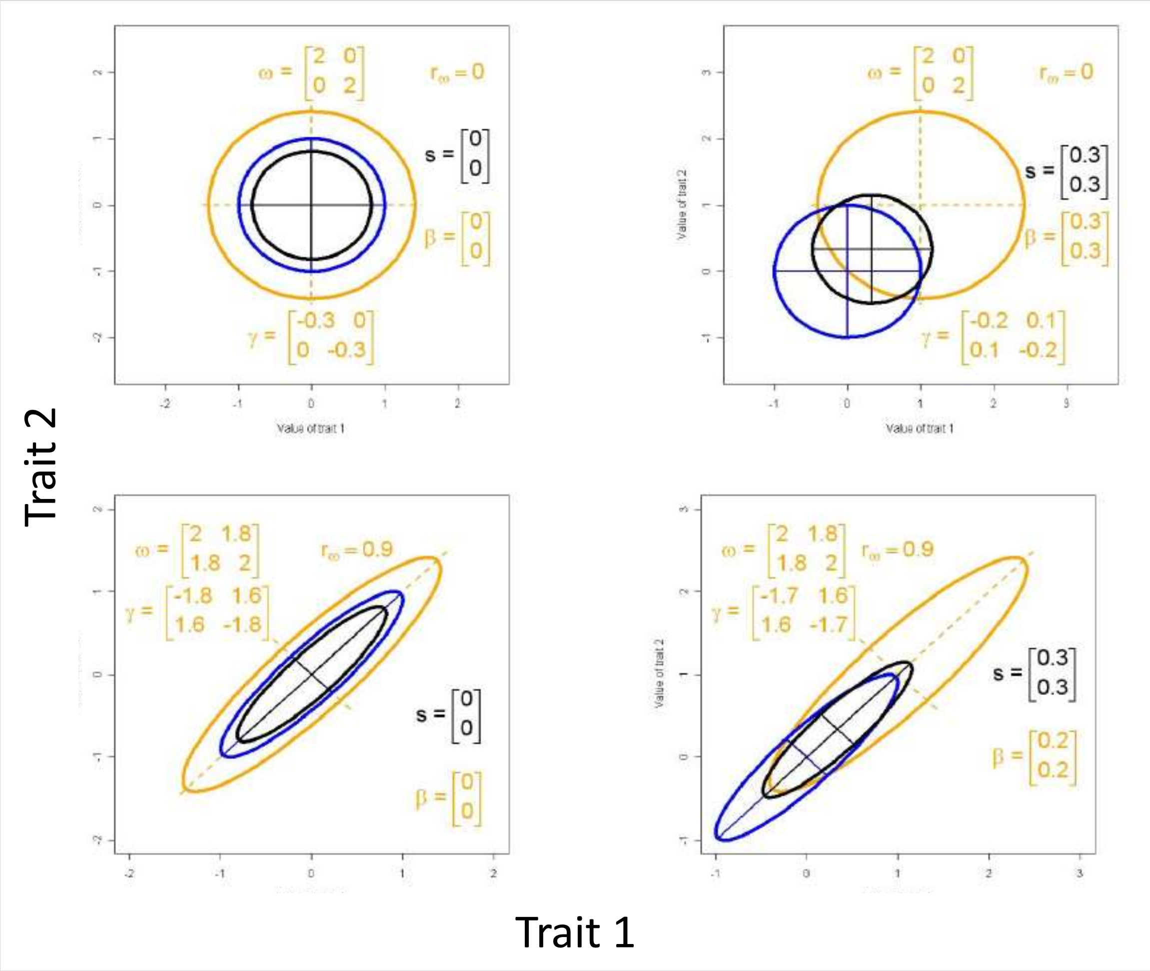
a. A hypothetical bivariate example



Animation 3

3. The multivariate individual selection surface, *ISS*

b. Some examples of bivariate ISSs and the selection they impose



[Animation 4]

4. Approximations to the multivariate ISS

a. Linear and quadratic approximations, a way to estimate β and y

For simplicity, we consider the two-trait case

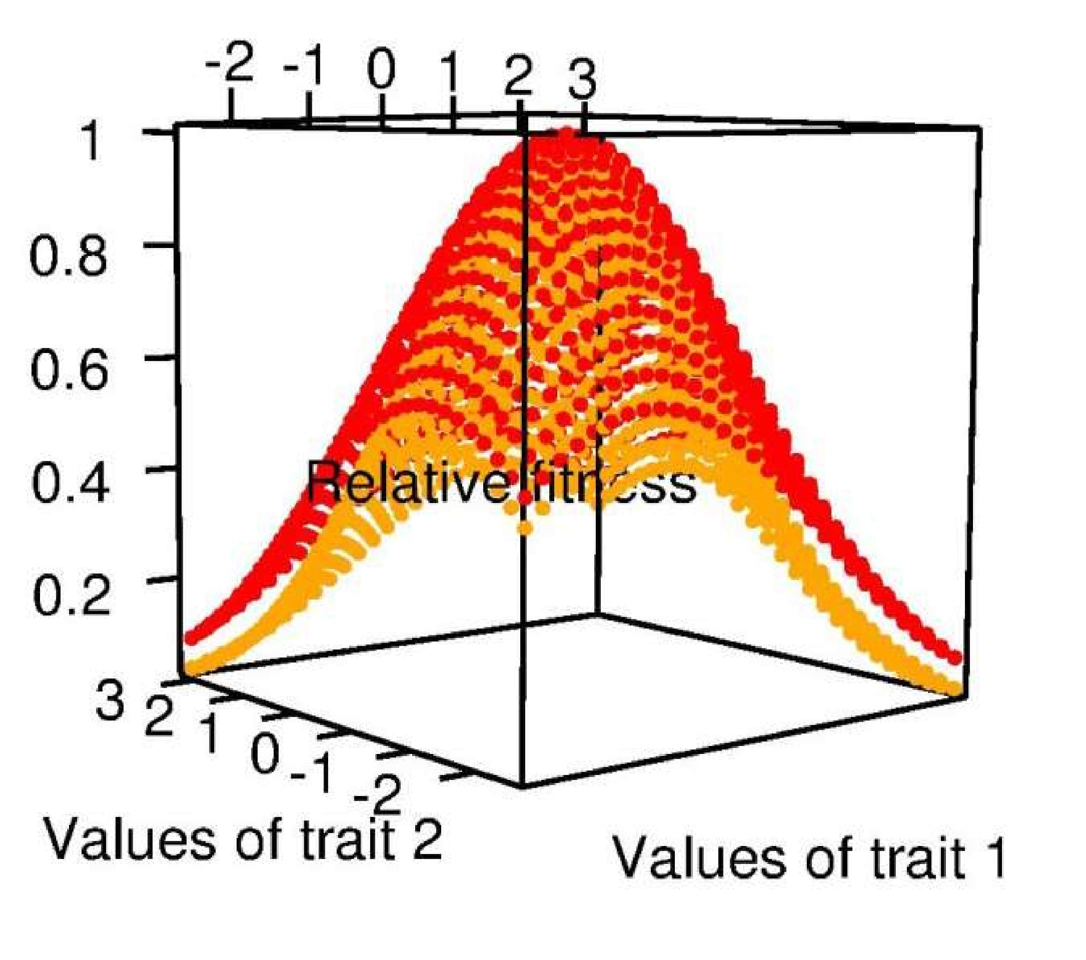
Linear approximation

$$w(z) = \alpha + \beta^T z + \varepsilon = \alpha + \beta_1 z_1 + \beta_2 z_2 + \varepsilon$$

Quadratic approximation

$$w(z) = \alpha + \beta^T + \tfrac{1}{2} z^T \gamma z + \varepsilon = \alpha + \beta_1 z_1 + \beta_2 z_2 + \tfrac{1}{2}\gamma_{11} z_1^{\,2} + \tfrac{1}{2}\gamma_{22} z_2^{\,2} + \gamma_{12} z_1 z_2 + \varepsilon$$

5. The adaptive landscape has less curvature than its ISS



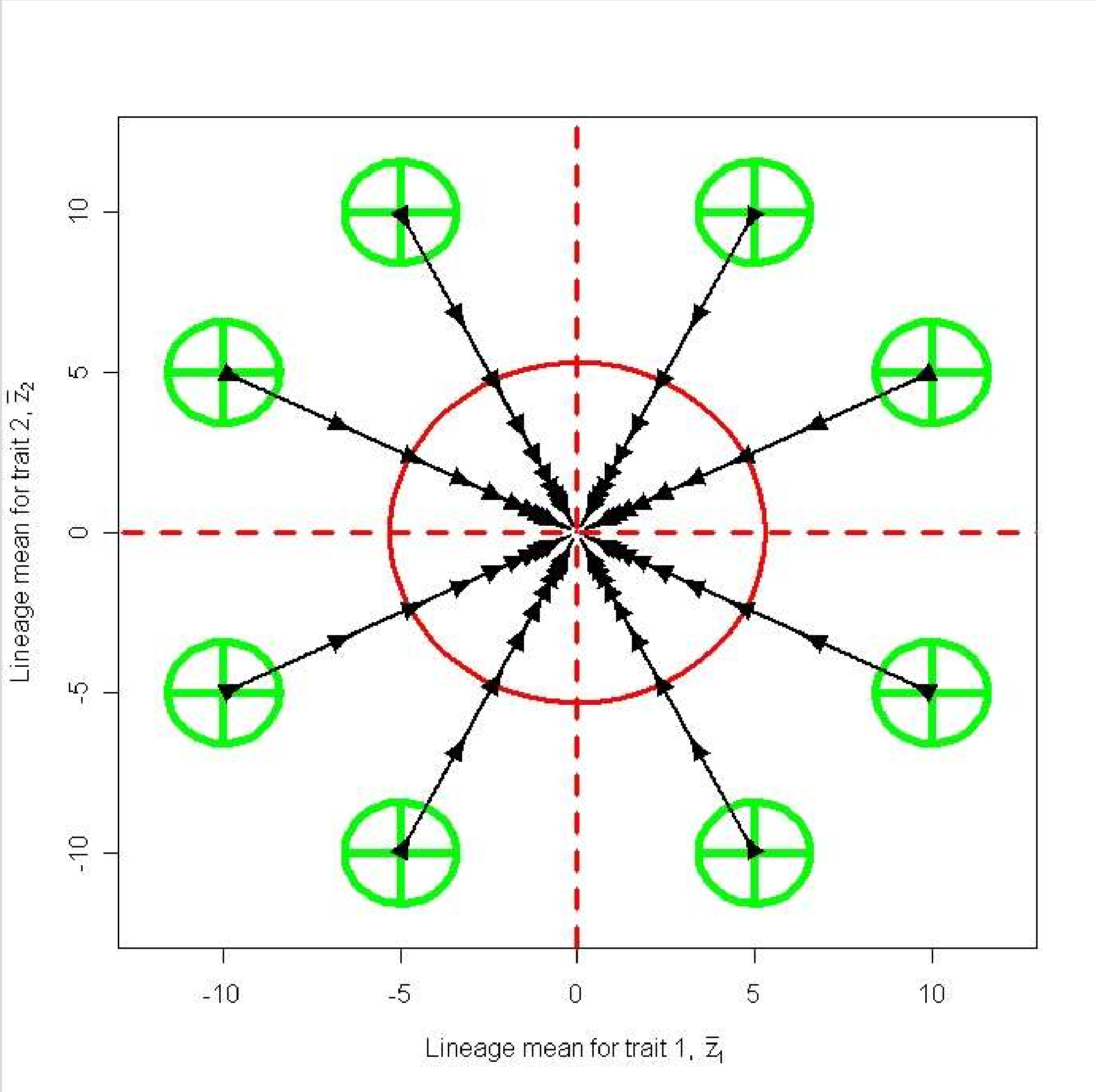
What have we learned?

1. Selection can be described with surfaces.

2. Some approximations of selection surfaces allow us to estimate key measures of selection (β and γ).

3. Those key measures in turn tell us about the adaptive landscape.

Evolution on Adaptive Landscapes



Thesis

- Models for adaptive radiation can be constructed with quantitative genetic parameters.
- The use of quantitative genetic parameters allows us to cross-check with the empirical literature on inheritance, selection, and population size.
- Stabilizing selection and peak movement appear to be necessary but may not be sufficient to account for evolution in deep time.

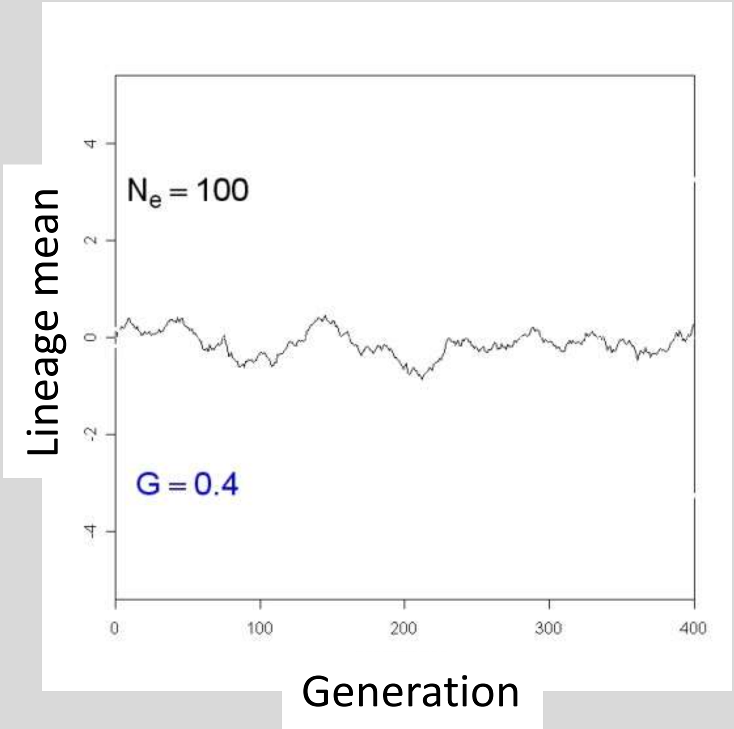
1. Evolution without selection, genetic drift

a. Sampling N_e individuals from a normal distribution of breeding values

$$Var(\bar{z}) = \frac{1}{N_e} G$$

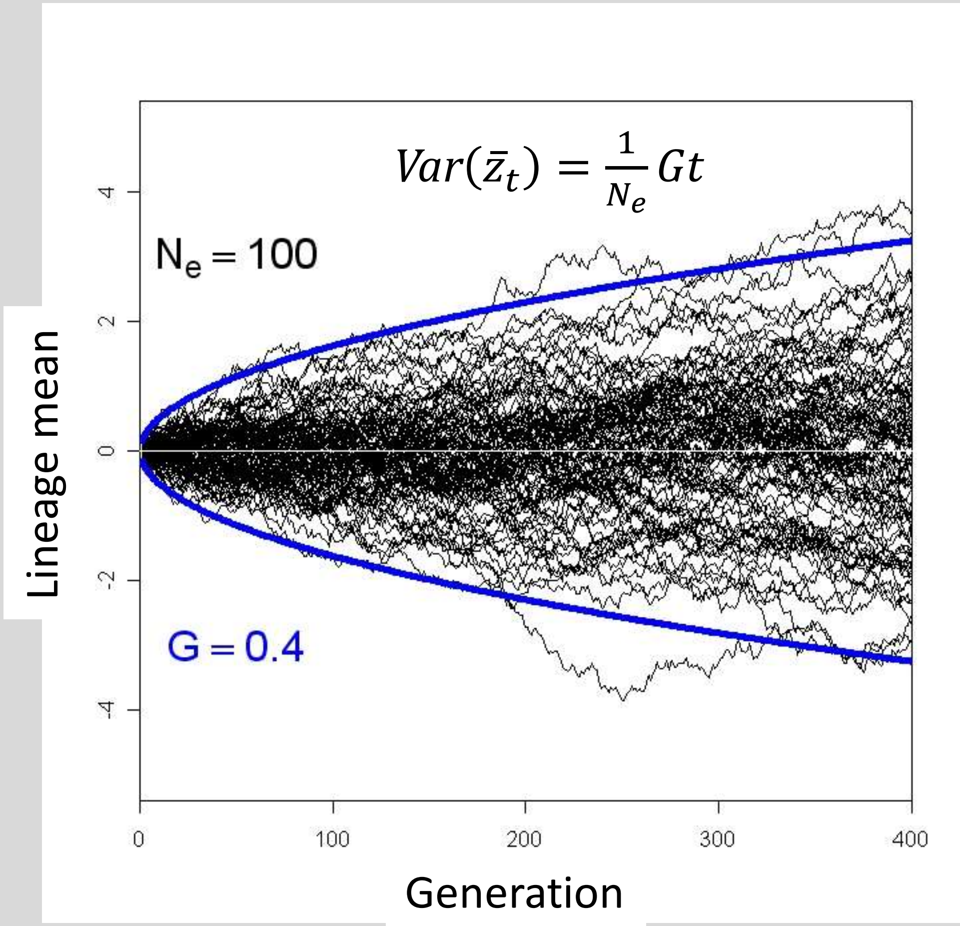
b. Projecting the distribution of breeding values into the future

$$Var(\bar{z}_t) = \frac{1}{N_e} G t$$



1. Evolution without selection, genetic drift

c. Many replicate populations evolving by drift



Animation 1

2. Univariate evolution about a stationary peak

a. Tendency to evolve uphill on the adaptive landscape

$$\Delta\bar{z} = G\beta = G\frac{\partial \ln \overline{W}}{\partial \bar{z}}$$

$$\Delta \ln \overline{W} \cong \Delta\bar{z}^T G^{-1} \Delta\bar{z} \geq 0$$

b. Stochastic dynamics with a single Gaussian, stationary peak

The Ornstein-Uhlenbeck, OU, process

Per generation change in mean

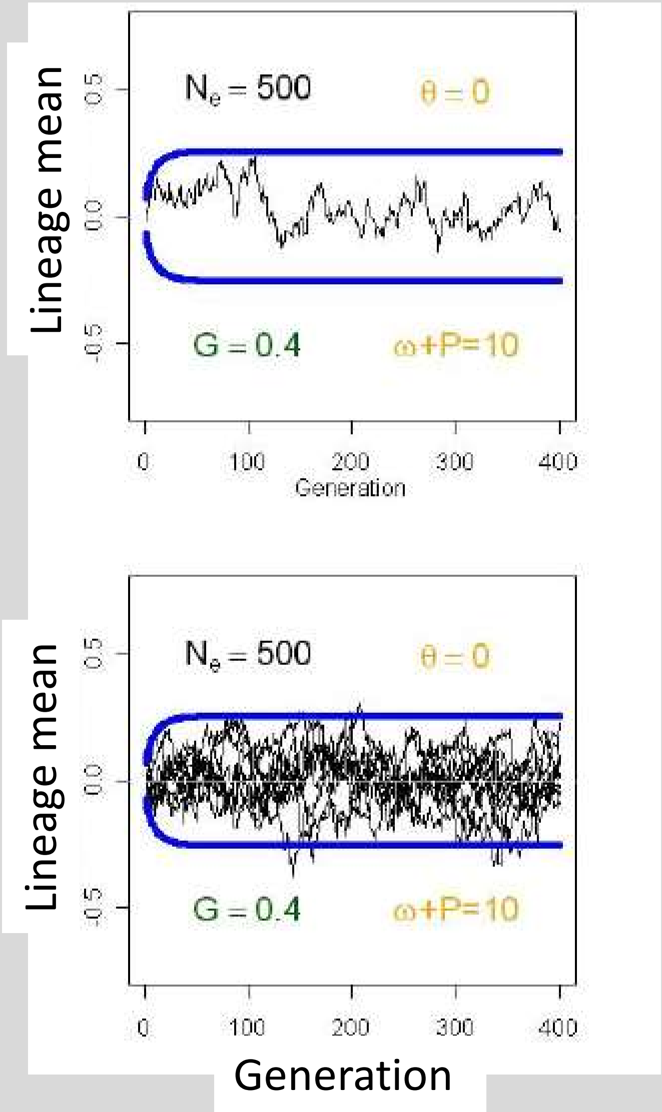
$$\bar{z}(t+1) = \bar{z}(t) + G\frac{[\theta - \bar{z}(t)]}{\omega + P} + N(0, G/N_e)$$

Variance among replicate lineages in trait mean

$$Var(\bar{z}_t) = \frac{\omega + P}{2N_e}\left\{1 - \exp\left[-2\left(\frac{G}{\omega + P}\right)t\right]\right\}$$

2. Univariate evolution about a stationary peak

b. Stochastic dynamics with a single, stationary peak



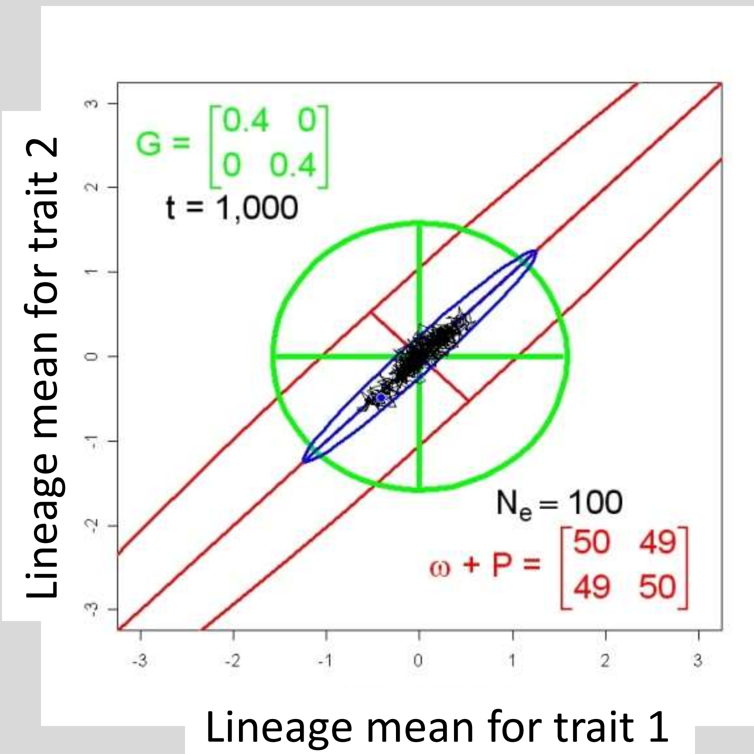
[Animation 2]

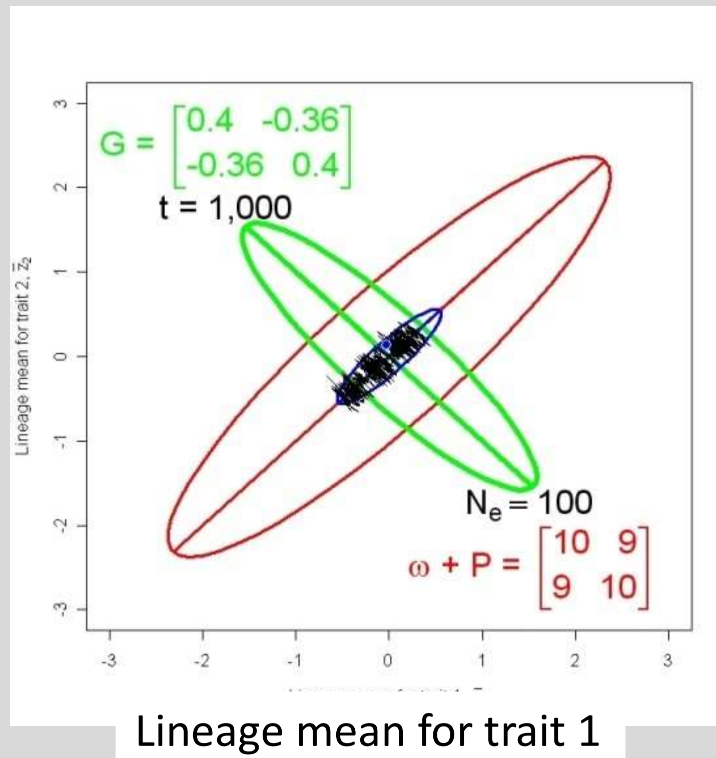
3. Bivariate evolution about a stationary peak

Replicate responses to a single Gaussian, stationary peak

The adaptive landscape trumps the G-matrix

$$Var(\bar{z}_t) = \frac{(\omega + P)}{2N_e}\left\{1 - \exp\left[-2tG(\omega + P)^{-1}\right]\right\}.$$



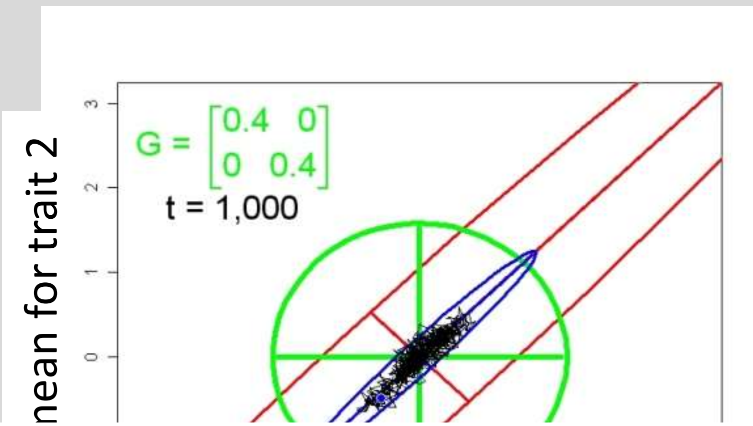


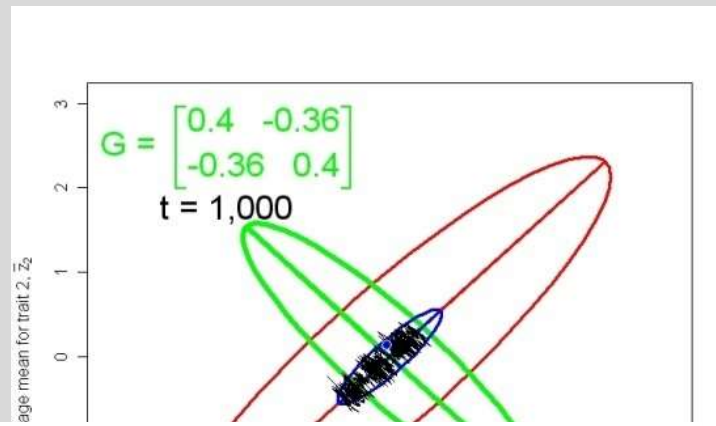
3. Bivariate evolution about a stationary peak

Stochastic response to a single Gaussian, stationary peak

The adaptive landscape trumps the G-matrix

$$Var(\bar{z}_t) = \frac{(\omega + P)}{2N_e}\left\{1 - \exp\left[-2tG(\omega + P)^{-1}\right]\right\}.$$





The heartbreak of OU: to account for data, requires small N_e or
very weak stabilizing selection (large ω)

Lineage mean for trait 1

Lineage mean for trait 1

4. Evolution when the peak moves

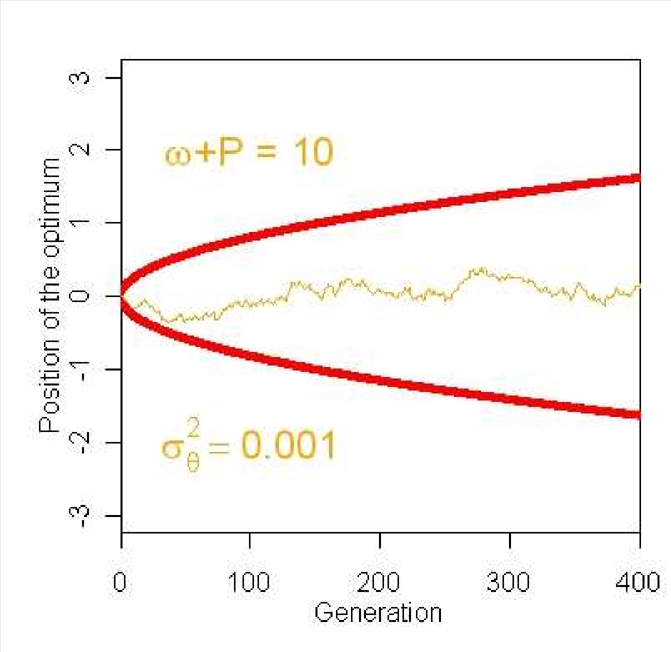
a. Brownian motion of a Gaussian adaptive peak

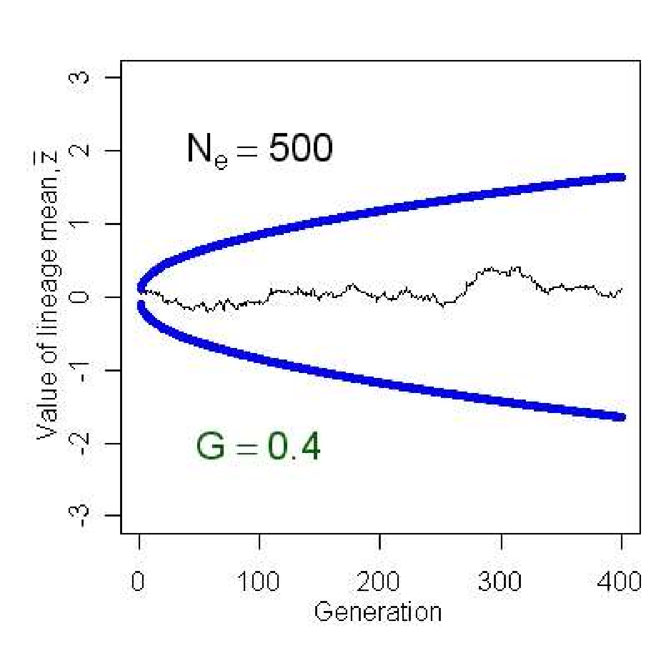
$$\theta_{t+1} = \theta_t + \varepsilon_\theta$$

The optimum, θ, undergoes Brownian motion

$$\Delta\bar{z}(t+1) = \left(\frac{\theta_t - \bar{z}_t}{\omega + P}\right)G + N(0, G/N_e)$$

The lineage mean chases the optimum





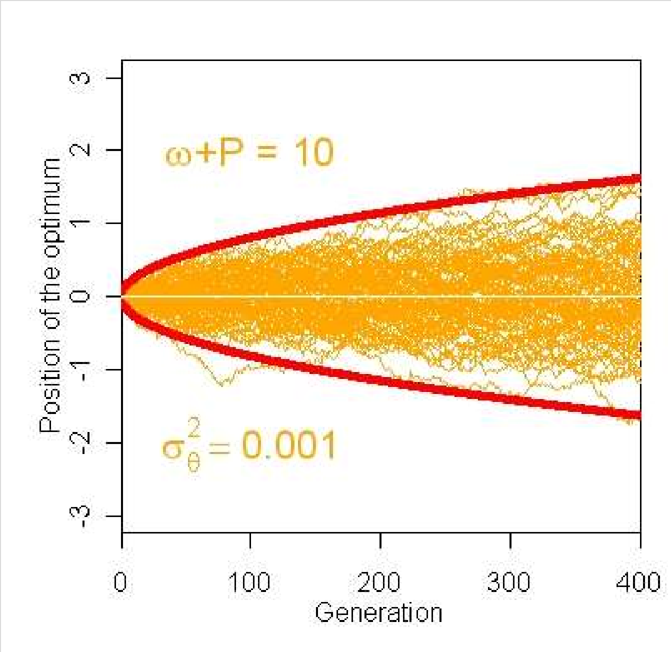
4. Evolution when the peak moves

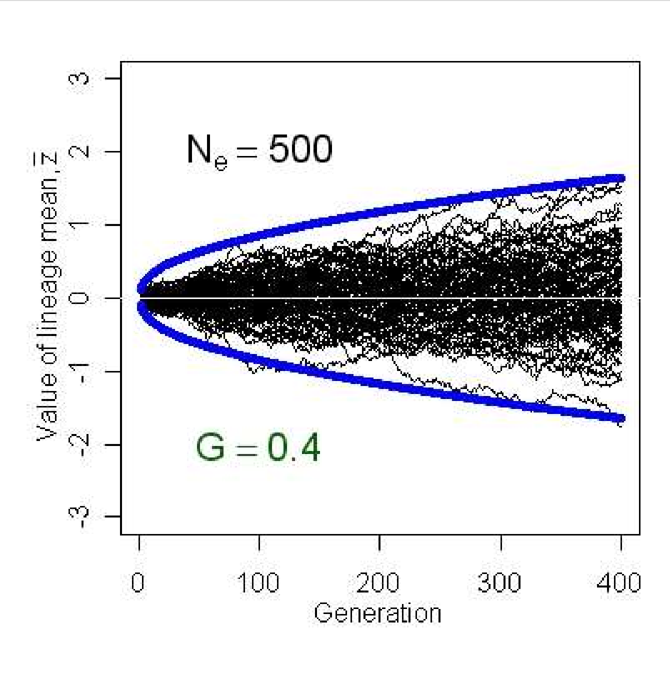
a. Brownian motion of a Gaussian adaptive peak

Replicate lineages respond to replicate peak movement

$$Var[\bar{z}(t)] = \frac{\sigma_\theta^2 + \frac{G}{N_e}}{2a}\{1 - exp[-2at]\} + \sigma_\theta^2 t\left\{1 - 2\frac{(1 - \exp[-at])}{at}\right\}$$

$$a = \frac{G}{\omega + P}$$



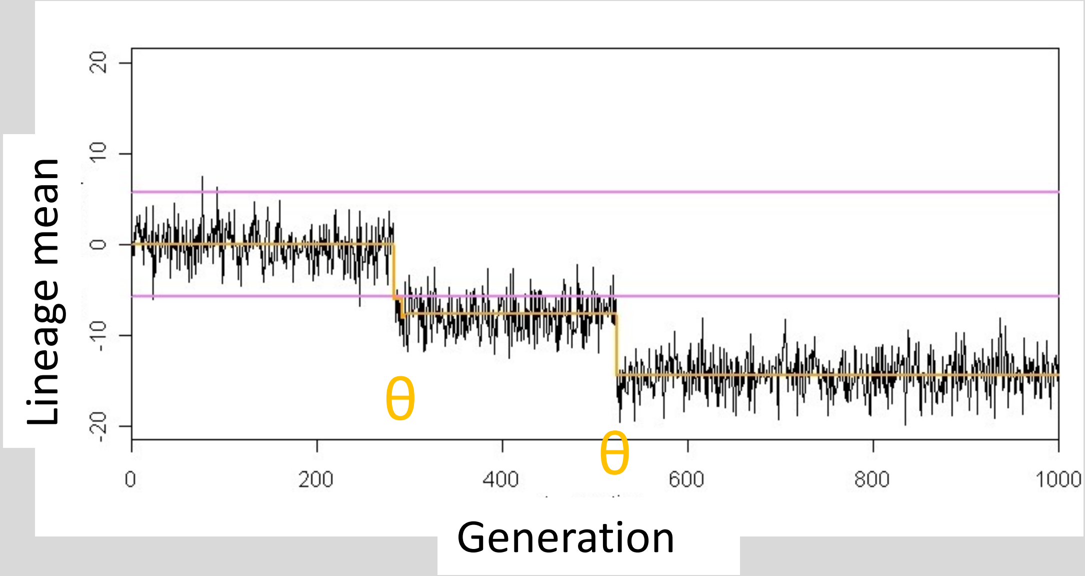


4. Evolution when the peak moves

b. Multiple burst model of peak movement

The optimum, θ, moves in rare bursts, governed by a Poisson process, but is otherwise stationary

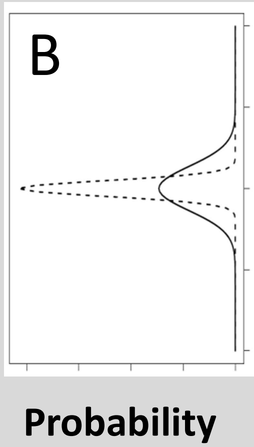
The lineage mean instantaneously tracks bursts in the optimum, but otherwise evolves according to a white noise process

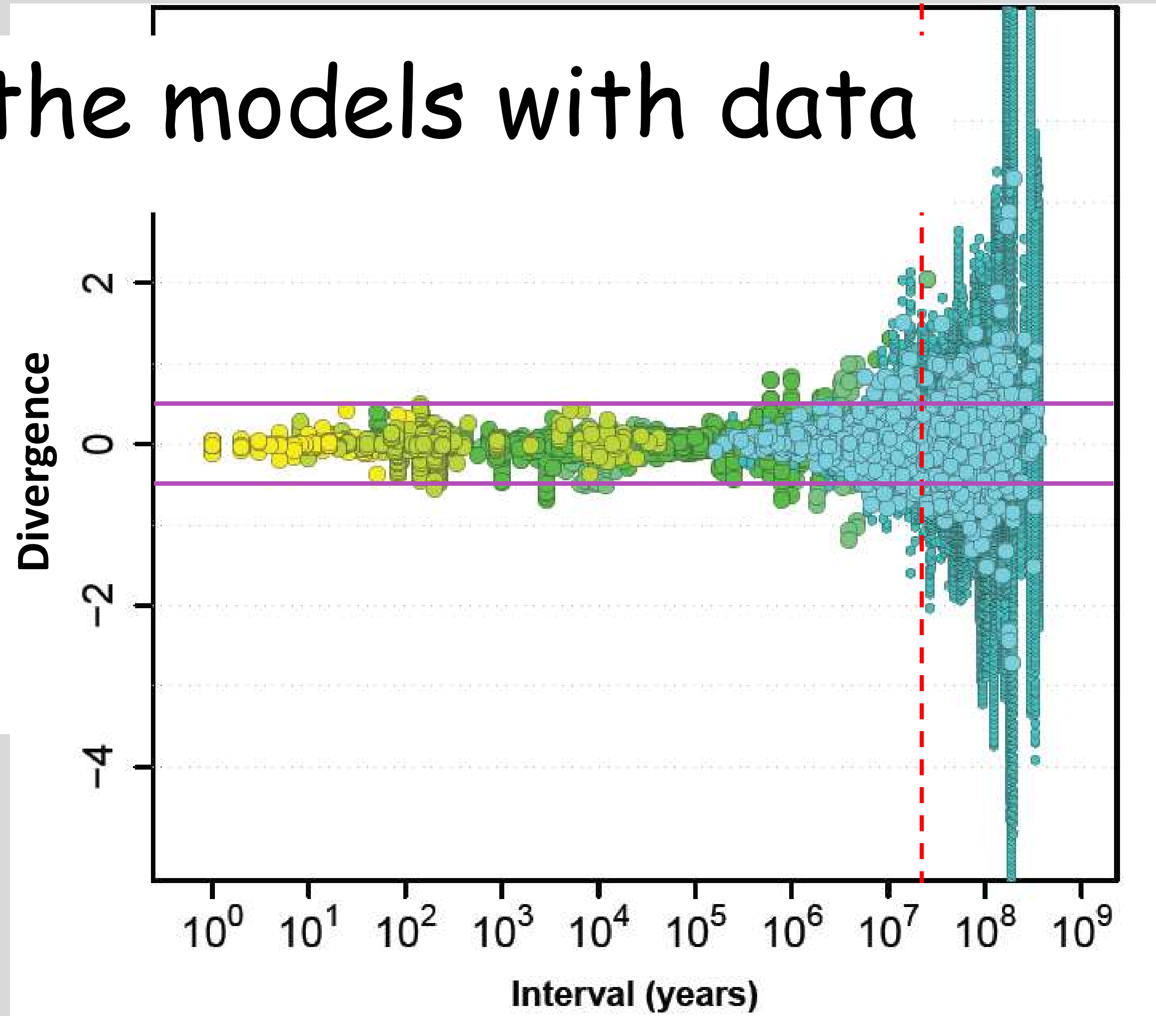


5. Challenging the models with data

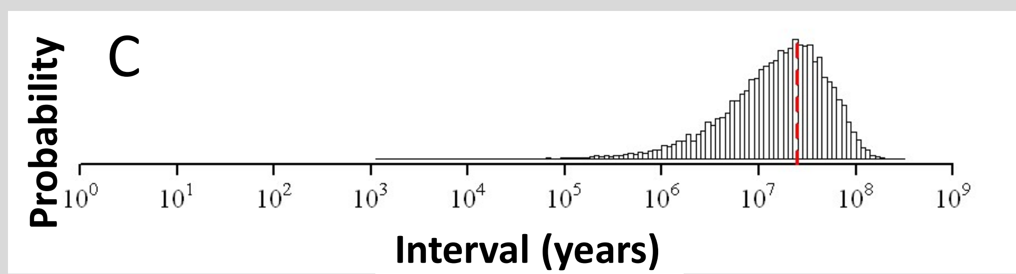
White noise distribution (dashed)

Burst size distribution (solid)





Burst timing distribution (mean time between bursts = 25 my)



What have we learned?

1. Quantitative genetic models can be used to model adaptive radiations.

2. Models in which an adaptive peak is stationary can not account for the scope of actual adaptive radiations.

3. Bounded evolution is a prevalent mode of evolution on all timescales.

4. Sudden departures from bounded evolution are rare but may account for the invasion of new adaptive zones.

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