I. What is local adaptation? How could local adaptation be measured?

What is local adaptation?

How could you measure local adaptation?

What do reciprocal transplant studies actually measure?

The difference between expected fitness at "home" and expected fitness "globally"

$$\Lambda = E[\bar{W}_{i\to i}] - E[\bar{W}_{i\to j}] \quad (1)$$

Although completely general, equation (1) provides little insight without specifying a fitness function. To make progress, let's use our favorite fitness function: Gaussian Stabilizing Selection on a *single trait*.

Assuming weak stabilizing selection:

$$W_i \approx 1 - \gamma(z_i - \theta_i)^2$$

$$\overline{W_i} = 1 - \gamma\left((\bar{z}_i - \theta_i)^2 + V_{z_i}\right)$$

$$\Lambda = E\left[1 - \gamma\left((\bar{z}_i - \theta_i)^2 + V_{z_i}\right)\right] - E\left[1 - \gamma\left(\left(\bar{z}_i - \theta_j\right)^2 + V_{z_i}\right)\right]$$

$$= -\gamma E[(\bar{z}_i - \theta_i)^2] + \gamma E\left[\left(\bar{z}_i - \theta_j\right)^2\right]$$

$$= -\gamma\left(\overline{\bar{z}_i{}^2} + \overline{\theta_i{}^2} - 2\overline{\bar{z}_i\theta_i}\right) + \gamma\left(\overline{\bar{z}_i{}^2} + \overline{\theta_j{}^2} - 2\bar{z}_i\bar{\theta}_j\right)$$

$$= 2\gamma\left(\overline{\bar{z}_i\theta_i}\right) - 2\gamma\left(\bar{z}_i\bar{\theta}_j\right)$$

$$\therefore$$

$$\Lambda = 2\gamma Cov[\bar{z}, \theta] \quad (2)$$

**Note that (2) assumes population mean fitness depends on only a single trait, z*

Conclusion: How cool! Local adaptation is just the covariance between population mean phenotype and the optimum phenotype.

II. What determines levels of local adaptation?

What evolutionary forces shape the evolution of $Cov[\bar{z},\theta]$?

How can we study the evolution of $Cov[\bar{z},\theta]$?

Integrating weak gaussian stabilizing selection with a spatially variable phenotypic optimum, gene flow, and drift into our evolutionary model yields the following expression for the population mean trait value in population i in the next generation:

$$\bar{z}_i' = \bar{z}_i + 2\gamma G(\theta - \bar{z}) + m(\mu_{\bar{z}} - \bar{z}_i) + \varepsilon \qquad (3)$$

where the first term is stabilizing selection, the second and third terms are gene flow, and the fourth term is drift. *Note that* (4) *assumes selection, gene flow, and drift are all "weak"*

What does (4) predict $\mathrm{Cov}[\bar{z},\theta]$ will be in the next generation?

$$\mathrm{Cov}[\bar{z}',\theta] = \mathrm{Cov}[\bar{z}_i + 2\gamma G(\theta - \bar{z}) - m\bar{z}_i + m\mu_{\bar{z}} + \varepsilon, \theta]$$

$$= \mathrm{Cov}[\bar{z},\theta] + 2\gamma G(\mathrm{Cov}[\theta,\theta] - \mathrm{Cov}[\bar{z},\theta]) - m\mathrm{Cov}[\bar{z},\theta] + m\mathrm{Cov}[\mu_{\bar{z}},\theta] + \mathrm{Cov}[\varepsilon,\theta]$$

$$= \mathrm{Cov}[\bar{z},\theta] + 2\gamma G\left(\sigma_\theta^2 - \mathrm{Cov}[\bar{z},\theta]\right) - m\mathrm{Cov}[\bar{z},\theta]$$

∴

$$\Delta Cov[\bar{z},\theta] = 2\gamma G\left(\sigma_\theta^2 - \mathrm{Cov}[\bar{z},\theta]\right) - m\mathrm{Cov}[\bar{z},\theta]$$

$$\Delta Cov[\bar{z},\theta] = 2\gamma G\sigma_\theta^2 - (m + 2\gamma G)\mathrm{Cov}[\bar{z},\theta] \qquad (4)$$

We can use (6) to solve for the equilibrium value of $\mathrm{Cov}[\bar{z},\theta]$:

$$0 = 2\gamma G\sigma_\theta^2 - (m + 2\gamma G)\mathrm{Cov}[\bar{z},\theta]$$

∴

$$\widehat{\mathrm{Cov}[\bar{z},\theta]} = \frac{2\gamma G\sigma_\theta^2}{m + 2\gamma G} \qquad (5)$$

Inserting (6) into (2) yields our final expression for local adaptation:

$$\hat{\Lambda} = \frac{4\gamma^2 G\sigma_\theta^2}{(m+2\gamma G)} \quad (6)$$

What does (7) *reveal about the forces that mould local adaptation?*

What must be true for local adaptation to occur?

Where did drift go?

Appendix I. The influence of gene flow

How can we incorporate movement of individuals?

Perhaps the simplest meaningful model is the "island model"

How does gene flow change the mean?

$$\bar{z}_i' = (1-m)\bar{z}_i + m\mu_{\bar{z}}$$
$$\therefore$$
$$\mu_{\bar{z}}' = E[(1-m)\bar{z}_i + m\mu_{\bar{z}}] = \mu_{\bar{z}}$$
$$\therefore$$
$$\Delta\mu_{\bar{z}} = 0 \qquad \text{(A1)}$$

How does gene flow change the variance?

$$\sigma_{\bar{z}}^{2\,\prime} = V[(1-m)\bar{z}_i + m\mu_{\bar{z}}] = (1-m)^2 V[\bar{z}_i] + m^2 V[\mu_{\bar{z}}] = (1-m)^2\sigma_{\bar{z}}^2$$
$$\therefore$$
$$\Delta\sigma_{\bar{z}}^2 = m(m-2)\sigma_{\bar{z}}^2$$

Which, assuming infrequent movement, gives:

$$\Delta\sigma_{\bar{z}}^2 \approx -2m\sigma_{\bar{z}}^2 \qquad \text{(A2)}$$