I. To this point, we have studied how phenotypes change in response to natural selection

What other forces may drive phenotypic evolution?

When are these forces important?

II. How does drift change the mean phenotype of a population?

Let's focus on a single trait, z, to keep things simple, and make the following assumptions:

1. The next generation is formed by sampling *n* individuals at random

2. No selection or gene flow

3. The additive genetic variance G is constant over time

With these assumptions, the mean phenotype in the next generation is:

$$\bar{z}' = \bar{z} + \varepsilon \qquad (1)$$

where ε is a random variable with a mean equal to zero and a variance equal to G/n

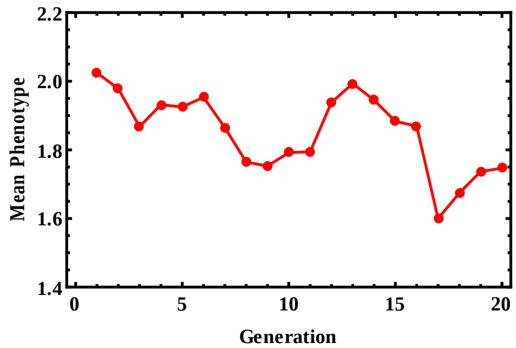
Why is the mean of ε equal to 0?

Drift increases phenotype and decreases phenotype with equal probability

Why is the variance of ε equal to G/n?

This is simply the variance of a sample mean. In other words, if we were to calculate the mean phenotype for a sample of n individuals randomly selected to form the next generation, and repeated this procedure in many independent replicate experiments, the variance of the mean phenotype across replicates would be equal to G/n.

What does equation (1) predict?



Conclusion: Although (1) is perfectly accurate, it is essentially useless for predicting phenotypic evolution

➔ **We need to take a statistical approach**

II. Can we predict phenotypic evolution in the presence of drift?

The key to this statistical approach is to replicate the evolutionary process in space or time (conceptually speaking), and to focus on the expected value of the population mean among replicates as well as the variance of the population mean among replicates.

What is the expected population mean phenotype in the next generation?

$$E[\bar{z}'] = E[\bar{z} + \varepsilon] = E[\bar{z}] + E[\varepsilon] = \mu_{\bar{z}}$$

$$\therefore$$

$$\Delta\mu_{\bar{z}} = 0 \qquad (2)$$

where $\mu_{\bar{z}}$ is the expected value of the population mean phenotype

What is the variance of population mean phenotype in the next generation?

$$V[\bar{z}'] = E[(\bar{z} + \varepsilon)^2] - E[\bar{z} + \varepsilon]E[\bar{z} + \varepsilon] = E[\bar{z}^2 + 2\bar{z}\varepsilon + \varepsilon^2] - {\mu_{\bar{z}}}^2$$

$$E[\bar{z}^2] + E[2\bar{z}\varepsilon] + E[\varepsilon^2] - {\mu_{\bar{z}}}^2 = \sigma_{\bar{z}}^2 + \sigma_{\varepsilon}^2 = \sigma_{\bar{z}}^2 + G/n$$

$$\therefore$$

$$\Delta\sigma_{\bar{z}}^2 = G/n \qquad (3)$$

where $\sigma_{\bar{z}}^2$ is the variance of population mean phenotype.

What do equations 2 and 3 tell us about drift when taken from the point of view of:

Multiple possible realizations of evolution run in series?

Multiple independent populations evolving in parallel?

III. Unifying Drift and Selection: Gaussian stabilizing selection in finite populations

For a population experiencing Gaussian stabilizing selection of strength γ toward a phenotypic optimum θ, absolute fitness can be written as:

$$W(z) = e^{-\gamma(z-\theta)^2} \tag{4}$$

where θ is the optimal phenotype and γ measures how rapidly fitness decreases as a function of phenotypic distance from the optimum.

If we are willing to assume that selection is "weak", such that γ is "small", (4) is approximately equal to:

$$W(z) \approx 1 - \gamma(z-\theta)^2 \tag{5}$$

and population mean fitness is thus equal to:

$$\bar{W} = \int W(z)\phi(z)d_z = 1 - \gamma[(\bar{z}-\theta)^2 + V_z] \tag{6}$$

where V_z is the phenotypic variance of the population.

Given (6), we can use Lande's formula:

$$\Delta\bar{z} = G\frac{1}{\bar{W}}\frac{\partial\bar{W}}{\partial\bar{z}} \tag{7}$$

to calculate the change the mean phenotype that occurs over a single generation:

$$\Delta\bar{z} \approx 2\gamma G(\theta-\bar{z}) \tag{8}$$

Thus, in a finite population experiencing stabilizing selection and drift, the population mean phenotype in the next generation will be:

$$\bar{z}' \approx \bar{z} + 2\gamma G(\theta-\bar{z}) + \varepsilon \tag{9}$$

where ε is, as before, a random deviation with mean zero and variance G/n.

Calculating evolutionary change in expected population mean phenotype

$$\mu'_{\bar{z}} = E[\bar{z} + 2\gamma G(\theta-\bar{z}) + \varepsilon] = \mu_{\bar{z}} + 2\gamma G(\theta-\mu_{\bar{z}}) \tag{10a}$$

$$\Delta\mu_{\bar{z}} = 2\gamma G(\theta-\mu_{\bar{z}}) \tag{10b}$$

Calculating the variance in population mean phenotype in the next generation

$$\sigma_{\bar{z}}^{2\,\prime} = V[\bar{z} + 2\gamma G(\theta - \bar{z}) + \varepsilon] = V[2\gamma G\theta] - V[(2\gamma G - 1)\bar{z}] + V[\varepsilon]$$

$$= 4\gamma^2 G^2 V[\theta] - (2\gamma G - 1)^2 V[\bar{z}] + V[\varepsilon]$$

which, as long as we view θ as a constant is equal to:

$$= -(2\gamma G - 1)^2 \sigma_{\bar{z}}^2 + \frac{G}{n} = -(4\gamma^2 G^2 + 4\gamma G - 1)\sigma_{\bar{z}}^2 + \frac{G}{n}$$

Remembering that we assumed selection was weak such that γ is small and terms of order γ^2 negligible, this reduces to:

$$\sigma_{\bar{z}}^{2\,\prime} = -(4\gamma G - 1)\sigma_{\bar{z}}^2 + \frac{G}{n} \qquad \text{(11a)}$$

which yields our final expression for the change in variance:

$$\Delta\sigma_{\bar{z}}^2 \approx -4\gamma G\sigma_{\bar{z}}^2 + G/n \qquad \text{(11b)}$$

What does 11 tell us about the interaction between stabilizing selection in finite populations?

Conclusions:

1. On average, drift does not interfere with stabilizing selection since the expected change in population mean phenotype is independent of drift

2. In contrast, the variation among population mean phenotypes is shaped by an interaction between drift and selection: drift always increases variation among populations or replicate runs of the evolutionary process, but stabilizing selection always decreases this variation (assuming θ is constant)