PRICE'S THEOREM & POPULATION GENETICS

DERIVATION OF THE PRICE EQUATION

• Price's Theorem is a universal law of evolution
  – describes how the mean of <u>any</u> trait changes from ancestor to descendent
    * ancestor & descendent can be broadly defined

• PT has been used primarily to address kin and group selection, but in recent times is being applied more widely, including in community ecology

• Consider N individuals with trait values (phenotypes) $z_1, z_2, \ldots, z_N$.
  – Have $\bar{z} = \dfrac{1}{N}\displaystyle\sum_{i=1}^{N} z_i$

• Individual i has W_i offspring. It's jth offspring has phenotype $z_i + \delta_{ij}$
  – i.e., δ_{ij} is the difference between the phenotypes the jth offpsring and its parent

  – average difference between individual i and all its offpsring is $\bar{\delta}_i = \dfrac{1}{W_i}\displaystyle\sum_{j=1}^{W_i}\delta_{ij}$

• The average phenotype of all the offspring of all individuals is

$$\bar{z}' = \frac{1}{\displaystyle\sum_{i=1}^{N}W_i}\sum_{i=1}^{N}\sum_{j=1}^{W_i}\left(z_i+\delta_{ij}\right) = \frac{1}{N\bar{W}}\sum_{i=1}^{N}W_i\left(z_i+\bar{\delta}_i\right) \ \text{ where } \ \bar{W} = \frac{1}{N}\sum_{i=1}^{N}W_i$$

  – Does *not* require $\bar{W} = 1$, so population size can change.

• $\Delta\bar{z} = \bar{z}' - \bar{z} = \dfrac{1}{\bar{W}}\left(\dfrac{1}{N}\displaystyle\sum_{i=1}^{N}W_i z_i + \dfrac{1}{N}\sum_{i=1}^{N}W_i\bar{\delta}_i\right) - \bar{z} = \dfrac{1}{\bar{W}}\left[E(Wz) + E\left(W\bar{\delta}\right) - \bar{z}\bar{W}\right]$

• This shows $\boxed{\Delta\bar{z} = \dfrac{1}{\bar{W}}\left[\mathrm{cov}(W,z) + E\left(W\bar{\delta}\right)\right]}$, which is known as the Price's Theorem

  – named after it's discoverer George R. Price
  – covariance term describes selection
  – 2nd term summarizes ancestor-descendent differences (for <u>any</u> reasons)

PRICE'S THEOREM APPLIED TO POPULATION GENETICS: MUTATION-SELECTION BALANCE

• Haploid locus with alleles A and a (freqs. p and q) with one-way mutation from A to a at rate u; fitnesses $w_A = 1$ and $w_a = 1-s$

- Let z = fraction of A alleles ("Indicator Variable")
    - if genotype A, then $z = 1$ and $z = 0$ if genotype a

- $\bar{z} = p \cdot 1 + q \cdot 0 = p$ so $\Delta \bar{z} = \Delta p$ in this case

- Computing components of the Price Equation:

$$\bar{W} = p \cdot 1 + q \cdot (1 - s) = 1 - qs$$

$$\begin{aligned}
\text{cov}(W, z) &= E(Wz) - \bar{W}\bar{z} \\
&= \left[p \cdot 1 \cdot 1 + q \cdot (1 - s) \cdot 0 \right] - \bar{W}p = p - p\bar{W} = p(1 - \bar{W}) = p(1 - 1 + qs) \\
&= pqs
\end{aligned}$$

$E(W\bar{\delta})$:
   - Let $\bar{z}_g^o$ be the average z among offspring of individual w/ genotype g; then $\bar{\delta}_g = \bar{z}_g^o - \bar{z}_g$
   - $\bar{z}_A^o = (1 - u) \cdot 1 + u \cdot 0 = (1 - u) \Rightarrow \bar{\delta}_A = \bar{z}_A^o - \bar{z}_A = (1 - u) - 1 = -u$
   - $\bar{z}_a^o = 0 \Rightarrow \bar{\delta}_a = \bar{z}_a^o - \bar{z}_a = 0 - 0 = 0$
   - $E(W\bar{\delta}) = p \cdot 1 \cdot \bar{\delta}_A + q \cdot (1 - s)\bar{\delta}_a = -pu$

- Putting everything together:

$$\Delta \bar{z} = \Delta p = \frac{1}{1 - qs}(pqs - pu) = \frac{p}{1 - qs}(qs - u)$$

- Mutation-selection balance when $\Delta p = 0$
   - From Price's Theorem, can see immediately that this holds when $q = \hat{q} = \dfrac{u}{s}$

THE BREEDER'S EQUATION (based on Rice)

- Price's Theorem can be re-written to emphasize the relation between parents and offspring as follows:

   - define $\bar{z}_i^o = z_i + \bar{\delta}_i$ (the mean phenotype of i's offspring)

   - then $\Delta \bar{z} = \dfrac{1}{\bar{W}}\left[\text{cov}(W, \bar{z}^o - \bar{\delta}) + E(W\bar{\delta}) \right] = \dfrac{1}{\bar{W}}\left[\text{cov}(W, \bar{z}^o) - \text{cov}(W, \bar{\delta}) + E(W\bar{\delta}) \right]$

   - So, $\boxed{\Delta \bar{z} = \dfrac{1}{\bar{W}}\text{cov}(W, \bar{z}^o) + \bar{\bar{\delta}}}$,   (*)

where $\bar{\bar{\delta}} = E(\bar{\delta}) = \frac{1}{N}\sum_{i=1}^{N}\bar{\delta}_i$ is the "transmission bias", i.e., the change that would occur at the population level by reproduction alone.

- Assume $\bar{\bar{\delta}} = 0$ and that the mean offspring phenotype is a linear function of the parental phenotype: $\bar{z}_i^o = \bar{z} + b_{\bar{z}^o,z}(z_i - \bar{z})$

  – then $\Delta\bar{z} = b_{\bar{z}^o,z}\frac{1}{\bar{W}}\mathrm{cov}(W,z)$

    – The selection differential S is defined as $S = \frac{1}{\bar{W}}\mathrm{cov}(W,z)$, thus we have the breeder's equation $\boxed{\Delta\bar{z} = b_{\bar{z}^o,z}S}$

    – As Rice points out, this result applies to both asexual and sexual organisms.

    – In the case of sexual organisms, z_i, should be interpreted as the mid-parent phenotype and the regression coefficent is equivalent to the heritability h^2.

- Since $b_{\bar{z}^o,z} = \mathrm{cov}(\bar{z}^o,z)/\mathrm{var}(z)$ and the selection gradient is, by definition, $\beta = S/\mathrm{var}(z)$, then we also have **Lande's Equation** $\boxed{\Delta\bar{z} = \mathrm{cov}(\bar{z}^o,z)\beta}$

  – β defines **directional selection** on the trait.

  – This version of Lande's equation applies to both asexual and sexual organisms!

  – In sexual organisms, $\mathrm{cov}(\bar{z}^o,z) = V_A$, the additive-genetic covariance. However, as Rice points out, there are situations in which $\mathrm{cov}(\bar{z}^o,z) \neq V_A$ and in those cases, the parent-offspring covariance determines the evolutionary response to selection.

FISHER'S FUNDAMENTAL THEOREM OF NATURAL SELECTION

- Since individual fitness, W, is a quantifiable phenotype, Price's Theorem applies to the change in the mean fitness of a population.

- Applying version (*) of Price's Theorem: $\Delta\bar{W} = \dfrac{\mathrm{cov}(W,\bar{W}^o)}{\bar{W}} + \bar{\bar{\delta}}$

- Since $\mathrm{cov}(W,\bar{W}^o) = V_A$, the additive-genetic variance for fitness, this immediately gives a

  version of Fisher's Fundamental Theorem of Natural Selection: $\boxed{\Delta\bar{W} = \dfrac{V_A}{\bar{W}} + \bar{\bar{\delta}}}$.

• If there is no transmission bias ($\bar{\bar{\delta}} = 0$), then $\Delta \bar{W} = V_A / \bar{W}$, like the equation we saw earlier.

• The version of FFTNS with transmission bias ($\bar{\bar{\delta}} \neq 0$) emphasizes the role of non-heritable causes of fitness changes (e.g., density or frequency dependence, environmental variation, phenotypic plasticity, learning, etc.)

EVOLUTION OF THE VARIANCE (& OTHER HIGHER MOMENTS)

• Suppose $\phi_i = (z_i - \bar{z})^k$. Then $\Delta \bar{\phi} = \dfrac{1}{\bar{W}}\left[\text{cov}(W, \phi) + E(W\bar{\delta}_\phi)\right]$ where

$$\bar{\delta}_{\phi i} = \frac{1}{W_i}\sum_{j=1}^{W_i}\left[\phi_{ij}^o - \phi_i\right] = \frac{1}{W_i}\sum_{j=1}^{W_i}\left[\left(z_{ij}^o - \bar{z}\right)^k - \left(z_i - \bar{z}\right)^k\right]$$

• If $k = 2$, $\bar{\phi} = E(z - \bar{z})^2 = \text{var}(z)$ which gives $\boxed{\Delta\, \text{var}(z) = \dfrac{1}{\bar{W}}\left\{\text{cov}\left[W, (z - \bar{z})^2\right] + E\left[W\bar{\delta}_{(z-\bar{z})^2}\right]\right\}}$.

• Similar equations can be developed for the skew, kurtosis, and so forth.

• Consider the regression of fitness on $(z - \bar{z})^2$: $\quad \beta_{W,(z-\bar{z})^2} \propto \text{cov}\left(W, (z - z)^2\right)$

  – If $\beta_{W,(z-\bar{z})^2} < 0$, selection is **stabilizing** since a phenotype's fitness decreases with its distance from the mean.

  – If $\beta_{W,(z-\bar{z})^2} > 0$, selection is **disruptive** since a phenotype's fitness increases with its distance from the mean.