Supplementary File A: Derivation of the Price equation

The Price equation, originally developed by George R. Price in 1970, can be used to describe trait change from an ancestral population to a descendant population by partitioning change into a component that gives the change due to differential survival and reproduction which is used to represent natural selection and a component that gives the change due to transmission bias (i.e. deviations between the parents and offspring due to imperfect transmission; Frank 2012). The latter component describes change due to mutation or recombination, but could also be due to plasticity responses if the offspring experience a different environment compared with the parental population. Here I give a simple derivation of the basic Price equation modified from OKASHA (2006). Consider a closed asexually reproducing parental population consisting of N entities, indexed by $i \in \{1, \ldots, N\}$. The entities (e.g. group, individuals, genotypes, etc.), no matter what they are, vary with respect to a measurable phenotypic character z. Denote with z_i (resp. w_i) the average character value (resp. the absolute fitness defined as total number of offspring) of entity i, and with $\bar{z} = \frac{1}{N}\sum_{i=1}^{N} z_i$ (resp. $\bar{w} = \frac{1}{N}\sum_{i=1}^{N} w_i$) the population average for character z (resp. fitness). The relative fitness of entity i is calculated as $\omega_i = w_i/\bar{w}$ and is the contribution of a parent to the descendant population. Now consider the offspring population which comprises all the offspring of the N entities of the parental population. Denote with z_i' the average character value for the offspring of entity i. The average value for z in the offspring population then equals $\bar{z}_o = \frac{1}{N}\sum_{i=1}^{N} \frac{w_i}{\bar{w}} z_i'$, which is the weighted average of all the mean trait values of the offspring. The observed trait change between the parental and offspring population can then be calculated as:

$$\Delta\bar{z} = \bar{z}_o - \bar{z} = \frac{1}{N}\sum_{i=1}^{N} \frac{w_i}{\bar{w}} z_i' - \frac{1}{N}\sum_{i=1}^{N} z_i.$$

Multiplying both sides by $\bar{w}$, the average absolute fitness, gives:

$$\bar{w}\Delta\bar{z} = \bar{w}(\bar{z}_o - \bar{z}) = \frac{1}{N}\sum_{i=1}^{N} w_i z_i' - \frac{1}{N}\sum_{i=1}^{N} \bar{w} z_i. \tag{A.1}$$

If transmission of character z between parents and offspring is perfect, then $z_i' = z_i$. However, if transmission is imperfect then $\Delta z_i = z_i' - z_i$ measures the transmission bias of entity i. Using this equality in equation (A.1) to substitute z_i' and rearranging terms gives:

$$\begin{aligned} \bar{w}\Delta\bar{z} &= \frac{1}{N}\sum_{i=1}^{N} w_i z_i + \frac{1}{N}\sum_{i=1}^{N} w_i \Delta z_i - \frac{1}{N}\sum_{i=1}^{N} \bar{w} z_i \\ &= \frac{1}{N}\sum_{i=1}^{N} z_i(w_i - \bar{w}) + \frac{1}{N}\sum_{i=1}^{N} w_i \Delta z_i \end{aligned} \tag{A.2}$$

Dividing both sides by $\bar{w}$ and using standard statistical definitions of covariance and expectation, we can reformulate the last line in eqn (A.2) in the usual form of the Price equation:

$$\Delta\bar{z} = cov(\omega, z) + E_w(\Delta z) \tag{A.3}$$

The first term in the right hand side of eqn (A.3) is the covariance between character value z_i and relative fitness and reflects the selection differential component (PRICE 1970; FRANK 1995, 2012). The second term is a fitness-weighted average of the transmission bias. Note that the main assumption of the Price equation is the focus in constructing categories for the parent individuals, and then connects all offspring in the next generation to their ancestors through this categorisation (LYNCH & WALSH 1998; FRANK 2012).

OKASHA (2006) derived a different decomposition of the Price equation by removing relative fitness (ω) from the second term on the right hand side of eqn (A.3) using $E_w[\Delta z] = E[\Delta z] + cov(\omega, \Delta z)$. Substituting the latter into eqn (A.3) gives:

$$\Delta\bar{z} = cov(\omega, z') + E[\Delta z] \tag{A.4}$$

In equation (A.4) the first term in the right hand side now only captures fitness and represents the total effect of natural selection (OKASHA 2006). Equation (A.4) only holds if both terms interact independently and additively from one another. If this, however, does not hold, the Price equation can be reformulated as follows:

$$\Delta\bar{z} = cov(\omega, z') + cov(\omega, \Delta z) + E[\Delta z]. \tag{A.5}$$

In eqn (A.5) $cov(\omega, z')$ represents fitness differences only, $E[\Delta z]$ represents transmission bias only, and $cov(\omega, \Delta z)$ combines both (GODFREY-SMITH 2007). If selection does not interact with transmission, then $cov(\omega, \Delta z)$ can be added to the first term (recovering eqn (A.4)) or to the last term (recovering eqn (A.3)).

Worked-out example

We next illustrate the Price equation with a hypothetical example of change in mean body size change for an asexually reproducing *Daphnia* population depicted in Figure A.1. The parental population (P) consists of 5 distinct *Daphnia* genotypes each corresponding to a specific body size value. Each genotype contributes a certain amount of offspring to the next generation and the average body size of the offspring might slightly deviate from the parent due to mutations or environmental effects. In this example, the mean body size in the parental population equals the average across the 5 genotypes, i.e. $\bar{z} = 2.68$. The relative fitness of each genotype is calculated as its number of offspring divided by the average number of offspring among all genotypes (i.e. $\bar{w} = 6.8$). For example, for the orange genotype $\omega_{orange} = 6/6.8 \approx 0.88$. We use the relative fitness and the offspring's average trait value of each genotype to calculate the mean body size in the offspring population, $\bar{z}_o = \frac{1}{N}\sum_{i=1}^{N}\frac{w_i}{\bar{w}}z'_i = 2.86$. Thus the observed change in mean body size in this hypothetical *Daphnia* population equals $\Delta\bar{z} = 0.18$. We next use the Price equation (A.3) to calculate the selection differential component and transmission bias, i.e.

$$\frac{1}{N}\sum_{i=1}^{N} z_i\Big(\frac{w_i}{\bar{w}} - 1\Big) = \frac{1}{5}\Big(2.5(\frac{6}{6.8} - 1) + 2.4(\frac{4}{6.8} - 1) + 2.9(\frac{8}{6.8} - 1)$$
$$+ 2.6(\frac{6}{6.8} - 1) + 3.0(\frac{10}{6.8} - 1)\Big) = 0.07$$
$$\frac{1}{N}\sum_{i=1}^{N} \frac{w_i}{\bar{w}}(z_i' - z_i) = \frac{1}{5}\Big(\frac{6}{6.8}(2.8 - 2.5) + \frac{4}{6.8}(2.4 - 2.4) + \frac{6}{6.8}(2.65 - 2.6)$$
$$+ \frac{10}{6.8}(3.1 - 3.0) + \frac{8}{6.8}(3.0 - 2.9)\Big) = 0.11$$

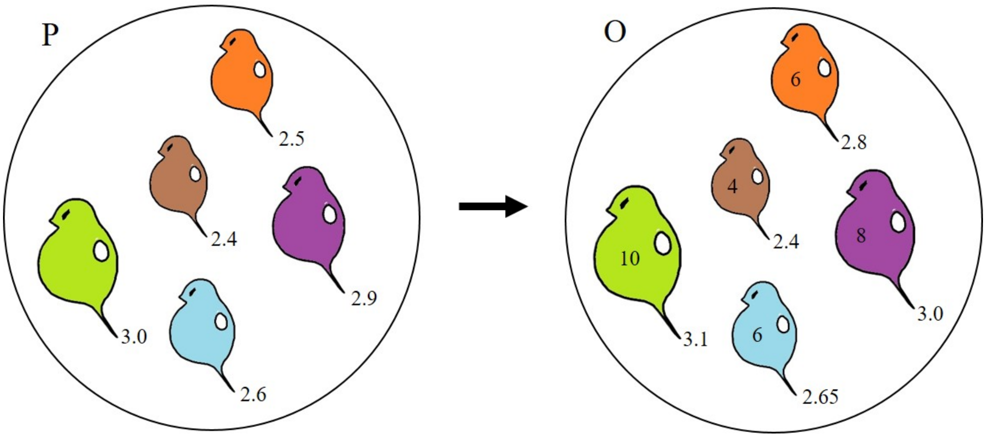

Figure A.1: Hypothetical example of change in mean body size for an asexually reproducing *Daphnia* population consisting of 5 distinct genotypes (indicated by orange, brown, green, blue and purple colour) to illustrate the use of the Price equation. P is the parental population, and O the Offspring population. The numbers attached to the individuals reflect the mean phenotypic body size of that genotype. The numbers within the individuals in the offspring population reflect the amount of offspring that genotype produced in the offspring population.

References

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