

Appendix C from S. Lion, “Class Structure, Demography, and Selection: Reproductive-Value Weighting in Nonequilibrium, Polymorphic Populations” (Am. Nat., vol. 191, no. 5, p. 620)

C.1. Discrete-Time Dynamics

Here I provide a derivation of the weighted and unweighted class-structured Price equations in discrete time.

Ecological Dynamics

As for the continuous time, the ecological dynamics of a class-structured population are given by a matrix equation:

$$\mathbf{n}(t + 1) = \mathbf{W}(t)\mathbf{n}(t), \quad (\text{C1})$$

where $\mathbf{n}(t)$ is the vector of densities in each class $n^k(t)$ and $\mathbf{W}(t)$ collects the quantities $\bar{w}^{kj}(t)$. This gives us

$$n^k(t + 1) = \sum_j \bar{w}^{kj}(t)n^j(t) = \bar{w}^k(t)n^k(t), \quad (\text{C2})$$

where $\bar{w}^k(t) = \sum_j \bar{w}^{kj}(t)n^j(t)/n^k(t)$. The total population size, $n(t)$, obeys the following equation:

$$n(t + 1) = \sum_k n^k(t + 1) = \sum_k \bar{w}^k(t)n^k(t) = \bar{w}(t)n(t), \quad (\text{C3})$$

where $\bar{w}(t) = \sum_k \bar{w}^k(t)n^k(t)/n(t)$. The equation for the class frequencies can be derived from equation (C2) by dividing by $n(t + 1)$. Using equation (C3), this leads to

$$\frac{n^k(t + 1)}{n(t + 1)} = \frac{\sum_j \bar{w}^{kj}(t)n^j(t)}{\bar{w}(t)n(t)},$$

which finally gives

$$\bar{w}(t)f^k(t + 1) = \sum_j \bar{w}^{kj}(t)f^j(t). \quad (\text{C4})$$

This equation can also be rewritten in matrix form to give equation (17b) in the main text.

Similarly, the dynamics of type i in class k can be written as

$$n_i^k(t + 1) = \sum_j w_i^{kj}(t)n_i^j(t) = w_i^k(t)n_i^k(t), \quad (\text{C5})$$

where

$$w_i^k(t) = \sum_j w_i^{kj}(t) \frac{n_i^j(t)}{n_i^k(t)}. \quad (\text{C6})$$

Change in Frequency

The frequency of type i in class k is $f_i^k = n_i^k/n^k$. The change in frequency is then

$$\begin{aligned}
 f_i^k(t+1) - f_i^k(t) &= \frac{n_i^k(t+1)}{n^k(t+1)} - f_i^k(t) \\
 &= \frac{\sum_j w_i^{kj}(t)n_j^i(t)}{\sum_j \bar{w}^{kj}(t)n^j(t)} - f_i^k(t) \\
 &= \left(\frac{w_i^k(t)}{\bar{w}^k(t)} - 1 \right) f_i^k(t).
 \end{aligned} \tag{C7}$$

Change in Trait Mean

The change in the trait mean $\bar{z}^k(t) = \sum_i z_i f_i^k(t)$ directly follows from the change in frequency:

$$\begin{aligned}
 \bar{z}^k(t+1) - \bar{z}^k(t) &= \sum_i z_i (f_i^k(t+1) - f_i^k(t)) \\
 &= \sum_i z_i \left(\frac{w_i^k(t)}{\bar{w}^k(t)} - 1 \right) f_i^k(t) \\
 &= \frac{\text{cov}_k(z_i, w_i^k(t))}{\bar{w}^k(t)}.
 \end{aligned} \tag{C8}$$

Using equation (C6), this can be expanded as follows:

$$\begin{aligned}
 \bar{z}^k(t+1) - \bar{z}^k(t) &= \frac{\text{cov}_k \left(z_i, \sum_j w_i^{kj}(t) \frac{n_j^i(t)}{n_i^k(t)} \right)}{\bar{w}^k(t)} \\
 &= \frac{\text{cov}_k \left(z_i, \sum_j w_i^{kj}(t) \frac{f_j^i(t) n^j(t)}{f_i^k(t) n^k(t)} \right)}{\bar{w}^k(t)} \\
 &= \frac{1}{\bar{w}^k(t)} \left[\sum_i (z_i - \bar{z}^k(t)) \sum_j w_i^{kj}(t) f_j^i(t) \frac{n^j(t)}{n^k(t)} \right] \\
 &= \frac{1}{\bar{w}^k(t)} \left[\sum_i \sum_j (z_i - \bar{z}^j(t) + \bar{z}^j(t) - \bar{z}^k(t)) w_i^{kj}(t) f_j^i(t) \frac{n^j(t)}{n^k(t)} \right] \\
 &= \frac{1}{\bar{w}^k(t)} \left[\sum_i \sum_j (z_i - \bar{z}^j(t)) w_i^{kj}(t) f_j^i(t) \frac{n^j(t)}{n^k(t)} + \sum_i \sum_j (\bar{z}^j(t) - \bar{z}^k(t)) w_i^{kj}(t) f_j^i(t) \frac{n^j(t)}{n^k(t)} \right],
 \end{aligned}$$

which finally gives

$$\bar{z}^k(t+1) - \bar{z}^k(t) = \frac{1}{\bar{w}^k(t)} \left[\sum_j \text{cov}_j(z_i, w_i^{kj}) \frac{n^j(t)}{n^k(t)} + \sum_j (\bar{z}^j(t) - \bar{z}^k(t)) \bar{w}^{kj}(t) \frac{n^j(t)}{n^k(t)} \right]. \tag{C9}$$

Change in Weighted Trait Mean

We now introduce the following weighted average:

$$\tilde{z}(t) = \sum_k c^k(t) \bar{z}^k(t). \quad (\text{C10})$$

Using equation (C9), the weighted average at $t + 1$ can be written as

$$\begin{aligned} \tilde{z}(t+1) &= \sum_k c^k(t+1) \bar{z}^k(t+1) \\ &= \sum_k c^k(t+1) \left[\bar{z}^k(t) + \sum_j \text{cov}_j \left(z_i, \frac{w_i^{kj}(t)}{\bar{w}^k(t)} \right) \frac{n^j(t)}{n^k(t)} + \sum_j (\bar{z}^j(t) - \bar{z}^k(t)) \frac{\bar{w}^{kj}(t) n^j(t)}{\bar{w}^k(t) n^k(t)} \right] \\ &= \sum_k c^k(t+1) \bar{z}^k(t) + \sum_j \text{cov}_j \left(z_i, \sum_k c^k(t+1) \frac{w_i^{kj}(t)}{\bar{w}^k(t)} \right) \frac{n^j(t)}{n^k(t)} \\ &\quad + \sum_k c^k(t+1) \sum_j (\bar{z}^j(t) - \bar{z}^k(t)) \frac{w_i^{kj}(t) n^j(t)}{\bar{w}^k(t) n^k(t)} \\ &= \sum_k c^k(t+1) \bar{z}^k(t) + \sum_j \text{cov}_j \left(z_i, \sum_k c^k(t+1) \frac{w_i^{kj}(t)}{\bar{w}^k(t)} \right) \frac{n^j(t)}{n^k(t)} \\ &\quad + \sum_j \bar{z}^j(t) \sum_k c^k(t+1) \frac{\bar{w}^{kj}(t) n^j(t)}{\bar{w}^k(t) n^k(t)} - \sum_k c^k(t+1) \bar{z}^k(t) \sum_j \frac{\bar{w}^{kj}(t) n^j(t)}{\bar{w}^k(t) n^k(t)}. \end{aligned}$$

Because the sum over j in the fourth term is equal to 1 by definition, the first and fourth term cancel out and we obtain

$$\tilde{z}(t+1) = \sum_j \text{cov}_j \left(z_i, \sum_k c^k(t+1) \frac{w_i^{kj}(t)}{\bar{w}^k(t)} \right) \frac{n^j(t)}{n^k(t)} + \sum_j \bar{z}^j(t) \sum_k c^k(t+1) \frac{\bar{w}^{kj}(t) n^j(t)}{\bar{w}^k(t) n^k(t)}. \quad (\text{C11})$$

Now if we choose the weights c^k such that they satisfy the recursion

$$c^j(t) = \sum_k c^k(t+1) \frac{\bar{w}^{kj}(t) n^j(t)}{\bar{w}^k(t) n^k(t)}, \quad (\text{C12})$$

we obtain

$$\tilde{z}(t+1) = \sum_j \text{cov}_j \left(z_i, \sum_k c^k(t+1) \frac{w_i^{kj}(t)}{\bar{w}^k(t)} \right) \frac{n^j(t)}{n^k(t)} + \sum_j \bar{z}^j(t) c^j(t), \quad (\text{C13})$$

which directly gives us the change in the weighted average as

$$\tilde{z}(t+1) - \tilde{z}(t) = \sum_j \text{cov}_j \left(z_i, \sum_k c^k(t+1) \frac{w_i^{kj}(t)}{\bar{w}^k(t)} \right) \frac{n^j(t)}{n^k(t)}. \quad (\text{C14})$$

A final rearrangement uses the fact that $n^k(t+1) = \bar{w}^k(t)n^k(t)$ and the definition $c^k(t) = v^k(t)f^k(t)$, so we have

$$\begin{aligned}\bar{z}(t+1) - \bar{z}(t) &= \sum_j \text{cov}_j \left(z_i, \sum_k v^k(t+1)f^k(t+1) \frac{w_i^{kj}(t)}{n^k(t+1)} \right) n^j(t) \\ &= \sum_j \text{cov}_j \left(z_i, \sum_k v^k(t+1) \frac{w_i^{kj}(t)}{n(t+1)} \right) n^j(t) \\ &= \sum_j \text{cov}_j \left(z_i, \sum_k v^k(t+1) \frac{w_i^{kj}(t)}{\bar{w}(t)n(t)} \right) n^j(t),\end{aligned}$$

and finally we obtain

$$\bar{z}(t+1) - \bar{z}(t) = \frac{1}{\bar{w}(t)} \sum_j \text{cov}_j \left(z_i, \sum_k v^k(t+1) w_i^{kj}(t) \right) f^j(t). \quad (\text{C15})$$

The latter equation thus shows that the change in the reproductive value-weighted trait can be written as a covariance between the trait and a weighted measure of fitness, obtained by weighting each offspring in the next generation by the reproductive value of the class in the next generation.

Noting that $\bar{w}^k(t)n^k(t) = n^k(t+1)$ (eq. [C2]), the recursion for class reproductive values is thus

$$c^j(t) = \sum_k c^k(t+1) \bar{w}^{kj}(t) \frac{n^j(t)}{n^{k+1}(t)}, \quad (\text{C16})$$

which can also be cast in matrix form (see eq. [16] in the main text). From this equation, we can obtain a recursion for the individual reproductives. Using the definition for $c^j(t)$, we get

$$v^j(t)f^j(t) = \sum_k v^k(t+1)f^k(t+1) \frac{\bar{w}^{kj}(t)n^j(t)}{n^k(t+1)}.$$

Because $n^k(t) = f^k(t)n(t)$, this can be simplified as

$$v^j(t) = \sum_k v^k(t+1) \frac{\bar{w}^{kj}(t)n(t)}{n(t+1)},$$

and using $n(t+1) = \bar{w}(t)n(t)$ yields

$$\bar{w}(t)v^j(t) = \sum_k v^k(t+1) \bar{w}^{kj}(t), \quad (\text{C17})$$

which can also be cast in matrix form as in equation (17a) in the main text.

C.2. Derivation of the Selection Gradient for Polymorphic and Periodic Resident Populations

The starting point of the derivation is the equation for the dynamics of the weighted trait mean,

$$\frac{d\bar{z}}{dt} = \mathbf{v}^\top \mathbf{C} \mathbf{f}, \quad (\text{C18})$$

where the covariance matrix has elements

$$C_{jk} = \text{cov}_k(z_i, r_i^{jk}) = \sum_i (z_i - \bar{z}^k)(r_i^{jk} - \bar{r}^{jk}) f_i^k. \quad (\text{C19})$$

In a resident population at equilibrium, the change in the weighted trait mean is 0. We are interested in the perturbation resulting from the introduction of a mutation with small phenotypic effect.

Monomorphic Population

In a monomorphic population, the covariance matrix \mathbf{C} is necessarily equal to the null matrix. Hence, in a population with two types w and m with the same trait value z_w , the change in weighted trait mean is 0. If we now assume that the mutant type has trait value $z_w + \varepsilon$, we can write the resulting perturbation of the covariance matrix as $\mathbf{C} = \mathbf{0} + \varepsilon^1 \mathbf{C}^{(1)} + \varepsilon^2 \mathbf{C}^{(2)} + O(\varepsilon^3)$, where $\mathbf{C}^{(1)}$ and $\mathbf{C}^{(2)}$ are the first- and second-order perturbation terms of the matrix \mathbf{C} .

If we assume that the resident population (when $\varepsilon = 0$) is on an ecological attractor, the perturbation of the reproductive values and class frequencies are $\hat{\mathbf{v}} + \varepsilon \mathbf{v}^{(1)} + O(\varepsilon^2)$ and $\hat{\mathbf{f}} + \varepsilon \mathbf{f}^{(1)} + O(\varepsilon^2)$, where $\hat{\mathbf{v}}$ and $\hat{\mathbf{f}}$ are calculated in the monomorphic population on its attractor. Plugging these expressions into equation (C18) yields the following perturbation of the change in weighted trait mean:

$$\frac{d\bar{z}}{dt} = \varepsilon \hat{\mathbf{v}}^\top \mathbf{C}^{(1)} \hat{\mathbf{f}} + \varepsilon^2 \hat{\mathbf{v}}^\top \mathbf{C}^{(2)} \hat{\mathbf{f}} + \varepsilon^2 \hat{\mathbf{v}}^\top \mathbf{C}^{(1)} \mathbf{f}^{(1)} + \varepsilon^2 (\hat{\mathbf{v}}^{(1)})^\top \mathbf{C}^{(1)} \hat{\mathbf{f}} + O(\varepsilon^3). \quad (\text{C20})$$

To calculate the perturbation of the covariance matrix, note that in a two-allele model the relationships $f_m^k + f_w^k = 1$, $\bar{r}^{jk} = r_w^{jk} f_w^k + r_m^{jk} f_m^k$, and $\bar{z}^k = z_w f_w^k + z_m f_m^k$ yield the following equality:

$$C_{jk} = (z_m - z_w)(r_m^{jk} - r_w^{jk})f_m^k(1 - f_m^k). \quad (\text{C21})$$

Now, if we assume that the mutation has only a weak effect on the ecological attractor, we can write the rates r_i^{jk} as a function of the trait z_i and of the resident monomorphic environment $\hat{\mathbf{E}}$. We then have

$$r_m^{jk} - r_w^{jk} = \varepsilon \frac{dr_m^{jk}}{d\varepsilon} + O(\varepsilon^2), \quad (\text{C22})$$

where the derivative is evaluated at $\varepsilon = 0$. Finally, this leads to

$$C_{jk} = [\varepsilon^2 f_m^k (1 - f_m^k)] \frac{dr_m^{jk}}{d\varepsilon} + O(\varepsilon^3). \quad (\text{C23})$$

The factor between square brackets is the trait variance within class k , σ_{zz}^k . Under weak selection in a deterministic model, σ_{zz}^k should be well approximated by the trait variance in the whole population, σ_{zz} (Lande 1982*b*; see also Barfield et al. 2011, eq. [B11]). Equation (C23) implies that $\mathbf{C}^{(1)} = \mathbf{0}$ and $\mathbf{C}^{(2)} = f_m(1 - f_m) d\mathbf{R}_m / d\varepsilon$. This finally yields

$$\frac{d\bar{z}}{dt} = \sigma_{zz} \hat{\mathbf{v}}^\top \frac{d\mathbf{R}_m}{d\varepsilon} \hat{\mathbf{f}} + O(\varepsilon^3). \quad (\text{C24})$$

Hence, the leading-order term of the perturbation is $O(\varepsilon^2)$ and depends only on the perturbation of the covariance matrix and not on the perturbation of the demographic variables \mathbf{v} and \mathbf{f} .

Periodic Environment

The derivations of equations (C20) and (C23) make no assumptions on the nature of the resident attractor. Thus, equation (C24) can be applied to a periodic monomorphic attractor, but now the vectors $\hat{\mathbf{v}}$ and $\hat{\mathbf{f}}$ are time dependent, and the matrix \mathbf{R}_m depends on the time-dependent resident attractor. In a deterministic model, the mutant frequency should not change in a neutral model, even in a periodic model, because the densities of the two types have exactly the same dynamics, so we can approximate the trait variance as a constant factor. Doing so and integrating over one period gives the change in the weighted trait mean over one period (eq. [23] in the main text).

Polymorphic Resident Populations

I now assume that M types coexist in the resident population at equilibrium. For such polymorphic resident populations, the perturbation of the covariance matrix can be calculated in different ways depending on how the mutation arises. For simplicity, I assume here that all individuals in type m mutate. The trait value in the mutant individuals is $z_m = z_m^0 + \varepsilon$.

Assuming that the per capita growth rates can be evaluated using the resident environment \hat{E} , we write

$$\begin{aligned} r_m^{jk} &= r_m^{jk,0} + \varepsilon \frac{dr_m^{jk}}{d\varepsilon} + \frac{\varepsilon^2}{2} \frac{d^2 r_m^{jk}}{d\varepsilon^2} + O(\varepsilon^3), \\ r_i^{jk} &= r_i^{jk,0} \quad \text{for } i \neq m, \\ \bar{r}^{jk} &= \bar{r}^{jk,0} + \varepsilon f_m^k \frac{dr_m^{jk}}{d\varepsilon} + \frac{\varepsilon^2}{2} f_m^k \frac{d^2 r_m^{jk}}{d\varepsilon^2} + O(\varepsilon^3), \end{aligned}$$

where the terms with a 0 superscript and the derivatives are calculated for $\varepsilon = 0$. In the following, we also denote $z_i = z_i^0$ the trait value for $i \neq m$. We then have $\bar{z}^k = \bar{z}^{k,0} + \varepsilon f_m^k$ and

$$\begin{aligned} C_{jk} &= \sum_i (z_i - \bar{z}^k) (r_i^{jk} - \bar{r}^{jk}) f_i^k \\ &= \sum_i (z_i^0 - \bar{z}^{k,0}) (r_i^{jk} - \bar{r}^{jk}) f_i^k + \varepsilon (r_m^{jk} - \bar{r}^{jk}) f_m^k - \varepsilon f_m^k \sum_i (r_i^{jk} - \bar{r}^{jk}) f_i^k \\ &= \sum_i (z_i^0 - \bar{z}^{k,0}) (r_i^{jk} - \bar{r}^{jk}) f_i^k + \varepsilon (r_m^{jk} - \bar{r}^{jk}) f_m^k \quad \text{because the last sum is 0 by definition} \\ &= \sum_i (z_i^0 - \bar{z}^{k,0}) (r_i^{jk,0} - \bar{r}^{jk,0}) f_i^k + \varepsilon (r_m^{jk} - \bar{r}^{jk}) f_m^k \\ &\quad - \varepsilon \sum_{i \neq m} (z_i^0 - \bar{z}^{k,0}) f_m^k \left[\frac{dr_m^{jk}}{d\varepsilon} + \frac{\varepsilon}{2} \frac{d^2 r_m^{jk}}{d\varepsilon^2} \right] f_i^k + \varepsilon (z_m^0 - \bar{z}^{k,0}) (1 - f_m^k) \left[\frac{dr_m^{jk}}{d\varepsilon} + \frac{\varepsilon}{2} \frac{d^2 r_m^{jk}}{d\varepsilon^2} \right] f_m^k \\ &= \sum_i (z_i^0 - \bar{z}^{k,0}) (r_i^{jk,0} - \bar{r}^{jk,0}) f_i^k + \varepsilon (r_m^{jk} - \bar{r}^{jk}) f_m^k \\ &\quad + \left(\varepsilon f_m^k \frac{dr_m^{jk}}{d\varepsilon} + \frac{\varepsilon^2}{2} f_m^k \frac{d^2 r_m^{jk}}{d\varepsilon^2} \right) \left[- \sum_{i \neq m} (z_i^0 - \bar{z}^{k,0}) f_i^k + (z_m^0 - \bar{z}^{k,0}) (1 - f_m^k) \right]. \end{aligned}$$

The first term is C_{jk}^0 , the covariance evaluated at $\varepsilon = 0$. The factor between brackets in the third term can be simplified as $-\sum_i f_i^k (z_i^0 - \bar{z}^{k,0}) + z_m^0 - \bar{z}^{k,0} = z_m^0 - \bar{z}^{k,0}$. Expanding the second term then yields

$$C_{jk} = C_{jk}^0 + \varepsilon (r_m^{jk,0} - \bar{r}^{jk,0}) f_m^k + \varepsilon (z_m^0 - \bar{z}^{k,0}) f_m^k \left[\frac{dr_m^{jk}}{d\varepsilon} + \frac{\varepsilon}{2} \frac{d^2 r_m^{jk}}{d\varepsilon^2} \right] + \varepsilon^2 f_m^k (1 - f_m^k) \frac{dr_m^{jk}}{d\varepsilon}. \quad (C25)$$

If the perturbations of the vectors \mathbf{v} and \mathbf{f} are assumed to be negligible compared to the perturbation of the covariance matrix, we can pre- and postmultiply by the vectors \mathbf{v}^0 and \mathbf{f}^0 calculated at equilibrium in the resident population with $\varepsilon = 0$. We then have

$$\begin{aligned} \frac{d\bar{z}}{dt} &= (\mathbf{v}^0)^\top \mathbf{C}^0 \mathbf{f}^0 + \varepsilon \sum_j \sum_k v^{j,0} f^{k,0} (r_m^{jk,0} - \bar{r}^{jk,0}) f_m^k \\ &\quad + \sum_j \sum_k v^{j,0} f^{k,0} \left(\varepsilon (z_m^0 - \bar{z}^{k,0}) f_m^k \left[\frac{dr_m^{jk}}{d\varepsilon} + \frac{\varepsilon}{2} \frac{d^2 r_m^{jk}}{d\varepsilon^2} \right] + \varepsilon^2 f_m^k (1 - f_m^k) \frac{dr_m^{jk}}{d\varepsilon} \right). \end{aligned}$$

The first term is the change in trait mean in the resident population, which is 0 because the resident population is at equilibrium. The second term can be simplified by noting that

$$\sum_j \sum_k v^{j,0} f^{k,0} (r_m^{jk,0} - \bar{r}^{jk,0}) f_m^k = \sum_j v^{j,0} \left(\sum_k r_m^{jk,0} f_m^k f^{k,0} \right) - \sum_k f^{k,0} f_m^k \left(\sum_j v^{j,0} \bar{r}^{jk,0} \right).$$

The first term between brackets is 0 because it is proportional to dn_m^i/dt calculated for a neutral mutant. The second term between brackets is 0 by definition of \mathbf{v} in the resident population at equilibrium. Hence, the dynamics of the weighted trait mean can be approximated as

$$\frac{d\tilde{z}}{dt} = \varepsilon \sum_j \sum_k v^{j,0} f^{k,0} (z_m^0 - \bar{z}^{k,0}) f_m^k \frac{dr_m^{jk}}{d\varepsilon} + \varepsilon^2 \sum_j \sum_k v^{j,0} f^{k,0} \left[f_m^k (1 - f_m^k) \frac{dr_m^{jk}}{d\varepsilon} + \frac{1}{2} (z_m^0 - \bar{z}^{k,0}) f_m^k \frac{d^2 r_m^{jk}}{d\varepsilon^2} \right] + O(\varepsilon^3). \quad (\text{C26})$$

Importantly, the leading-order term is $O(\varepsilon)$, which is of the same order as the perturbations of \mathbf{v} and \mathbf{f} . Hence, to neglect the perturbation of demography compared to the perturbation of the covariance matrix, we need to make a more stringent assumption than in the monomorphic case. If this assumption does not hold, we need to compute the perturbation of the reproductive values and class frequencies.

Note that if the population consists of only two types w and m with traits z_w and $z_m = z_w + \varepsilon$ (so that when $\varepsilon = 0$ the population is monomorphic), equation (C23) can be recovered using the relationship $\bar{z}^{k,0} = z_w = z_m^0$.

C.3. Continuous Age Structure and Fisher's Original Concept of Reproductive Value

Consider a population with continuous age structure. The density of type- i individuals with age a at time t is $n_i(a, t)$. These individuals die at rate $d_i(a, t)$ and give birth at rate $b_i(a, t)$. These assumptions yield the partial differential equation

$$\frac{\partial n_i}{\partial t}(a, t) + \frac{\partial n_i}{\partial a}(a, t) = -d_i(a, t)n_i(a, t) \quad (\text{C27})$$

along with the boundary condition

$$n_i(0, t) = \int_0^\infty b_i(a, t)n_i(a, t)da. \quad (\text{C28})$$

The total density of individuals at age a and time t is $n(a, t) = \sum_i n_i(a, t)$.

Now, for a focal trait z with value z_i in type- i individuals, we denote the average trait value in age- a individuals at time t as $\bar{z}(a, t)$. Denoting the class reproductive value at age a and time t as $c(a, t)$, we calculate the weighted average

$$\tilde{z} = \int_0^\infty c(a, t)\bar{z}(a, t)da = \sum_i z_i \int_0^\infty c(a, t)f_i(a, t)da,$$

where $f_i(a, t) = n_i(a, t)/n(a, t)$. In this specific case, it is easier to work with the individual reproductive values. Using the relationship $c(a, t) = v(a, t)f(a, t)$, where $f(a, t) = n(a, t)/n(t)$ is the frequency of individuals with age a at t in the population, we write

$$\tilde{z} = \sum_i z_i \frac{\int_0^\infty n_i(a, t)v(a, t)da}{n(t)}.$$

With these assumptions, the dynamics of the weighted trait mean are

$$\begin{aligned} \frac{d\tilde{z}}{dt} &= \sum_i z_i \frac{1}{n(t)} \int_0^\infty \frac{\partial(v(a, t)n_i(a, t))}{\partial t} da - \sum_i z_i \frac{\int_0^\infty n_i(a, t)v(a, t)da}{n(t)} \bar{r}(t) \\ &= \sum_i z_i \int_0^\infty \frac{n_i(a, t)}{n(t)} \frac{\partial v}{\partial t} da + \sum_i z_i \int_0^\infty \frac{v(a, t)}{n(t)} \frac{\partial n_i}{\partial t} da - \sum_i z_i \frac{\int_0^\infty n_i(a, t)v(a, t)da}{n(t)} \bar{r}(t) \\ &= \int_0^\infty \bar{z}(a, t)f(a, t) \left[\frac{\partial v}{\partial t} - \bar{r}(t)v(a, t) \right] da + \sum_i z_i \int_0^\infty \frac{v(a, t)}{n(t)} \frac{\partial n_i}{\partial t} da, \end{aligned}$$

where $\bar{r}(t) = d \ln(n)/dt$ is the per capita growth rate of the total population.

Now, using equation (C27), the last term becomes

$$\sum_i z_i \int_0^\infty \frac{v(a, t)}{n(t)} \frac{\partial n_i}{\partial t} da = - \sum_i z_i \int_0^\infty \frac{v(a, t)}{n(t)} \frac{\partial n_i}{\partial a} da - \sum_i z_i \int_0^\infty v(a, t) d_i(a, t) f_i(a, t) f(a, t) da.$$

The first term on the right-hand side of the latter equation can be integrated by parts, which yields

$$\begin{aligned} \sum_i z_i \int_0^\infty \frac{v(a, t)}{n(t)} \frac{\partial n_i}{\partial t} da &= - \sum_i z_i \frac{1}{n(t)} [v(a, t) n_i(a, t)]_{a=0}^\infty + \sum_i z_i \int_0^\infty \frac{\partial v}{\partial a} f_i(a, t) f(a, t) da \\ &\quad - \sum_i z_i \int_0^\infty v(a, t) d_i(a, t) f_i(a, t) f(a, t) da \\ &= \sum_i z_i v(0, t) \frac{n_i(0, t)}{n(t)} + \sum_i z_i \int_0^\infty \frac{\partial v}{\partial a} f_i(a, t) f(a, t) da \\ &\quad - \sum_i z_i \int_0^\infty v(a, t) d_i(a, t) f_i(a, t) f(a, t) da. \end{aligned}$$

Plugging this into the dynamics for \tilde{z} gives

$$\begin{aligned} \frac{d\tilde{z}}{dt} &= \int_0^\infty \bar{z}(a, t) f(a, t) \left[\frac{\partial v}{\partial t} + \frac{\partial v}{\partial a} - \bar{r}(t) v(a, t) \right] da \\ &\quad + \sum_i z_i v(0, t) \frac{n_i(0, t)}{n(t)} - \sum_i z_i \int_0^\infty v(a, t) d_i(a, t) f_i(a, t) f(a, t) da. \end{aligned}$$

Using the boundary condition (C28) for $n_i(0, t)$, we obtain

$$\begin{aligned} \frac{d\tilde{z}}{dt} &= \int_0^\infty \bar{z}(a, t) f(a, t) \left[\frac{\partial v}{\partial t} + \frac{\partial v}{\partial a} - \bar{r}(t) v(a, t) \right] da \\ &\quad + \sum_i z_i v(0, t) \int_0^\infty b_i(a, t) f_i(a, t) f(a, t) da - \sum_i z_i \int_0^\infty v(a, t) d_i(a, t) f_i(a, t) f(a, t) da. \end{aligned}$$

Finally, we introduce the age-specific covariances

$$\text{cov}_a(z_i, b_i(a, t)) = \sum_i (z_i - \bar{z}(a, t))(b_i(a, t) - \bar{b}(a, t)) f_i(a, t) \quad (\text{C29})$$

and similar expressions for the covariances between the trait and the death rate. Doing so results in the following equation:

$$\begin{aligned} \frac{d\tilde{z}}{dt} &= \int_0^\infty \bar{z}(a, t) f(a, t) \left[\frac{\partial v}{\partial t} + \frac{\partial v}{\partial a} + \bar{b}(a, t) v(0, t) - \bar{d}(a, t) v(a, t) - \bar{r}(t) v(a, t) \right] da + v(0, t) \int_0^\infty \text{cov}_a(z_i, b_i(a, t)) f(a, t) da \\ &\quad - \int_0^\infty v(a, t) \text{cov}_a(z_i, d_i(a, t)) f(a, t) da. \end{aligned}$$

Thus, if the individual reproductive values satisfy the partial differential equation

$$\frac{\partial v}{\partial t} + \frac{\partial v}{\partial a} + \bar{b}(a, t) v(0, t) - \bar{d}(a, t) v(a, t) - \bar{r}(t) v(a, t) = 0, \quad (\text{C30})$$

the dynamics of the weighted trait mean take the simple form

$$\frac{d\tilde{z}}{dt} = v(0, t) \int_0^\infty \text{cov}_a(z_i, b_i(a, t)) f(a, t) da - \int_0^\infty v(a, t) \text{cov}_a(z_i, d_i(a, t)) f(a, t) da. \quad (\text{C31})$$

This is the equivalent of equation (C18) for a continuous age structure. Note that the selective effects due to birth events are weighted by the reproductive values of newborns, $v(0, t)$, and the frequency of adults with age a , $f(a, t)$, whereas

the selective effect due to death events at age a are weighted by the reproductive value at age a , $v(a, t)$, and the frequency $f(a, t)$.

Equation (C30) was previously derived by Bacaër and Abdurahman (2008) in a periodic epidemiological model structured by infectious age (their eq. [7]). Equation (C30) generalizes their finding to polymorphic populations. As in Bacaër and Abdurahman (2008), equation (C30) is coupled to an adjoint partial differential equation for $f(a, t)$, with normalization condition $\int_0^\infty f(a, t)v(a, t)da = 1$.

Note that it is straightforward to show that if the reproductive values satisfy equation (C30), the weighted population size $\tilde{n}(t) = \int_0^\infty n(a, t)v(a, t)da$ always grows as

$$\frac{d\tilde{n}}{dt} = \bar{r}(t)\tilde{n}(t). \quad (\text{C32})$$

A special solution of equation (C30) can be found under the assumption that the birth and death rates are independent of time. When this is assumed, the solution of equation (C30) is

$$v(a) = v(0) \frac{e^{ra}}{\ell(a)} \int_a^\infty e^{-rs} \ell(s) \bar{b}(s) ds, \quad (\text{C33})$$

with $\ell(s) = \exp(-\int_0^s \bar{d}(x)dx)$ the probability to survive to age s .² Expression (C33) is the original definition of reproductive value given by Fisher (Fisher 1930; Charlesworth 1994) but with average birth and death rates. Note that in Fisher's (1930) version, the normalization constant $v(0)$ was omitted, but this was corrected in the 1958 version of the book.

2. An equivalent expression, with time-dependent coefficients, can be derived if the age distribution is assumed to stabilize quickly relative to the timescale on which $\bar{b}(a, t)$ and $\bar{d}(a, t)$ change (see, e.g., Day et al. 2011).