On the dynamics of reproductive values and phenotypic traits in class-structured populations

Sébastien Lion

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Centre d'Écologie Fonctionnelle et Évolutive, CNRS UMR 5175
1919, route de Mende 34293 Montpellier Cedex 5, France
sebastien.lion@cefe.cnrs.fr

Abstract

Natural populations are structured according to the physiological, demographic or ecological state of individuals. This class structure has important evolutionary consequences because the fitness of individuals with the same genetic background may vary depending on their class. These intrinsic differences between classes are classically taken into account by weighting classes by their reproductive values, which are generally constant weights calculated in exponentially growing populations or in invasion dynamics in populations at demographic equilibrium. This yields a simpler Price equation where the non-selective effects of between-class transitions are removed from the dynamics of the trait. Here, I show that, for large populations and clonal reproduction, this result can be extended using time-dependent reproductive values. In contrast to previous studies, this holds in a large class of ecological scenarios, out of equilibrium and for arbitrary trait distributions. I discuss the role of these reproductive values for prospective and retrospective analyses of the dynamics of phenotypic traits. This study extends and clarifies the central role of reproductive values in evolutionary ecology.

Keywords: reproductive value, Price equation, selection gradient, population dynamics, neutrality

Evolution is fuelled by the genetic variance of populations. However, natural populations also display non-genetic sources of heterogeneity, when individuals of a given genotype belong to distinct classes representing different demographic, physiological or ecological states, with different demographic or ecological impacts on the population dynamics. This occurs for instance in in age-structured populations (e.g. when older individuals have a lower fecundity than younger individuals), in species with distinct developmental stages (e.g. when a species' life cycle may consist of a dispersing and a sessile morph), or in size-structured populations. The spatial location of an individual, or the quality of its habitat, may also be used to partition the population into distinct classes. In demography and ecology, this has led to a vast theoretical literature aiming at describing the population dynamics of such class-structured populations (Metz & Diekmann, 1986; Caswell, 2001).

In most theoretical analyses, intrinsic differences between classes of individuals are taken into account by weighting individuals by their reproductive values (Fisher, 1930; Price & Smith, 1972; Taylor, 1990; Rousset, 1999; Leturque & Rousset, 2002; Rousset, 2004; Rousset & Ronce, 2004; Engen et al., 2009; Engen et al., 2014). These reproductive values are typically calculated as a left eigenvector associated with the dominant eigenvalue of a constant projection matrix (Tuljapurkar, 1989; Taylor, 1990; Caswell, 2001; Rousset, 2004). Hence, the reproductive values are associated to the long-term growth rate of an exponentially growing population. Reproductive values play a key role in evolutionary game theory and inclusive fitness theory, where one seeks to compute the invasion fitness of a rare mutant arising in a monomorphic resident population that has reached its ecological attractor (Metz et al., 1992; Rousset, 2004; Metz, 2008; Gardner et al., 2011; Lehmann & Rousset, 2014). Under weak selection, the resulting selection gradient takes the form of a weighted sum of selective effects, where the weights are the class frequencies and the reproductive values calculated in the resident population (Taylor & Frank, 1996; Frank, 1998; Rousset, 1999; Rousset, 2004; Lehmann & Rousset, 2014; Gardner, 2015).

Reproductive values have also been used in combination with the Price equation (Price, 1970) in attempts to isolate the effect of natural selection from the effects of transitions between demographic classes (Crow, 1979; Engen et al., 2014; Grafen, 2015b). The motivation for doing so is the realisation that, in class-structured populations, the mean trait may change even in a neutral model where the vital rates do not depend on the trait, due to the dynamics of class structure itself. Following Grafen (2015b), I will refer to this latter effect as "passive changes", to distinguish it from the effect of selection. In models with constant projection matrices, passive changes in mean trait are typically transient and disappear when a stable class structure is reached (reviewed in Tuljapurkar, 1989; Caswell, 2001). As first suggested by Fisher (1930), it is possible to get rid of this transient effect *from the start* if one

uses reproductive values as weights when calculating the average phenotypic trait (Engen et al., 2014; Gardner, 2015). However, it is not clear how this property extends to models with density dependence or environmental feedbacks.

In this manuscript, I derive a class-structured Price equation coupled with a general ecological model in both continuous and discrete time. This extends previous works by Day & Gandon (2006) and Gandon & Day (2007), and gives an ecological underpinning to some results of Grafen (2015b). I then show, using only minimal ecological assumptions, that the purely demographic effect of class dynamics can be removed from the dynamics of the mean trait if one weights the mean trait in each class at time t by the reproductive value of that class at time t. This result is valid for large population sizes and clonal reproduction, but holds generally for any out-of-equilibrium ecological model, allowing for density-dependence, environmental feedbacks and environmental stochasticity. The requirement is that reproductive values are not calculated asymptotically in a population at equilibrium, but from a dynamical equation depending on *average* transition rates between classes, where the average is taken over all the genotypes. Related dynamical equations have been derived before in monomorphic populations (Tuljapurkar, 1989; Rousset, 2004; Rousset & Ronce, 2004; Barton & Etheridge, 2011), but to my knowledge their implications for the Price equation under general ecological scenarios have not been discussed. I discuss the usefulness of reproductive-value weighting for more practical studies, distinguishing between backward studies where one is interested in detecting selection in a known temporal series, and forward studies where one is interested in making predictions about the future change in a trait of interest. In particular, I show how these results extend previous results on the selection gradient calculated from traditional invasion analyses (Taylor, 1990; Metz et al., 1992; Taylor & Frank, 1996; Rousset, 1999; Rousset, 2004).

1 Ecological dynamics

The key points of the argument are easier to grasp using a population with a discrete structure and continuous-time dynamics. These assumptions will therefore be used in the primary derivation of the results, but extensions to discrete-time dynamics and continuous population structure will be discussed at a later stage. Table 1 provides a summary of the mathematical symbols used in this article.

I consider an infinitely large population, such that demographic stochasticity can be ignored. The population consists of M clonally reproducing types. A type can represent an allele, a genotype, or a phenotype, depending on the level of interest. The population is further structured into K classes. Throughout the article, I use the subscript i to refer to types and superscripts j and k to refer to classes. Hence, I denote the total density of individuals in class k as n^k and the density of type i

individuals in class k as n_i^k. These densities are collected in the vectors $\mathbf{n}_i = \begin{pmatrix} n_i^1 & \dots & n_i^K \end{pmatrix}^\top$ and $\mathbf{n} = \begin{pmatrix} n^1 & \dots & n^K \end{pmatrix}^\top$.

Apart from clonal reproduction and large population densities, I will make only minimal ecological assumptions. The results are only expressed in terms of the transition rates r_i^{kj} of i individuals from class j to class k. These transitions may be due to reproduction, survival, maturation, or dispersal depending on the biological context. In general, the rates r_i^{kj} will depend on the vital rates of the focal type (fecundity, mortality, migration, infection...), but also on the vital rates of the other types. More importantly, the rates r_i^{kj} also depend on the environment $\mathbf{E}(t)$. The environment is defined from an individual-centred perspective (Metz et al., 1992; Mylius & Diekmann, 1995) and collects all the relevant information necessary to compute the reproduction and survival of individuals. Basically, the vector $\mathbf{E}(t)$ collects the densities of the various types in the population, through the vectors $\mathbf{n}_i$, but also any ecological effects that are external to the focal population, which are collected in a vector $\mathbf{e}$. These external effects may represent predation, parasitism, interspecific competition, or changes in abiotic factors.

In continuous time, the dynamics of the total densities in each class can be written in matrix form as

$$\frac{\mathrm{d}\mathbf{n}}{\mathrm{d}t} = \mathbf{R}(\mathbf{E}(t))\mathbf{n}. \tag{1}$$

The matrix $\mathbf{R}$ has element $\bar{r}^{kj}$ on the kth line and jth column, where $\bar{r}^{kj} = \sum_i r_i^{kj} n_i^j / n^j$ is the average transition rate from class j to class k. Coupled with a dynamical equation for the vector of external densities $\mathbf{e}$, equation (1) forms the basis for ecological studies of class-structured populations (e.g. Caswell, 2001). For simplicity, I will omit the dependency of the transition rates on the environment $\mathbf{E}(t)$ in the following, but it is important to keep in mind the generality of this formulation.

2 Dynamics of a phenotypic trait

2.1 The class-structured Price equation

To study evolutionary change, I will focus on the change in the average of a focal trait, $\bar{z}$, which can be calculated as a weighted sum of class means, $\bar{z} = \sum_k f^k \bar{z}^k$, where $\bar{z}^k$ is the mean trait in class k, and f^k is the relative frequency of class k. The relative frequencies of each class can be calculated as $f^k = n^k/n$, where $n = \sum_k n^k$ is the total density of individuals. In Appendix A, I show that the

Table 1: Definition of mathematical symbols used in the text

Mathematical symbol	Description
n_i^k	Density of individuals of type i in class k
$n^k = \sum_i n_i^k$	Density of individuals in class k
$n = \sum_k n^k$	Total density of individuals
$f_i^k = n_i^k / n^k$	Relative frequency of i individuals within class k
$f^k = n^k / n$	Relative frequency of individuals in class k (with respect to the total population)
$f_i = \sum_k n_i^k / n = \sum_k f_i^k f^k$	Relative frequency of type i (with respect to the total population)
$\bar{z}^k = \sum_i z_i f_i^k$	Mean value of trait z within class k
$\bar{z} = \sum_i z_i f_i = \sum_k f^k \bar{z}^k$	Mean value of trait z in the total population
$\tilde{z} = \sum_k c^k \bar{z}^k$	Weighted average of trait z with time-dependent weights $c^k(t)$ for each class.
r_i^{jk}	Rate at which type-i individuals in class k produce type-i individuals in class j.
$\bar{r}^{jk} = \sum_i r_i^{jk} f_i^k$	Average rate at which individuals in class k produce individuals in class k.

dynamics of $\bar{z}$ are given by the following differential equation,

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = \sum_k f^k \underset{k}{\mathrm{cov}}\left(z_i, r_i^{\bullet k}\right) + \sum_k (\bar{z}^k - \bar{z}) \bar{r}^{\bullet k} f^k + \text{mutation term.} \tag{2}$$

Equation (2) is the class-structured version of Price equation and shows that the change in mean trait can be partitioned into three components. The first term is the weighted average of the within-class covariances between the trait and the total contribution of individuals of type i in class k, $r_i^{\bullet k} = \sum_j r_i^{jk}$. The second term is the between-class covariance between the mean trait in a class and the total contribution of individuals in that class. This term depends on the phenotypic differentiation between a given class and the total population, $\bar{z}^k - \bar{z}$, and on the total contribution of individuals in class k, $\bar{r}^{\bullet k}$. Hence, equation (2) partitions the change in mean trait into a within-class and a between-class component. Finally, the third component of equation (2) represents the effect of mutation, recombination, or possibly external immigration events. In the following, I will neglect the mutation term and focus on the effects of natural selection and demographic changes on the dynamics of the mean trait, but a more complete description of the mutation term can be found in Appendix A.

Equation (2) confirms that, even in the absence of selection (for instance if the per-capita growth rates are independent of the trait, so that the covariances in the first term are zero), one may still observe directional change in the mean trait due to the second term. Following Grafen (2015b), I will refer to this effect as the "passive changes in mean trait".

Further insight can be gained by writing the equation giving the dynamics of the mean trait in

class k, $\bar{z}^k$ (Appendix A). Dropping the mutation term for simplicity, this gives:

$$\frac{\mathrm{d}\bar{z}^k}{\mathrm{d}t} = \sum_j \underset{j}{\mathrm{cov}}\left(z_i, r_i^{kj}\right)\frac{f^j}{f^k} + \sum_j \left(\bar{z}^j - \bar{z}^k\right)\bar{r}^{kj}\frac{f^j}{f^k}. \tag{3}$$

This shows that there are two components driving the dynamics of between-class differentiation. Even when the per-capita growth rates r_i^{kj} are independent of the trait, so that the covariance terms are zero, the mean trait within class k may still change due to between-class demographic transitions between class k and the other classes. This can lead to changes in the phenotypic differentation across classes, measured by the deviation of the class averages $\bar{z}^k$ from the population average $\bar{z}$. Hence, the second term of equation (2) conflates the consequences of natural selection and of other ecological or genetical mechanisms causing phenotypic differentiation between classes.

2.2 The class-structured Price equation for a weighted average

Equation (2) is derived by giving each individual weight unity. In order to extract the signal of natural selection from equation (2), a common approach has been to consider the dynamics of a weighted average of the focal trait, by giving each individual a class-specific weight (Fisher, 1930; Crow, 1979; Taylor, 1990; Leturque & Rousset, 2002; Rousset, 2004; Rousset & Ronce, 2004; Engen et al., 2014; Grafen, 2015b). Here, I follow this approach but I consider that the weights are not constant through time. I therefore consider the weighted average at time t

$$\tilde{z}(t) = \sum_k c^k(t)\bar{z}^k(t) \tag{4}$$

where the weight $c^k(t) = v^k(t)f^k(t)$ is assigned to class k at t and scaled such that $\sum_k c^k(t) = 1$. (Note that, when all the v^k's are set to the constant value 1, we recover the results of the previous paragraph.) Then, the change in the weighted mean trait can be written as (Appendix A)

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \sum_k f^k \underset{k}{\mathrm{cov}}\left(z_i, \sum_j v^j r_i^{jk}\right) + \sum_k \bar{z}^k\left[\frac{\mathrm{d}c^k}{\mathrm{d}t} - c^k\sum_j \bar{r}^{kj}\frac{f^j}{f^k} + \sum_j c^j\bar{r}^{jk}\frac{f^k}{f^j}\right]. \tag{5}$$

Equation (5) shows that if the c^k's satisfy the following system of differential equations

$$\frac{\mathrm{d}c^k}{\mathrm{d}t} = c^k\sum_j \bar{r}^{kj}\frac{f^j}{f^k} - \sum_j c^j\bar{r}^{jk}\frac{f^k}{f^j}, \tag{6}$$

the change in weighted mean trait takes the following simple form:

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \sum_k f^k \underset{k}{\mathrm{cov}} \left(z_i, \sum_j v^j r_i^{jk} \right). \tag{7}$$

Hence, for a well-chosen set of weights, we can write the change in mean trait as the average across all classes of the covariance between the trait and the (weighted) mean contribution of individuals in that class. The change in a neutral trait with no effect on the vital rates will therefore be exactly zero. Comparing the covariance term in equation (7) to the covariance term in equation (2), we note that the only difference is that the sum $r_i^{\bullet k} = \sum_j r_i^{jk}$ is replaced with the weighted sum $\sum_j v^j r_i^{jk}$.

Importantly, the elimination of passive changes holds if the c^k's satisfy equation (6), irrespective of initial or final conditions. As a result, the vector of weights is not unique, and additional considerations are required to choose the relevant initial condition. I will come back to this point when presenting the numerical applications of this approach.

3 Dynamics of reproductive values

3.1 General ecological scenarios

Equation (6) takes the form of a master equation describing the time-evolution of a vector of probabilities. The previous analysis shows that these probabilities can be used as time-dependent weights that guarantee the elimination of the passive changes in mean trait at any time.

A biological interpretation of $c^k(t)$ can be given as the probability that a random gene sampled at some time in the future has its ancestor in class k at time t when we look backward in the past. In other words, $c^k(t)$ represents the (relative) number of descendants left by genes present in class k at time t, from t onwards (Tuljapurkar, 1989; Caswell, 2001; Rousset, 2004; Barton & Etheridge, 2011). This is exactly the definition of reproductive value as a measure of relative long-term contribution used in population genetics and demography (going back to Fisher (1930) and Goodman (1968)). Following previous terminology, the weights $c^k(t)$ will be called "class reproductive values", and the weights $v^k(t)$ the "individual reproductive values" (Taylor, 1990; Rousset, 2004).

In matrix form, equation (6) can be written compactly as

$$\frac{\mathrm{d}\mathbf{c}^\top}{\mathrm{d}t} = -\mathbf{c}^\top \mathbf{Q}(\mathbf{E}(t)) \tag{8}$$

where $\mathbf{E}(t)$ is the vector of environmental variables and $\mathbf{Q}(\mathbf{E}(t))$ is the matrix with elements $q_{jk} = \bar{r}^{jk} f^k / f^j$ for $j \neq k$ and $q_{kk} = -\sum_{j \neq k} q_{kj}$ (Appendix B). A similar equation holds for individual

reproductive values (Appendix B)

$$\frac{\mathrm{d}\mathbf{v}^\top}{\mathrm{d}t} = -\mathbf{v}^\top \mathbf{R}(\mathbf{E}(t)). \tag{9}$$

Equations (8) and (9) can be seen as generalisations of previous dynamical equations proposed in the literature (Tuljapurkar, 1989; Rousset, 2004; Barton & Etheridge, 2011; Lehmann, 2014). However, while Tuljapurkar (1989) explicitly defined reproductive values as a function of time, usage in evolutionary theory has typically reserved the word "reproductive value" for the asymptotic behaviour of the dynamical equations, yielding a time-independent definition (Charlesworth, 1994; Rousset, 2004; Barton & Etheridge, 2011; Lehmann, 2014). This asymptotic definition of reproductive values hinges on additional demographic or genetic assumptions, although it has been noted that, in principle, reproductive values could be defined as time-dependent weights (see Lehmann & Rousset (2014), note 3). Equations (8) and (9) provide a general construction of these time-dependent reproductive values from purely demographic considerations.

Compared with most classical accounts of reproductive value, the definition of reproductive values given by equation (8) and (9) holds for a broad class of models, irrespective of the genetic composition of the population, of the trait distribution, and of the underlying population and environmental dynamics. In particular, the $c^k(t)$ are not calculated in a neutral or monomorphic population, nor under any limiting assumption of mutant rarity. The next section discusses the connection with previous usages of reproductive values.

3.2 Recovering classical limiting cases

The classical asymptotic definition of reproductive value can be recovered from equation (9) under additional ecological assumptions. This is most easily seen if we assume that the matrix $\mathbf{R}$ is constant (in which case population growth is exponential). Then, it is well known that, asymptotically, the vector $\mathbf{v}$ will become proportional to the left eigenvector associated with the dominant eigenvalue of the matrix $\mathbf{R}$ (Goodman, 1968; Tuljapurkar, 1989; Caswell, 2001). Reproductive value can then be defined as this left eigenvector, which gives the long-term contribution of individuals in a given class to the future of the population, relative to the contribution of other individuals in the population. When the matrix $\mathbf{R}$ explicitly depends on a density-independent environment, a similar result holds more generally provided the environment is ergodic (Tuljapurkar, 1989).

Another frequent assumption in the literature is that the population is at a stable demographic equilibrium. Then, the dynamics of reproductive values also depend on constant projection matrices $\mathbf{Q}(\hat{\mathbf{E}})$ and $\mathbf{R}(\hat{\mathbf{E}})$, where the environmental vector $\hat{\mathbf{E}}$ is calculated at equilibrium. The class and individual reproductive values at demographic equilibrium can be easily obtained from equation (6).

We then have $dc^k/dt = 0$, $dn/dt = 0$ and $df^k/dt = \sum_j \bar{r}^{kj} f^j = 0$. As a result, the c^j's are the solutions of

$$\sum_j c^j \bar{r}^{jk} \frac{f^k}{f^j} = 0. \tag{10}$$

Equation (10) shows that the vector $\mathbf{c}$ is a left eigenvector of the matrix $\mathbf{Q}$ associated with eigenvalue 0. Similarly, the individual reproductive values are given by a left eigenvector of $\mathbf{R}$ associated with eigenvalue 0. These results are continuous-time versions of some widely used results in evolutionary game theory and inclusive fitness theory (Taylor, 1990; Rousset, 2004). In contrast with previous studies, however, equation (10) holds good for polymorphic populations with arbitrary trait distribution, instead of being calculated in a monomorphic population.

4 Reproductive values for predictive theoretical analyses

The previous results show that the effect of selection in class-structured populations is best captured by weighting each class with time-dependent reproductive values. Using this weighting yields a compact expression for the dynamics of mean phenotypic traits, (7), which can also be written in matrix form as follows

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \mathbf{v}^\top \mathbf{C}\mathbf{f}, \tag{11}$$

where $\mathbf{C}$ is the matrix of covariances with components $C_{jk} = \underset{k}{\mathrm{cov}}(z_i, r_i^{jk})$. The aim of this section is to give a brief overview of the potential usefulness of equation (11) to make predictions on long-term evolution.

4.1 Separation of time scales

By construction, reproductive values quantify class contributions to the future demography of the population. Equations (8) and (9) show that they can be calculated from backward dynamical equations. As a result, equation (11) appears to have little predictive power as the change in the mean trait at a given time depends on the whole future we are precisely trying to predict. However, this problem can be solved if we are only interested in long-term evolution and assume a separation of time scales between evolutionary and ecological time scales, as is typical when computing invasion fitness (Metz et al., 1992; Geritz et al., 1998; Lehmann & Rousset, 2014; Van Cleve, 2015). If evolution is slow compared to the ecological dynamics, we only need to evaluate equation (11) on the population's ecological attractor, which can be a point equilibrium, a limit cycle, or more complicated objects. On the ecological attractor, the future is predictable, and the reproductive values give information about the long-term contribution of each class, as required to analyse long-term evolution.

Assuming such a separation of time scales, previous studies have derived important results for the invasion fitness of a mutant strategy in populations at demographic equilibrium that are formally similar to equation (11) (e.g. Taylor, 1990; Taylor & Frank, 1996; Rousset, 2004). Equation (11) allows to generalise these previous results in two important ways. First, equation (11) is valid for polymorphic populations with arbitrary trait distributions, whereas previous results were derived for quasi-monomorphic populations. Second, the time-dependent definition of reproductive values allows to consider more complex ecological attractors, such as periodic environments. I will illustrate these ideas in the remainder of this section.

4.2 Equilibrium ecological attractor

I will first recall a classical result of evolutionary game theory obtained under the assumption of a vanishingly small variance in the population. Consider two types w and m with traits z_w and $z_m = z_w + \varepsilon$. When $\varepsilon = 0$, we assume that the population settles on a demographic equilibrium. If ε is small (i.e. the mutation has a small phenotypic effect), the covariances can be approximated as $C_{jk} \approx \sigma_{zz} dr_M^{jk}/d\varepsilon + O(\varepsilon^3)$, where σ_{zz} is the trait variance and the derivative is evaluated at $\varepsilon = 0$. Because the variance is small, the dynamics of the mean trait unfolds on a slow time scale compared to the ecological dynamics and we can approximate equation (11) as

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \sigma_{zz} \hat{\mathbf{v}}^\top \frac{\mathrm{d}\mathbf{R}_m}{\mathrm{d}\varepsilon} \hat{\mathbf{f}} + O(\varepsilon^3), \tag{12}$$

where the vectors $\hat{\mathbf{v}}$ and $\hat{\mathbf{f}}$ in equation (12) are the equilibrium values of $\mathbf{v}$ and $\mathbf{f}$ computed in the monomorphic resident population.

Equations (11) and (12) have the same form, but the second is only valid as an approximation under weak selection. Expanding the matrix product in equation (12) then yields the classical expression for the selection gradient as a weighted sum of the effects of selection on class transitions (Taylor, 1990; Rousset, 1999; Rousset, 2004),

$$\mathcal{S} = \sum_k \sum_j \hat{f}^k \hat{v}^j \frac{\mathrm{d}r_m^{jk}}{\mathrm{d}\varepsilon}. \tag{13}$$

Note that Barfield et al. (2011) provide a related expression which takes the form of Lande (1982)'s theorem. Their approach uses the mean demographic matrix, as I do here, but with the additional assumption of normally distributed traits and exponentially growing populations. Finally, similar expressions can be obtained for a rare mutant and arbitrary strength of selection, provided the population is quasi-monomorphic (i.e. the resident population contains only one type) (Taylor, 1990; Lehmann et al., 2016). Quasi-monomorphism typically arises in two-allele models when the mutant

allele is rare compared to the resident allele (as in Taylor, 1990), or in models with a continuous trait distribution, when the trait distribution is assumed to be tightly clustered around the mean (weak selection).

4.3 Periodic ecological attractor

Using equation (11), we can generalise this classical result in two ways. First, although many theoretical models consider populations at equilibrium, realistic ecological dynamics may converge to more complex ecological attractors, such as limit cycles or chaotic attractors. Limit cycles can be thought of as a continous-time description of periodic environments, as needed for instance for taking into account seasonality. Equation (11) provides a straightforward extension of the selection gradient for periodic attractors. Assuming as before that selection is weak and the population has settled on a limit cycle with period T, it follows directly from equation (11) that the average change in the mean trait over one period is proportional to

$$\mathcal{S} = \sum_k \sum_j \int_0^T \hat{f}^k(t)\hat{v}^j(t)\frac{\mathrm{d}r_m^{jk}(t)}{\mathrm{d}\varepsilon}dt. \tag{14}$$

The reproductive values and class frequencies are time-dependent and computed using the matrix $\mathbf{R}(\hat{\mathbf{E}}(t))$, where $\hat{\mathbf{E}}(t)$ for $0 \leq t \leq T$ is the periodic environment generated by the resident population. The use of time-dependent reproductive values for periodic matrix models has been suggested before for continuous-time exponentially growing populations (Bacaër & Abdurahman, 2008) and discrete-time density-regulated populations (Brommer et al., 2000) but to my knowledge equation (14) has not been previously derived. Compared to earlier approaches that have dealt with complex demographies by incorporating the demographic states into the class-structure (Brommer et al., 2000; Rousset & Ronce, 2004; Lehmann et al., 2016), equation (14) provides a lower-dimensional invasion criterion in which classes are defined independently of the population dynamical model. For instance, if we study an ecological model with different attractors depending on parameter values, we do not need to change the class structure and the dimension of the projection matrix to analyse the different regions of parameter space. The connections between this result and previous characterisations of invasion fitness in periodic environments (Tuljapurkar, 1985; Ferrière & Gatto, 1995) is left for future work.

4.4 Polymorphic populations

A second generalisation of classical theory is possible from equation (11) when we relax the assumption that the population is quasi-monorphic. Consider for instance a polymorphic population with traits z_i and frequencies f_i for $i \leq 1 \leq M$. Assuming stable coexistence of this population, we ask what is

the effect of a slight perturbation of the trait distribution on the change in mean trait. For example, we may consider that a new mutant type arises from type M, with trait $z_M + \varepsilon$. If we can further assume that the effect of the mutation on the population demography is negligible compared to the perturbation of the covariance matrix $\mathbf{C}$, we can approximate equation (11) as

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} \approx \hat{\mathbf{v}} \frac{\mathrm{d}\mathbf{C}}{\mathrm{d}\varepsilon} \hat{\mathbf{f}}. \tag{15}$$

As in equation (13), the vectors $\hat{\mathbf{v}}$ and $\hat{\mathbf{v}}$ are computed at equilibrium for $\varepsilon = 0$. However, equation (15) is valid for arbitrary trait distributions in the resident population. The reproductive values and class frequencies must therefore be computed from the mean demographic matrix of the resident population, which is the natural extension of the "neutral" reproductive values typically considered when the resident population contains only one type. Of course, additional work is needed to investigate the domain of validity of this approximation, which is far beyond the scope of this paper. However, the present considerations shed light on the potential utility of equation (11) for deriving analytical expressions for long-term measures of selection in class-structured populations.

5 Reproductive values for retrospective data analyses

The previous section has emphasised that, to predict long-term evolution, we can neglect transient ecological dynamics and focus on the ecological attractor. However, when studying short-term eco-evolutionary dynamics, these transient dynamics can be critical. The concept of reproductive value may then lose its predictive power, although it is still potentially useful for retrospectively analysing time series. In this section, I first provide a discrete-time extension of equations (7) and (8), before applying them to simulated data as a proof-of-concept.

5.1 Discrete time dynamics

So far, I have considered a continous-time model, but the cancellation of passive changes from the dynamics of the mean trait also holds for discrete time dynamics. In Supporting Information S.1, I show that the change in weighted mean trait can be written in discrete time as

$$\tilde{z}(t+1) - \tilde{z}(t) = \sum_k f^k(t) \operatorname*{cov}_k \left(z_i, \sum_j v^j(t+1) \frac{w_i^{jk}(t)}{\bar{w}(t)} \right). \tag{16}$$

Compared to equation (7), the per-capita growth rates r_i^{jk} are replaced by the relative fitnesses $w_i^{jk}/\bar{w}(t)$, where $\bar{w}(t)$ is the average fitness in the population. Equation (16) more clearly shows

that the reproductive-value weighting needs to be applied to the offspring generation: each offspring is valued by its current contribution to the future of the population. The class reproductive values satisfy the following recursion:

$$c^j(t) = \sum_k c^k(t+1) \frac{\bar{w}^{kj}(t) n^j(t)}{\bar{w}^k(t) n^k(t)}, \tag{17}$$

which is a discrete-time analog of equation (6) (see also Rousset, 2004; Rousset & Ronce, 2004, where related recursions are derived).

5.2 Numerical illustrations

As a proof-of-concept, I consider a discrete-time three-class model, with class densities n_t^1, n_t^2 and n_t^3. The transition matrix for type i at time t is given by

$$\mathbf{W}_i(t) = \begin{pmatrix} 0 & \phi_2 F_2(\mathbf{E}_t, t) & \phi_3 F_3(\mathbf{E}_t, t) \\ s_1 + \omega z_i & 0 & 0 \\ 0 & s_2 S_2(\mathbf{E}_t, t) & s_3 S_3(\mathbf{E}_t, t) \end{pmatrix} \tag{18}$$

The elements of $\mathbf{W}_i$ are the w_i^{jk} of equation (16). The reproduction and survival of stages 2 and 3 depend on the environmental dynamics through the fecundity functions $F_2(\mathbf{E}_t, t)$ and $F_3(\mathbf{E}_t, t)$, and the survival functions $S_2(\mathbf{E}_t, t)$ and $S_3(\mathbf{E}_t, t)$. Individuals are characterised by a trait z, which is a property of the type and confers a survival advantage to the first stage. The parameter ω measures the strength of selection.

General method Starting from some initial conditions, the model can be run forward in time from time 0 to time T to provide a sequence of data. The details of the model are irrelevant, but what matters in the end is that we get a time series for the mean traits in each class, $\bar{z}^k(t)$, and for the average fitnesses $\bar{w}^{kj}(t)$, which determine between-class transitions. These quantities can in principle be measured in the field without any knowledge of the genetic variation in the population. Knowing this, recursion (17) can be iterated backward in time, starting from a given final condition $\mathbf{c}(T)$, yielding the weights $\mathbf{c}(t)$ that need to be applied to the mean traits $\bar{z}^k(t)$ at each time step. I will first present some illustrating results using two distinct models, before discussing the choice of the final condition.

Model 1 The first model assumes that survival of stage 2 is density-dependent and that fecundities of stages 2 and 3 are affected by environmental fluctuations in the availability of a resource, as follows:

$$F_2(\mathbf{E}_t, t) = F_3(\mathbf{E}_t, t) = G(t) \tag{19a}$$

$$S_2(\mathbf{E}_t, t) = e^{-\alpha n_t} \tag{19b}$$

$$S_3(\mathbf{E}_t, t) = 1 \tag{19c}$$

where $G(t) = u(1 + cos(\nu t) + \rho_t)$ represents the density of the fluctuating resource, with a periodic component and a random component ρ_t representing environmental stochasticity. The dynamics of the total density and mean trait in this model are shown in figure 1. In the neutral model (figure 1a, $\omega = 0$), a transient increase in mean trait is observed before stabilisation. A naive observer may interpret this transient increase as directional selection, but in fact this is only due to demographic transitions between classes. The absence of selection is revealed by plotting the reproductive-value weighted mean trait, which is a flat line. In the model with selection (figure 1b, $\omega = 0.05$), the reproductive-value weighting also irons out the passive changes due to class structure and allows for a more rigorous evaluation of the action of selection. For comparison, the lower panels of figure 1b also show the dynamics of the mean trait weighted with constant reproductive values calculated from the time-averaged projection matrix (gray lines). In the model with selection, the blue dashed line also shows the trajectory of the mean trait calculated with the time-dependent neutral reproductive values from figure 1ba. For this model, the effect of selection on the efficiency of the reproductive value weighting appears to be relatively weak.

Model 2 The second model is a variation on the classical Larva-Pupae-Adult (LPA) model for the dynamics of *Tribolium* populations (Dennis et al., 1995) and makes the following assumptions:

$$F_2(\mathbf{E}_t, t) = S_3(\mathbf{E}_t, t) = 1 \tag{20a}$$

$$F_3(\mathbf{E}_t, t) = e^{-c_{el} n_t^1 - c_{ea} n_t^3} \tag{20b}$$

$$S_2(\mathbf{E}_t, t) = e^{-c_{pa} n_t^3}, \tag{20c}$$

where following traditional notation, c_{el} (resp. c_{ea} and c_{pa}) reflects the intensity of cannibalism of eggs by larvae (resp. eggs by adults and pupae by adults). Figure 2a shows that, even for a neutral trait ($\omega = 0$), the model exhibits sustained fluctuations in the mean trait. Applying reproductive value weighting to the trait reveals that these changes are solely due to passive changes due to between-class transitions. In the model with selection (figure 2b), the change in mean trait initially shows some transient fluctuations before following a more linear trajectory. In contrast, the dynamics of the

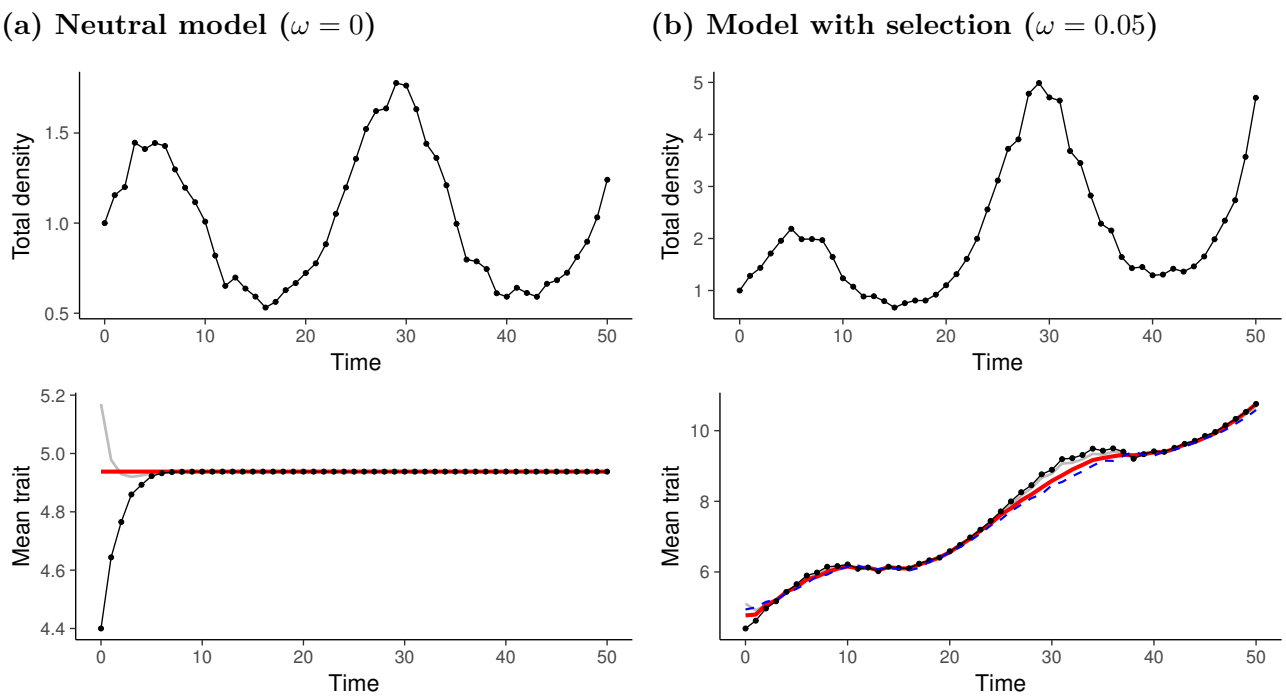

Figure 1: The dynamics of total population density and mean trait are shown for Model 1 at neutrality (left panel) and in the presence of selection (right panel). The dynamics of the model are given by equation $\mathbf{n}_i(t+1) = \mathbf{W}_i(t)\mathbf{n}_i(t)$, where the transition matrix is defined in equation (18) and (19). The upper panel gives the dynamics of the total population size, $n(t)$. The lower panel gives the dynamics of the arithmetic mean of the trait (dots), of the weighted mean trait using time-dependent reproductive-value (red line), and of the weighted mean trait using constant reproductive values computed from the average matrix over time (gray line). In figure (b), the blue dashed line shows the dynamics of the weighted mean trait using the neutral reproductive values. The initial densities for each class are $n^1(0) = 0.3$, $n^2(0) = 0.3$, $n^3(0) = 0.4$. The initial distribution of the types is Poissonian with means $\bar{z}^1(0) = \bar{z}^2(0) = 2$ and $\bar{z}^3(0) = 8$, so that $n_i^k(0) = n^k(0)(\bar{z}^k(0))^i e^{-\bar{z}^k(0)}/(i!)$ and $0 \leq i \leq 49$. The effect of environmental stochasticity, ρ_t, is modelled as a uniformly distributed random variable between -0.5 and 0.5. Parameters: $\phi_2 = 2$, $\phi_3 = 1$, $s_1 = 0.6$, $s_2 = s_3 = 0.9$, $\alpha = 0.5$ and $\nu = 0.25$.

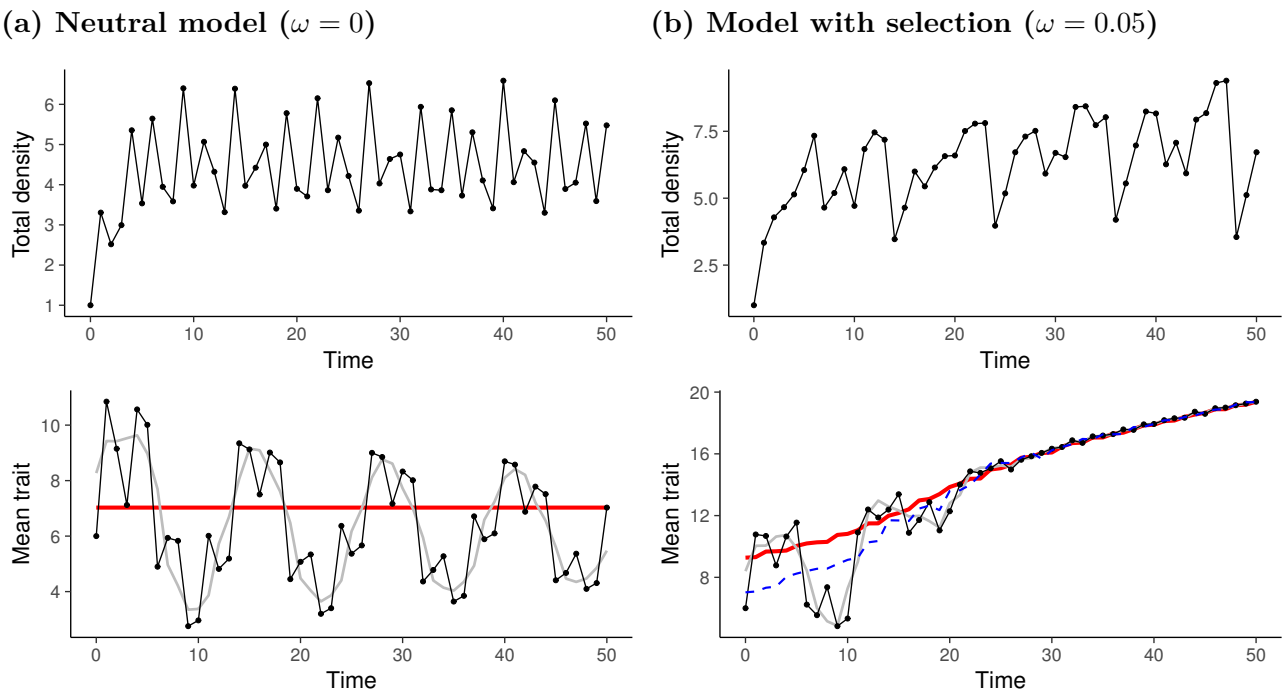

Figure 2: The dynamics of total population density and mean trait are shown for Model 2 at neutrality (left panel) and in the presence of selection (right panel). The dynamics of the model are given by equation $\mathbf{n}_i(t+1) = \mathbf{W}_i(t)\mathbf{n}_i(t)$, where the transition matrix is defined in equation (18) and (20). The upper panel gives the dynamics of the total population size, $n(t)$. The lower panel gives the dynamics of the arithmetic mean of the trait (dots), of the reproductive-value weighted trait (red line), and of the weighted mean trait using constant reproductive values computed from the average matrix over time (gray line). In figure (b), the blue dashed line shows the dynamics of the weighted mean trait using the neutral reproductive values. . The initial densities for each class are $n_1(0) = 0.3$, $n_2(0) = 0.3$, $n_3(0) = 0.4$. The initial distribution of the types is Poissonian with means $\bar{z}^1(0) = \bar{z}^2(0) = 2$ and $\bar{z}^3(0) = 12$, so that $n_i^k(0) = n^k(0)(\bar{z}^k(0))^i e^{-\bar{z}^k(0)}/(i!)$ and $0 \leq i \leq 49$. Parameters: $\phi_2 = 0$, $\phi_3 = 10$, $s_1 = 0.6$, $s_2 = 1$, $s_3 = 0.05$, $c_{ea} = 0.5$, $c_{pa} = 1$, $c_{el} = 0.4$.

weighted mean trait shows that the trait is under directional selection from the start, and that these transient fluctuations are not driven by selection. Using constant reproductive values calculated from the time-averaged projection matrix does not eliminate the passive changes in mean trait (gray lines). Furthermore, using the time-dependent neutral reproductive values as weights leads to a different prediction for the trajectory of the trait (blue dashed line).

Finally, the effect of non-linear dependencies of vital rates on the trait can be investigated by replacing z_i with $z_i/(1 + 0.2z_i)$ in the matrix $\mathbf{W}_i(t)$ (equation (18)). Figure 3 clearly shows that only the time-dependent non-neutral reproductive values produce a good smoothing of the trajectory.

Choice of the final condition As noted above, the choice of the final condition is irrelevant when deriving equations (7) and (16). In fact, for a neutral trait, the dynamics of the weighted mean trait should be a flat line, irrespective of the final condition. With selection, however, different final conditions will yield different trajectories for the weighted trait. In the two examples above, I used the final condition $\mathbf{c}(T) = \mathbf{f}(T)$ to compute the class reproductive values and weighted mean trait at each

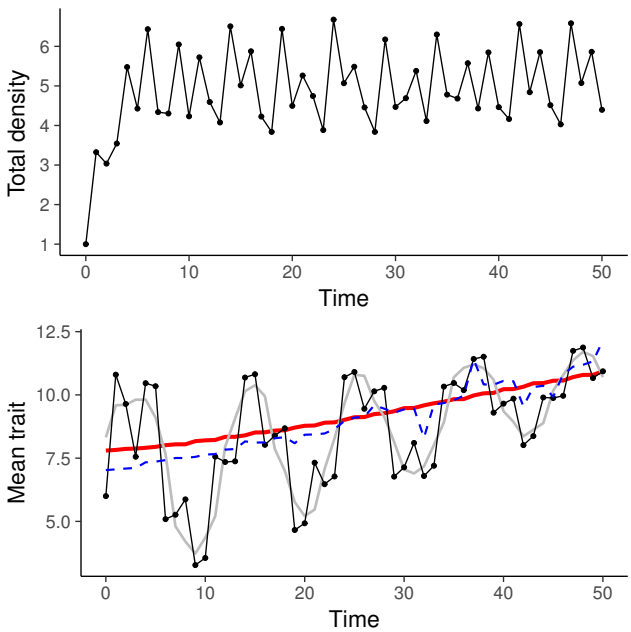

Figure 3: The dynamics of total population density and mean trait are shown for Model 2 with a non-linear effect of the trait. Compared with figure 2b, the only change is that the matrix $\mathbf{W}_i(t)$ depends non-linearly on the trait, as explained in the main text.

time. The choice of this particular final condition is equivalent to setting the relative contribution of each class to the present generation to 1 (Barton & Etheridge, 2011), but also guarantees that the trajectory of the weighted mean trait converges to the value measured at the end of the time series. In other words, from the final state of the population under study, we trace backward in time the trajectory corresponding to the change in mean trait in an ideal population where the passive changes have been removed.

A further motivation for choosing this final conditions comes from the consideration of the limiting regime where selection is weak. The influence of the passive changes in mean trait should decay rapidly under weak selection. As a result, if we have enough data points, we can expect the weighted dynamics to converge to those of the unweighted mean trait, as in figure 2b.

6 Discussion

In class-structured populations, changes in gene frequencies or mean phenotypes may be brought about through three distinct routes. First, natural selection may act within each class through the covariance between the focal trait and the vital rates of each type within that class. Second, directional changes in the mean trait may occur due to the dynamics of between-class differentiation, as measured by the difference between the mean trait in a class and the mean trait in the total population. The dynamics of between-class differentiation is itself the resultant of natural selection and of "passive changes" due to transitions between classes. These passive changes may be observed even in the absence of

natural selection, either transiently or on longer time scales, depending on genetic constraints and environmental feedback. Third, mutation or recombination may introduce some directional change in the mean trait, an effect that I have ignored in this article and should be kept in mind. In the Price equation for class-structured populations, these three terms combine additively to give the evolutionary change in the mean phenotype. This article proposes a general formulation that clarifies this decomposition of the Price equation, both in discrete time and in continuous time. A key aspect of my treatment is that the evolutionary dynamics encapsulated by the Price equation are explicitly coupled with a set of equations describing the ecological dynamics.

An influential idea in the theoretical literature, going back to Fisher (1930), is that the effect of selection is best captured by tracking the change in a weighted average rather than the more intuitive change in the arithmetic mean of the phenotype of interest. So far, this idea has been applied to exactly or approximately linear dynamics, where a focal population grows exponentially (Crow, 1979; Charlesworth, 1994; Engen et al., 2014). These systems are characterised asymptotically by a stable class structure (a right eigenvector of the constant projection matrix) and a stable set of reproductive values (a left eigenvector) associated with the long-term growth rate. Using these constant reproductive values as weights, the weighted density of the population grows *from the start* as it would when the stable class structure is reached. Furthermore, these constant weights can be used to cancel out the passive changes in the mean trait and therefore extract the signal of natural selection from the purely demographic consequences of class dynamics (Engen et al., 2014; Grafen, 2015b).

This article provides a general extension of this result, provided a dynamical and demographic definition of reproductive values is used. At a conceptual level, we need a clear distinction between types and classes, but to compute reproductive values we only need to work at the demographic level, using the between-class transition rates obtained by averaging over all types. The results hold for a large class of ecological models, allowing for density- and frequency-dependence, non-equilibrium population dynamics and environmental fluctuations. In addition, although I have focussed on discrete trait and state distributions, the derivation of Appendix A carries out unchanged if the trait averages are computed over a continuous distribution. This provides a direct connection with previous quantitative genetics models of age- and stage-structured populations (Lande, 1982; Barfield et al., 2011). Furthermore, the result also extends to populations structured by continuous states, such as age-structured or size-structured populations studied by integral projection models (Rees & Ellner, 2016; results not shown). However, in practice, it may often be more useful to segregate a population into discrete classes, as this allows each class to be sufficiently populated.

The definition of reproductive values used in this paper departs from the classical usage in two ways. First, class reproductive values are not defined asymptotically, but as functions of time. However, the classical computation of reproductive values as an eigenvector of a constant projection matrix is obtained as a special case of the dynamical definition when the transition matrix for the ecological dynamics is constant. This occurs in particular when populations are at ecological equilibrium, as typically assumed in invasion analyses. Second, I emphasise a purely demographic notion of reproductive value. In particular, there is no need to assign a reproductive value to each genotype in the population. Rather, the relevant weights need to be calculated from the demographic dynamics where the genotype-specific vital rates are averaged within each class. This use of reproductive values contrasts with other definitions (e.g. Crow, 1979), but appears to match the definition attributed to Fisher (1930) by Grafen (2015a) and Grafen (2015b). Defining reproductive values at a demographic level allows to circumvent the need for fitting models with phenotype- or genotype-dependent vital rates. Instead, we only need to estimate demographic projection matrices from the aggregated data where individuals of different genotypes are grouped by classes.

An important question to ask is whether the properties of reproductive values discussed here are of relevance for practical studies of natural selection. The value of reproductive value clearly depends on the biological question. First, one may be interested in detecting patterns of natural selection in demographic and genetic data, as collected for instance in field or controlled experimental studies. Then, it is possible to compute reproductive values by iterating estimated projection matrices backward in time, and use them as weights to detect deviation from neutrality. This use of reproductive values has been discussed by Engen et al. (2014), in the more restrictive setting of exponentially growing populations where reproductive values can simply be calculated as an eigenvector. In this article, I present an illustration using simulated data. Thus, if we are interested in understanding past events, reproductive-value weighting provides a useful way to test for the presence of selection without mistaking for selection the passive changes in mean trait resulting from class dynamics.

Alternatively, one may be interested in predicting patterns of evolutionary change for a particular trait of interest. If, for instance, one seeks to make predictions about how the virulence of a pathogen can be expected to change after the introduction of a vaccination campaign, the transient dynamics are of direct relevance as they allow to capture a potentially deadly short-term epidemic by a virulent strain that will eventually go extinct in the long run. Whether these changes are caused by natural selection or by class dynamics is a secondary issue. In addition, reproductive values can only be computed by backward iteration, so it is not clear how the concept is compatible with forward predictions on short-term dynamics. For this type of forward-looking questions, the unweighted Price equation appears to

be more useful. In particular, the unweighted Price equation arises naturally when studying short-term evolution in spatially structured population. For example, when studying the evolution of virulence during spatial epidemics on networks, Lion & Gandon (2016) found that the change in mean virulence depends on the build-up of a difference between the (local) virulence measured in hosts that have at least one susceptible neighbour and the (global) virulence measured at the population level. This term, which was interpreted as spatial differentiation in virulence, is the exact equivalent of the $\bar{z}^k - \bar{z}$ terms in equation (2).

For long-term evolution, the predictive power of reproductive values rests upon additional assumptions. For instance, if ecological dynamics take place on a fast time scale compared to evolutionary dynamics, the effect of transient ecological dynamics may be neglected and reproductive values can be computed on the ecological attractor. Thus, as for exponentially growing populations, we are interested in reproductive values in a "stable" population. Equation (11) gives a general description of the dynamics of a weighted mean trait that can be combined with other genetic or ecological assumptions to derive expressions for the selection gradient. For example, when the population is close to monomorphic (e.g., if the trait distribution is tightly clustered around the mean), it is sufficient to compute reproductive values under the assumption that all types have the mean trait value. The results of this paper suggests that, for polymorphic populations with arbitrary trait distribution, reproductive values should be calculated from the mean demographic matrix. In this case, the genetic variation is eliminated by averaging over all types, rather than letting the variance in the trait go to zero. Finally, the time-dependent definition of reproductive values allows to consider complex population dynamics, such as periodic environments, without altering the class structure of the population.

The effect of class transitions on the mean trait has been named "passive changes" by Grafen (2015b), and "transient quasi-selection" by Engen et al. (2014). The former formulation appears preferable, because the effect of class structure need not be transient, although they disappear quickly in haploid linear models. In more realistic models, ecological feedbacks and genetic constraints may potentially sustain fluctuations in allele frequencies among classes on longer time scales, at least long enough for these fluctuations to become relevant for empirical or experimental studies. An example is given in figure 2, based on the classical LPA model for *Tribolium* dynamics. Haplodiploid systems of inheritance provide another example of this phenomenon (Gardner, 2015).

Many results on evolution in class-structured populations have been derived using an inclusive fitness formalism (Taylor, 1990; Rousset, 2004; Lehmann & Rousset, 2014; Lehmann et al., 2016). The results of this article are valid also when the rates r_i^{kj} depends on the genetic or demographic spatial structure of the population. Spatial structure can be handled more explicitly in two ways. First,

space can be incorporated in the class structure (Rousset & Ronce, 2004). Second, it can be dealt with through the environment, as is typically done in spatial moment equations (Lion, 2016). Then, equations for $\mathbf{n}_i$ should be thought of as giving the dynamics of the zeroth-order spatial moments, and the r_i^{kj} would depend on the dynamcs of higher-order spatial moments. However, this has no conceptual impact on the definition and property of reproductive values.

The derivation of the weighted Price equation also extends to multiple traits and environmental stochasticity. First, because the reproductive values do not depend on the trait one considers, the extension to several jointly evolving traits is straightfoward. However, potential correlations between traits will need to be accounted for in the transition rates. Second, the results extend directly to environmental stochasticity. In practice, if we have a random sequence of environmental variables $\mathbf{E}_t$ and associated demographic and genetic data, we can still use the backward recursion to compute reproductive values at different time steps, and then compute the reproductive-value-weighted mean forward. This is illustrated in figure 1. At a theoretical level, the asymptotic value of reproductive values under environmental stochasticity matches the results of Tuljapurkar (1989) in a density-independent model.

In contrast, the derivation is only valid for large populations of clonally reproducing types. More precisely, we need to have a sufficiently large number of individuals in each class. To account for the effect of small population sizes, we would need to model demographic stochasticity explicitly. Dynamical equations for reproductive values have been derived under demographic stochasticity (Rousset & Ronce, 2004; Lehmann, 2012), and this could provide a way forward. In principle, it should also be possible to extend the results to other genetic systems, including sexual reproduction or recombination, by using alleles as types and incorporating the genetic background into the class structure. Such potential extensions are left for future work.

Historically, the use of reproductive values has also been advocated in two ways. In demography, reproductive values are often characterised as the weights v^k that need to be applied to the densities of each class (or age) so that the total reproductive value $\sum_k v^k n^k$ grows from the start with the long-term growth rate r (Fisher, 1930; Price & Smith, 1972; Samuelson, 1977; Crow, 1979; Charlesworth, 1994). However, the generality of this result has been debated, as this property of reproductive values seems tied to linear models (Samuelson, 1977; see also Bacaër & Abdurahman (2008) for an extension to periodic environments). Alternatively, in evolutionary theory, reproductive values have been discussed in relation to Fisher's Fundamental Theorem of Natural Selection (FTNS; Crow, 1979; Grafen, 2015a; Grafen, 2015b; Lessard & Soares, 2016), which states that the change in mean fitness *due to natural selection* is given by the genetic variance in fitness. In this literature, a focus of attention has been

to determine whether Fisher's intention in the FTNS was to use reproductive values as weights. In principle, we could obtain two different FTNS by substituting the growth rate r_i of type i for the trait z_i in the two Price equations derived above (Gandon & Day, 2009). However, these Price equations are derived for constant traits, whereas the growth rate r_i is a function of the environment $\mathbf{E}(t)$, and possibly of time itself if vital rates are functions of time. This will contribute an additional term to the Price equation, representing the feedback of the environment on the change in mean "fitness" (Frank & Slatkin, 1992; Gandon & Day, 2009). Hence, as has long been recognised, the FTNS only captures a partial change in mean fitness, with or without reproductive-value weighting.

The results of this article confirm that reproductive values are best viewed as weights allowing to decouple the changes due to selection from the passive changes due to class dynamics. This allows to measure selection in distinct classes with potentially different evolutionary value using a single, time-dependent currency. The power of this approach is that the relevant weights at each time can always be calculated from time series, even for complex population dynamics.

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Appendix A: Derivation of the class-structured Price equation

A.1 No mutation

The mean trait in the K-class model is $\bar{z} = \sum_k \bar{z}^k f^k$ where $f^k = n^k/n$ is the frequency of class k, and $\bar{z}^k$ is the mean trait among individuals in class k. Introducing the frequency of i-individuals within

class k, which is $f_i^k = n_i^k/n^k$, we have $\bar{z}^k = \sum_i z_i f_i^k$. We first compute the dynamics of frequencies. Using the fact that $dn_i^k/dt = r_i^k n_i^k$, we have

$$\frac{\mathrm{d}f_i^k}{\mathrm{d}t} = f_i^k(r_i^k - \bar{r}^k)$$

where the per-capita growth rate of type i in class k is

$$r_i^k = \sum_j r_i^{kj} \frac{n_i^j}{n_i^k} = \sum_j r_i^{kj} \frac{f_i^j}{f_i^k} \frac{f^j}{f^k}.$$

Noting that $f_i = \sum_k f_i^k f^k$, we have

$$\begin{aligned}
\frac{\mathrm{d}f_i}{\mathrm{d}t} =& \sum_k f^k \frac{\mathrm{d}f_i^k}{\mathrm{d}t} + \sum_k f_i^k \frac{\mathrm{d}f^k}{\mathrm{d}t} \\
=& \sum_k f^k f_i^k (r_i^k - \bar{r}^k) + \sum_k f_i^k \left(\sum_j \bar{r}^{kj} f^j - f^k \frac{1}{n} \frac{\mathrm{d}n}{\mathrm{d}t} \right) \\
=& \sum_k f^k f_i^k \sum_j r_i^{kj} \frac{f_i^j}{f_i^k} \frac{f^j}{f^k} - \sum_k f^k f_i^k \sum_j \bar{r}^{kj} \frac{f^j}{f^k} \\
&+ \sum_k f_i^k \sum_j \bar{r}^{kj} f^j - f_i \sum_k \sum_j \bar{r}^{kj} f^j \\
=& \sum_k \sum_j r_i^{kj} f_i^j f^j - f_i \sum_k \sum_j \bar{r}^{kj} f^j \\
=& \sum_k \sum_j (r_i^{kj} - \bar{r}^{kj}) f_i^j f^j + \sum_k \sum_j (f_i^j - f_i) \bar{r}^{kj} f^j
\end{aligned}$$

Multiplying by z_i and summing over i yields the dynamics of the mean trait

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = \sum_j \operatorname*{cov}_j(z_i, \sum_k r_i^{kj}) f^j + \sum_j (\bar{z}^j - \bar{z}) \sum_k \bar{r}^{kj} f^j. \tag{A.1}$$

The dynamics of the mean trait in class k can be derived from the dynamics of f_i^k. This gives

$$\begin{aligned}
\frac{\mathrm{d}\bar{z}^k}{\mathrm{d}t} =& \operatorname*{cov}_k(z_i, r_i^k) \\
=& \sum_i \sum_j (z_i - \bar{z}^k) r_i^{kj} f_i^j \frac{f^j}{f^k} \\
=& \sum_j \sum_i (z_i - \bar{z}^j) r_i^{kj} f_i^j \frac{f^j}{f^k} + \sum_j (\bar{z}^j - \bar{z}^k) \sum_i r_i^{kj} f_i^j \frac{f^j}{f^k} \\
=& \sum_j \operatorname*{cov}_j(z_i, r_i^{kj}) \frac{f^j}{f^k} + \sum_j (\bar{z}^j - \bar{z}^k) \bar{r}^{kj} \frac{f^j}{f^k} && \text{(A.2)} \\
=& \sum_j \operatorname*{cov}_j(z_i, r_i^{kj}) \frac{f^j}{f^k} + \sum_j (\bar{z}^j - \bar{z}) \bar{r}^{kj} \frac{f^j}{f^k} - (\bar{z}^k - \bar{z}) \frac{\sum_j \bar{r}^{kj} f^j}{f^k} && \text{(A.3)}
\end{aligned}$$

From equations (A.1) and (A.3), we can also derive the dynamics of $\bar{z}^k - \bar{z}$, which gives:

$$\frac{\mathrm{d}}{\mathrm{d}t}(\bar{z}^k - \bar{z}) = \sum_j \operatorname*{cov}_j \left(z_i, \frac{r_i^{kj}}{f^k} - \sum_k r_i^{kj} \right) f^j + \sum_j (\bar{z}^j - \bar{z}) \left(\bar{r}^{kj} \frac{f^j}{f^k} - \sum_k \bar{r}^{kj} f^j \right) - (\bar{z}^k - \bar{z}) \frac{\sum_j \bar{r}^{kj} f^j}{f^k} \quad \text{(A.4)}$$

A.2 Mutation

Let us consider the following mutation model: mutations occur at rate μ and with probability $m_{\ell i}$ a parent of type i can produce an offspring of type ℓ, conditional on mutation. The change in the density n_i^k can then be written as

$$\frac{\mathrm{d}n_i^k}{\mathrm{d}t} = (1-\mu) r_i^k n_i^k + \mu \sum_\ell m_{i\ell} r_\ell^k n_\ell^k = r_i^k n_i^k + \mu \left(\sum_\ell m_{i\ell} r_\ell^k n_\ell^k - r_i^k n_i^k \right)$$

Thus, mutation contributes an additional term to the dynamics of $\bar{z}^k$

$$\frac{\mathrm{d}\bar{z}^k}{\mathrm{d}t} = \operatorname{cov}(z_i, r_i^k) + \mu \sum_i z_i \left(\sum_\ell m_{i\ell} r_\ell^k f_\ell^k - r_i^k f_i^k \right)$$

which can be rewritten as

$$\frac{\mathrm{d}\bar{z}^k}{\mathrm{d}t} = \operatorname{cov}(z_i, r_i^k) + \mu \sum_i \left(\sum_\ell z_\ell m_{\ell i} - z_i \right) r_i^k f_i^k.$$

Hence, because $\bar{z} = \sum_k f^k \bar{z}^k$, mutation contributes the following additional term to the dynamics of $\bar{z}$

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = \text{RHS of (A.1)} + \mu \sum_i \left(\sum_\ell z_\ell m_{\ell i} - z_i \right) r_i f_i$$

where $r_i = \sum_k r_i^k n_i^k / n$ is the average growth rate of type i across all classes, and $f_i = \sum_k n_i^k / n$ is the global frequency of type i. Note that the above derivation assumes that the rate and distribution of mutations are constant across classes.

A.3 Weighted Price equation

We now calculate the dynamics of a weighted average frequency, $\tilde{f}_i = \sum_k c^k f_i^k$, with weights $c^k(t)$ such that $c^k = v^k f^k$ and $\sum c^k = 1$. In the absence of mutation, this yields

$$\begin{aligned}
\frac{\mathrm{d}\tilde{f}_i}{\mathrm{d}t} &= \sum_k c^k \frac{\mathrm{d}f_i^k}{\mathrm{d}t} + \sum_k f_i^k \frac{\mathrm{d}c^k}{\mathrm{d}t} \\
&= \sum_k c^k f_i^k r_i^k + \sum_k f_i^k \left[\frac{\mathrm{d}c^k}{\mathrm{d}t} - c^k \bar{r}^k\right] \\
&= \sum_k c^k f_i^k \sum_j r_i^{kj} \frac{f_i^j}{f_i^k}\frac{f^j}{f^k} + \sum_k f_i^k \left[\frac{\mathrm{d}c^k}{\mathrm{d}t} - c^k \sum_j \bar{r}^{kj}\frac{f^j}{f^k}\right] \\
&= \sum_k c^k f_i^k \sum_j r_i^{kj} \frac{f_i^j}{f_i^k}\frac{f^j}{f^k} - \sum_k f_i^k \sum_j c^j \bar{r}^{jk}\frac{f^k}{f^j} + \sum_k f_i^k \left[\frac{\mathrm{d}c^k}{\mathrm{d}t} - c^k \sum_j \bar{r}^{kj}\frac{f^j}{f^k} + \sum_j c^j \bar{r}^{jk}\frac{f^k}{f^j}\right]
\end{aligned}$$

If the c^k's satisfy the system

$$\frac{\mathrm{d}c^k}{\mathrm{d}t} = -\sum_j c^j \bar{r}^{jk}\frac{f^k}{f^j} + c^k \sum_j \bar{r}^{kj}\frac{f^j}{f^k}, \tag{A.5}$$

we then have the following simple equation for the dynamics of the weighted frequency

$$\frac{\mathrm{d}\tilde{f}_i}{\mathrm{d}t} = \sum_j f^j \sum_k v^k (r_i^{kj} - \bar{r}^{kj}) f_i^j.$$

Multiplying by z_i and summing over i yields the dynamics of the weighted average $\tilde{z} = \sum_k c^k \bar{z}^k = \sum_k c^k \sum_i f_i^k z_i$:

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \sum_j \operatorname*{cov}_j\left(z_i, \sum_k v^k r_i^{kj}\right) f^j, \tag{A.6}$$

or in matrix form as

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \mathbf{v}^\top \mathbf{C}\mathbf{f} \tag{A.7}$$

where $\mathbf{C}$ is the matrix of covariances with elements $C_{kj} = \operatorname*{cov}_j(z_i, r_i^{kj})$. Taking into account mutation would only contribute an additional term, which is simply the second term of equation (A.2) with $\tilde{r}_i$ and $\tilde{f}_i$ substituted for r_i and f_i.

Appendix B: Reproductive values

Equation (A.5) can be rewritten in matrix form as

$$\frac{\mathrm{d}\mathbf{c}^\top}{\mathrm{d}t} = -\mathbf{c}^\top \mathbf{Q} \tag{B.1}$$

where the matrix $\mathbf{Q}$ has elements

$$q_{jk} = \bar{r}^{jk} \frac{f^k}{f^j} \qquad \text{if } j \neq k,$$

$$q_{kk} = -\sum_{j \neq k} \bar{r}^{kj} \frac{f^j}{f^k} = -\sum_{j \neq k} q_{kj}.$$

Similarly, we can find a dynamical equation for the v^k's. Because $c^k = v^k f^k$ by definition, we have

$$\begin{aligned}
\frac{\mathrm{d}v^k}{\mathrm{d}t} f^k =& \frac{\mathrm{d}c^k}{\mathrm{d}t} - v^k \frac{\mathrm{d}f^k}{\mathrm{d}t} \\
=& -\sum_j c^j \bar{r}^{jk} \frac{f^k}{f^j} + c^k \sum_j \bar{r}^{kj} \frac{f^j}{f^k} - v^k \sum_j \bar{r}^{kj} f^j \\
=& -\sum_j v^j \bar{r}^{jk} f^k
\end{aligned}$$

which gives us the following equation for the vector $\mathbf{v}$

$$\frac{\mathrm{d}\mathbf{v}^\top}{\mathrm{d}t} = -\mathbf{v}^\top \mathbf{R} \tag{B.2}$$

Equations (B.1) and (B.2) show that the vector $\mathbf{c}$ (resp. $\mathbf{v}$) can be calculated at equilibrium as the left eigenvector of the matrix $\mathbf{Q}$ (resp. $\mathbf{R}$), associated with eigenvalue 0.

Appendix S: Supporting Information for "On the dynamics of reproductive values and phenotypic traits in class-structured populations"

S.1 Discrete time dynamics

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

S.1.1 Ecological dynamics

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

$$\mathbf{n}(t+1) = \mathbf{W}(t)\mathbf{n}(t) \tag{S.1}$$

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

$$n^k(t+1) = \sum_j \bar{w}^{kj}(t)n^j(t) = \bar{w}^k(t)n^k(t) \tag{S.2}$$

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

$$n(t+1) = \sum_k n^k(t+1) = \sum_k \bar{w}^k(t)n^k(t) = \bar{w}(t)n(t) \tag{S.3}$$

where $\bar{w}(t) = \sum_k \bar{w}^k(t)n^k(t)/n(t)$.

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

$$n_i^k(t+1) = \sum_j w_i^{kj}(t)n_i^j(t) = w_i^k(t)n_i^k(t) \tag{S.4}$$

where

$$w_i^k(t) = \sum_j w_i^{kj}(t)\frac{n_i^j(t)}{n_i^k(t)} \tag{S.5}$$

S.1.2 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

$$\begin{aligned} f_i^k(t+1) - f_i^k(t) &= \frac{n_i^k(t+1)}{n^k(t+1)} - f_i^k(t) \\ &= \frac{\sum_j w_i^{kj}(t) n_i^j(t)}{\sum_j \bar{w}^{kj}(t) n^j(t)} - f_i^k(t) \\ &= \left(\frac{w_i^k(t)}{\bar{w}^k(t)} - 1\right) f_i^k(t) \end{aligned} \tag{S.6}$$

S.1.3 Change in mean trait

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

$$\begin{aligned} \bar{z}^k(t+1) - \bar{z}^k(t) &= \sum_i z_i \left(f_i^k(t+1) - f_i^k(t)\right) \\ &= \sum_i z_i \left(\frac{w_i^k(t)}{\bar{w}^k(t)} - 1\right) f_i^k(t) \\ &= \frac{\underset{k}{\mathrm{cov}}(z_i, w_i^k(t))}{\bar{w}^k(t)} \end{aligned} \tag{S.7}$$

Using equation (S.5), this can be expanded as follows

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

which gives finally

$$\bar{z}^k(t+1) - \bar{z}^k(t) = \frac{1}{\bar{w}^k(t)} \left[\sum_j \underset{j}{\mathrm{cov}}(z_i, w_i^{kj}) \frac{n^j(t)}{n^k(t)} + \sum_j (\bar{z}^j(t) - \bar{z}^k(t)) \bar{w}^{kj}(t) \frac{n^j(t)}{n^k(t)}\right] \tag{S.8}$$

S.1.4 Change in weighted mean trait

We now introduce the following weighted average

$$\tilde{z}(t) = \sum_k c^k(t)\bar{z}^k(t). \tag{S.9}$$

Using equation (S.8), the weighted average at $t+1$ can be written as

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

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

$$\tilde{z}(t+1) = \sum_j \operatorname*{cov}_j\left(z_i, \sum_k c^k(t+1)\frac{w_i^{kj}(t)}{\bar{w}^k(t)}\right)\frac{n^j(t)}{n^k(t)} + \sum_j \bar{z}^j(t)\sum_k c^k(t+1)\frac{\bar{w}^{kj}(t)}{\bar{w}^k(t)}\frac{n^j(t)}{n^k(t)} \tag{S.10}$$

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

$$c^j(t) = \sum_k c^k(t+1)\frac{\bar{w}^{kj}(t)}{\bar{w}^k(t)}\frac{n^j(t)}{n^k(t)}, \tag{S.11}$$

we obtain

$$\tilde{z}(t+1) = \sum_j \operatorname*{cov}_j\left(z_i, \sum_k c^k(t+1)\frac{w_i^{kj}(t)}{\bar{w}^k(t)}\right)\frac{n^j(t)}{n^k(t)} + \sum_j \bar{z}^j(t)c^j(t) \tag{S.12}$$

which gives us directly the change in the weighted average as

$$\tilde{z}(t+1) - \tilde{z}(t) = \sum_j \operatorname*{cov}_j\left(z_i, \sum_k c^k(t+1)\frac{w_i^{kj}(t)}{\bar{w}^k(t)}\right)\frac{n^j(t)}{n^k(t)} \tag{S.13}$$

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

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

and we have finally

$$\boxed{\tilde{z}(t+1) - \tilde{z}(t) = \frac{1}{\bar{w}(t)} \sum_j \operatorname*{cov}_j \left(z_i, \sum_k v^k(t+1) w_i^{kj}(t) \right) f^j(t)}. \tag{S.14}$$

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.