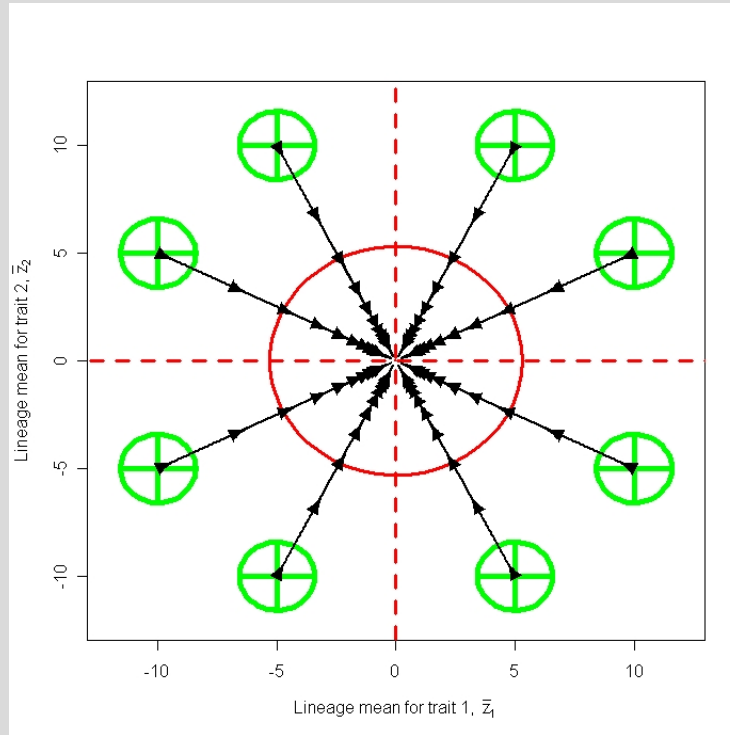


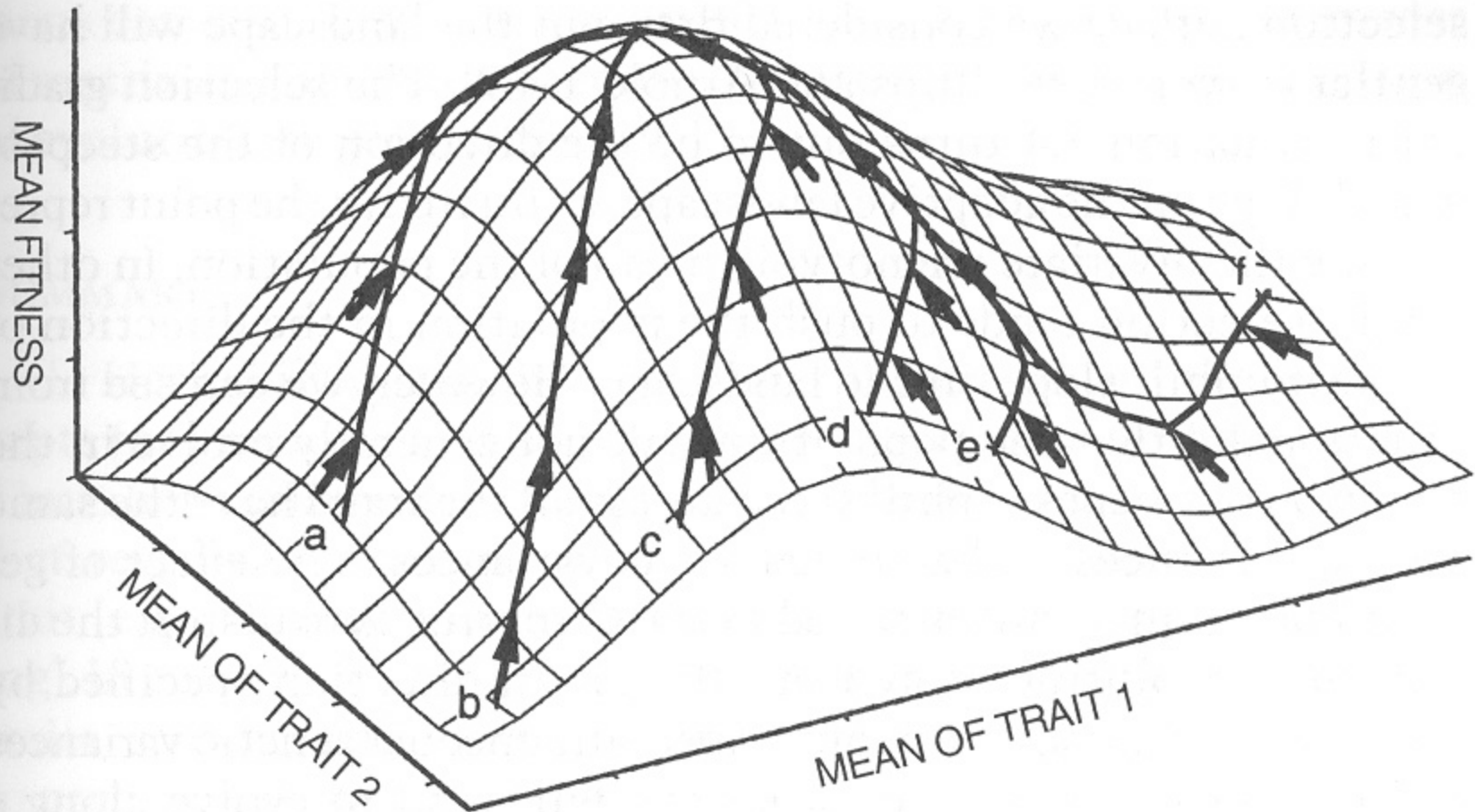
2.3 Evolution on a Surface



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



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.

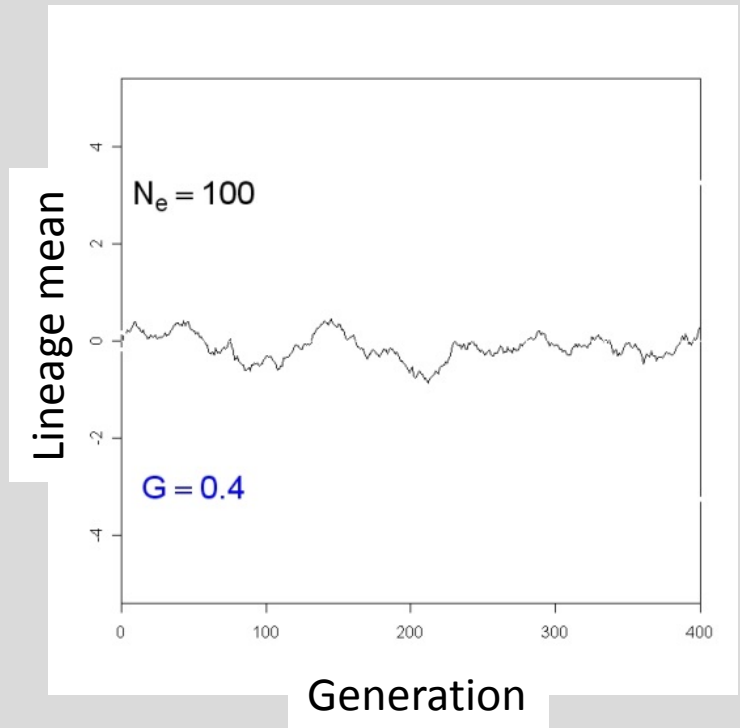
1. Evolution without selection, genetic drift

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

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

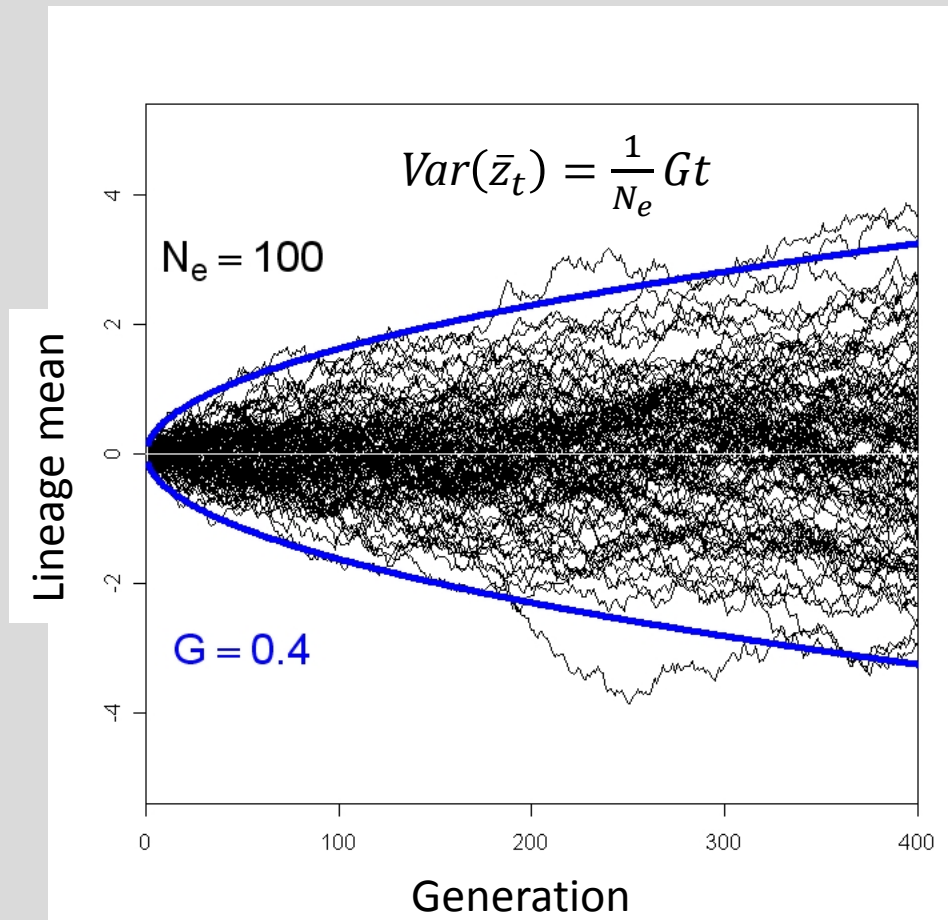
b. Projecting the distribution of breeding values into the future

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



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



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

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

b. Stochastic dynamics with a single Gaussian, stationary peak

The Ornstein-Uhlenbeck, OU, process

Per generation change in mean

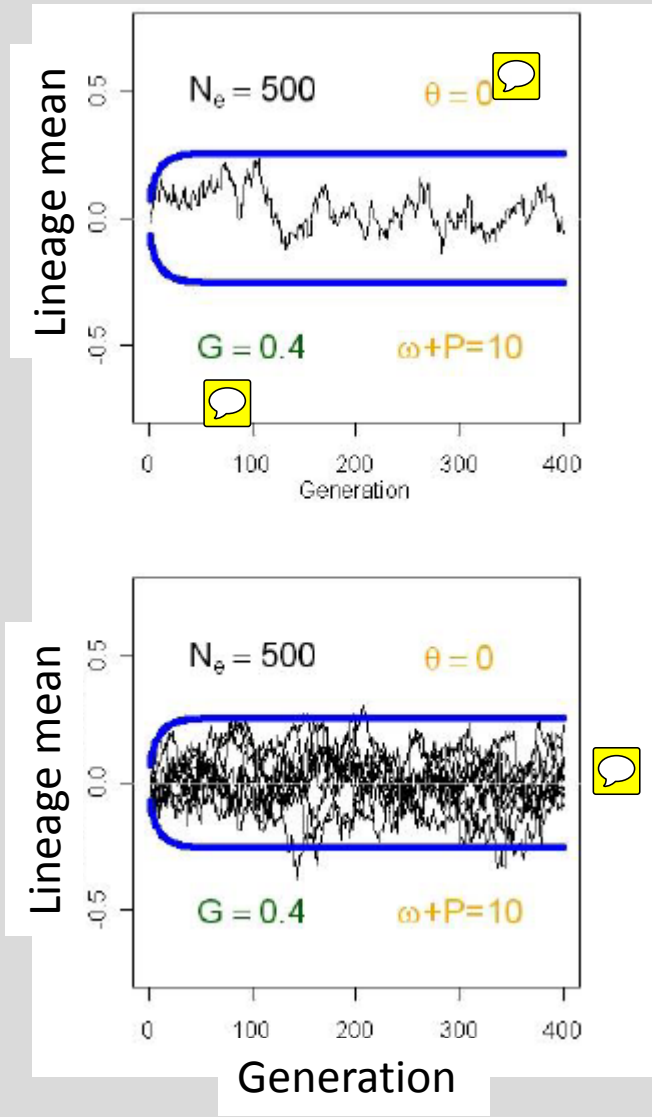
$$\bar{z}(t+1) = \bar{z}(t) + G \frac{[\theta - \bar{z}(t)]}{\omega + P} + N(0, G/N_e)$$

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



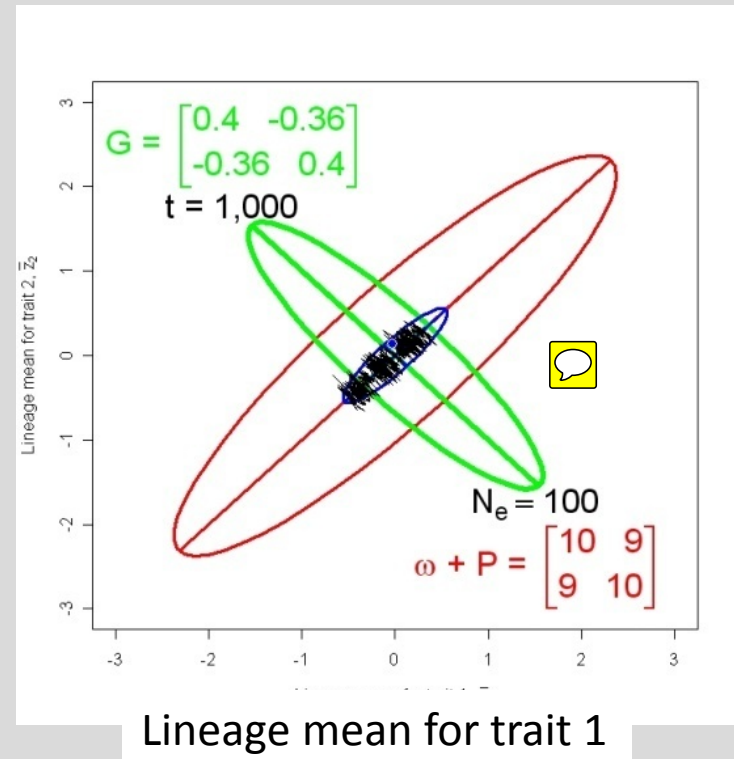
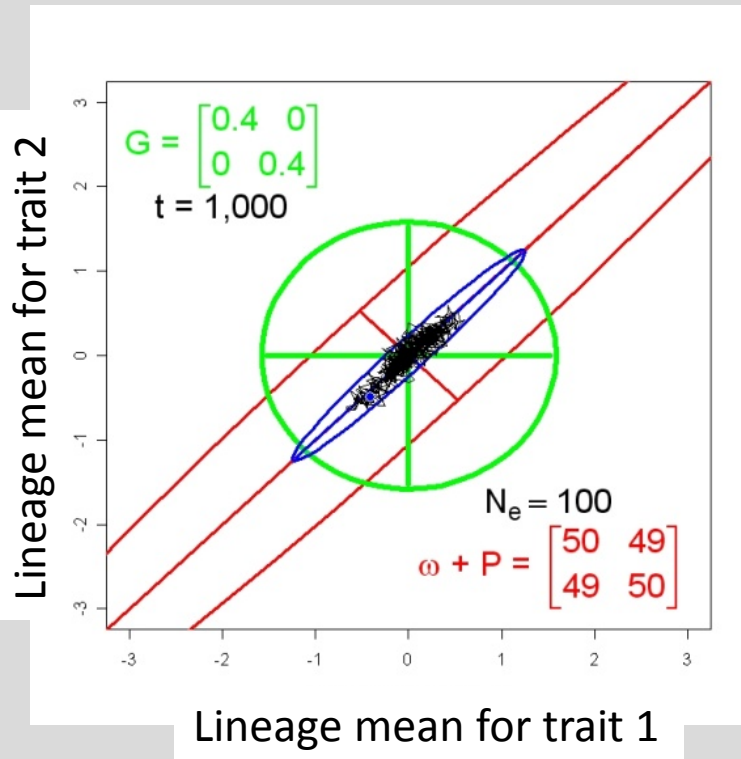
[Animation 2](#)

3. Bivariate evolution about a stationary peak

Replicate responses to a single Gaussian, stationary peak

The adaptive landscape trumps the G -matrix

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

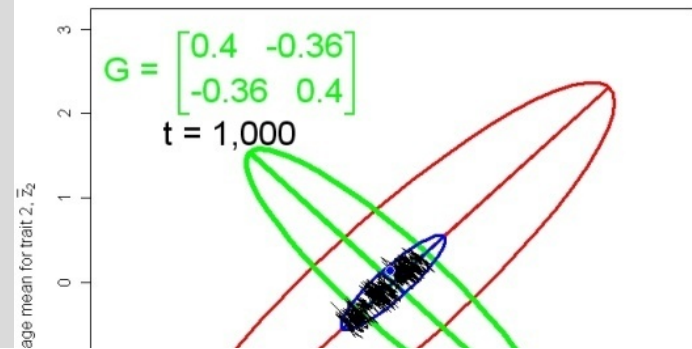
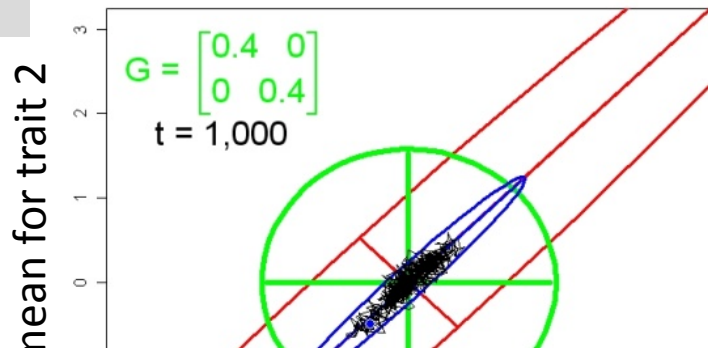


3. Bivariate evolution about a stationary peak

Stochastic response to a single Gaussian, stationary peak

The adaptive landscape trumps the G -matrix

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



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

Lineage mean for trait 1

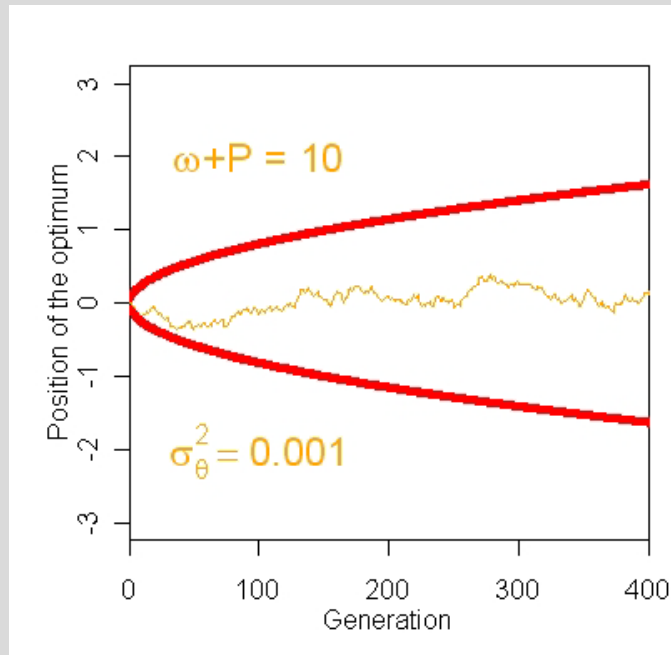
Lineage mean for trait 1

4. Evolution when the peak moves

a. Brownian motion of a Gaussian adaptive peak

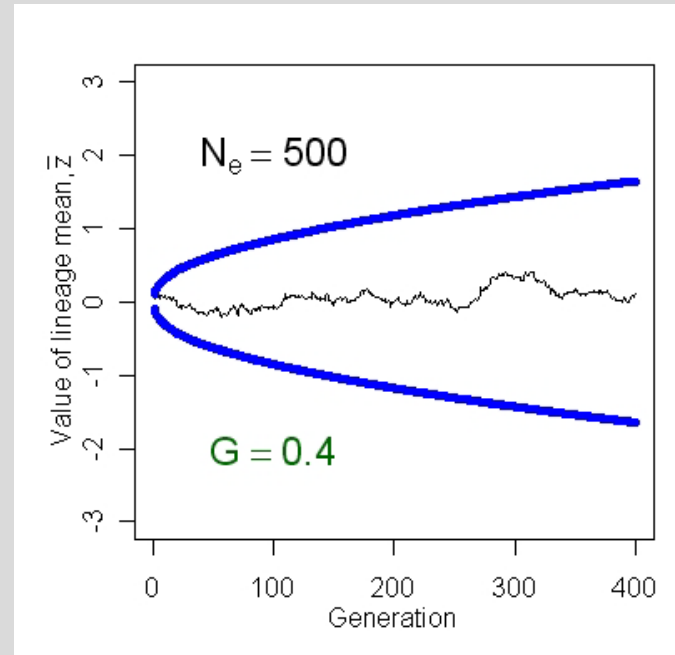
$$\theta_{t+1} = \theta_t + \varepsilon_\theta$$

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



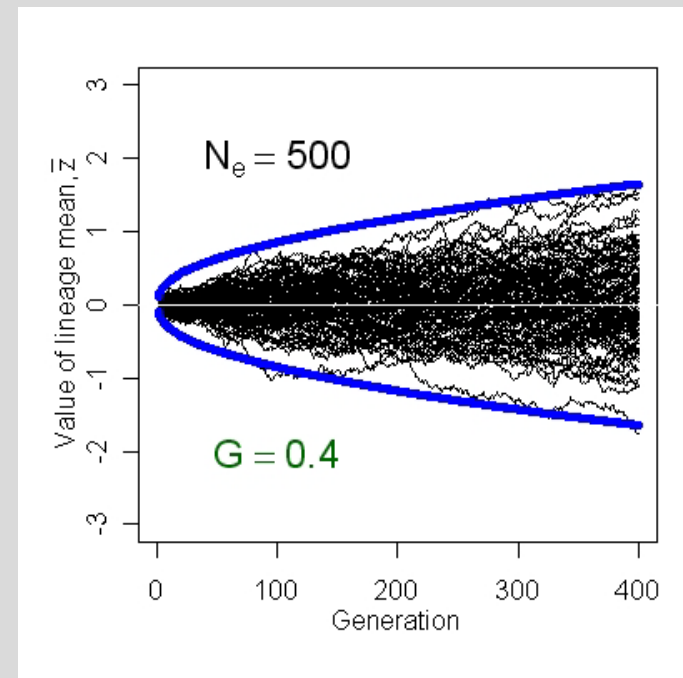
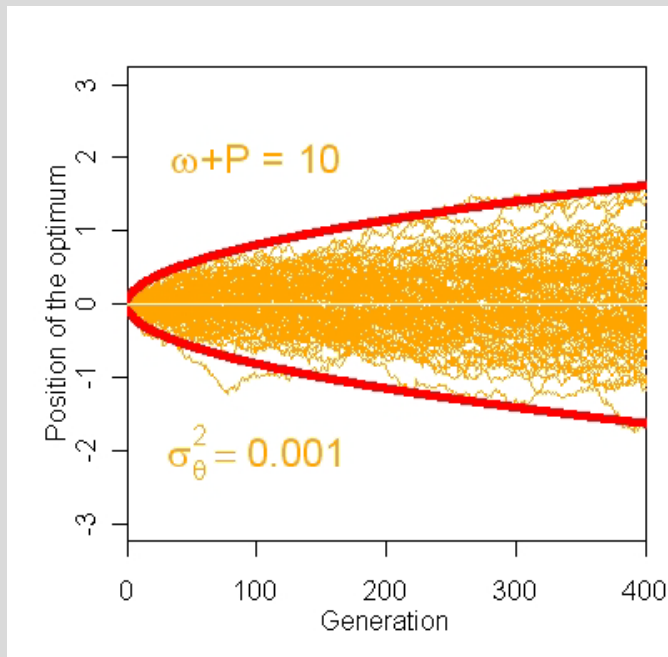
4. Evolution when the peak moves

a. Brownian motion of a Gaussian adaptive peak

Replicate lineages respond to replicate peak movement

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

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

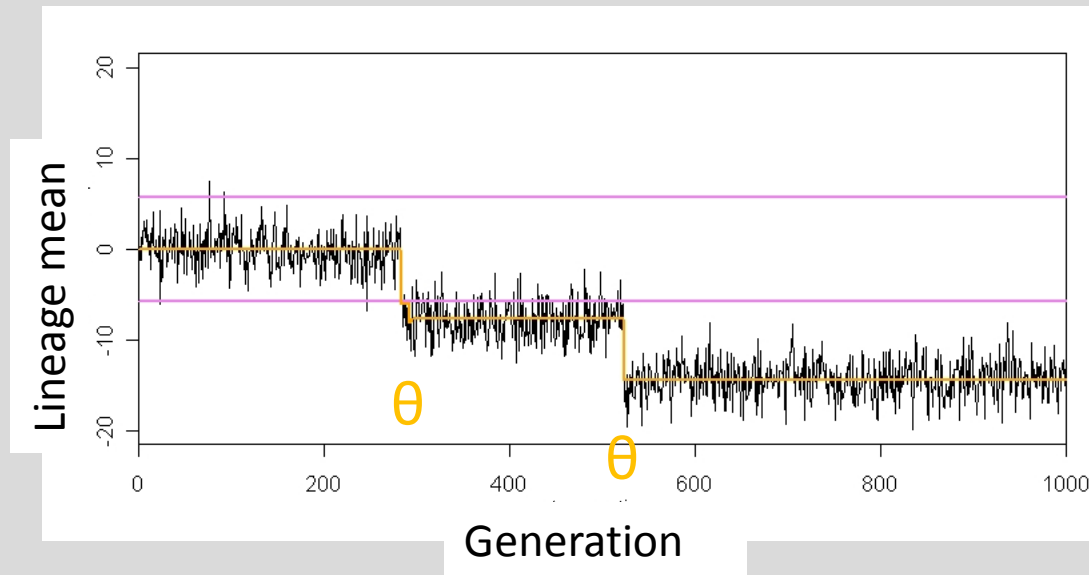


4. Evolution when the peak moves

b. Multiple burst model of peak movement

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

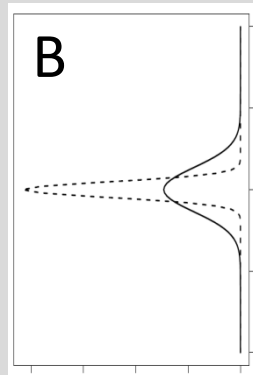
The lineage mean instantaneously tracks bursts in the optimum, but otherwise evolves according to a white noise process



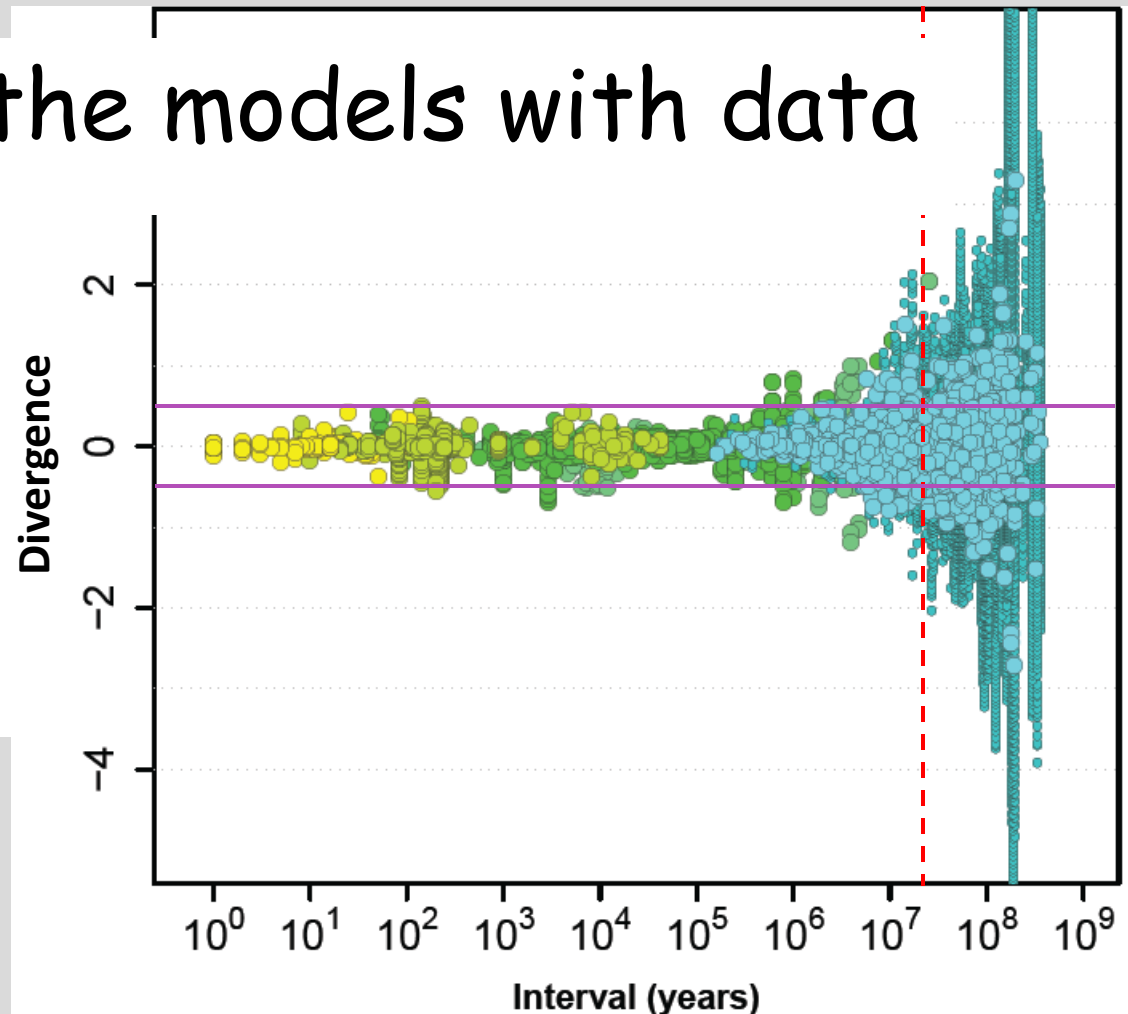
5. Challenging the models with data

White noise
distribution
(dashed)

Burst size
distribution
(solid)



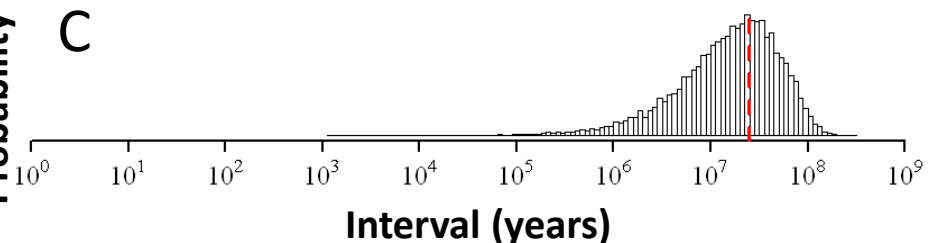
Probability



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

Probability

C



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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