

Class Structure, Demography, and Selection: Reproductive-Value Weighting in Nonequilibrium, Polymorphic Populations

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ABSTRACT: In natural populations, individuals of a given genotype may belong to different classes. Such classes can represent different age groups, developmental stages, or habitats. Class structure has important evolutionary consequences because the fitness of individuals with the same genetic background may vary depending on their class. As a result, demographic transitions between classes can cause fluctuations in the trait mean that need to be removed when estimating selection on a trait. Intrinsic differences between classes are classically taken into account by weighting individuals by class-specific reproductive values, defined as the relative contribution of individuals in a given class to the future of the population. These reproductive values are generally constant weights calculated from a constant projection matrix. Here, I show for large populations and clonal reproduction that reproductive values can be defined as time-dependent weights satisfying dynamical demographic equations that depend only on the average between-class transition rates over all genotypes. Using these time-dependent demographic reproductive values yields a simple Price equation where the nonselective effects of between-class transitions are removed from the dynamics of the trait. This generalizes previous theory to a large class of ecological scenarios, taking into account density dependence, ecological feedbacks, arbitrary strength of selection, and arbitrary trait distributions. I discuss the role of reproductive values for prospective and retrospective analyses of the dynamics of phenotypic traits.

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

Introduction

Evolution is fueled by the genetic variance of populations. However, natural populations also display nongenetic 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 an age-structured population (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 consists 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 structured populations (Metz and 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 and Smith 1972; Taylor 1990; Rousset 1999, 2004; Leturque and Rousset 2002; Rousset and Ronce 2004; Engen et al. 2009, 2014). These reproductive values are defined as 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. 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 with 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 and 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 and Frank 1996; Frank 1998; Rousset 1999, 2004; Lehmann and 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;

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Grafen 2015*b*). The motivation for doing so is the realization that in class-structured populations the trait mean can 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 (2015*b*), 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 trait mean 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 article, I derive class-structured Price equations coupled with a general ecological model in both continuous and discrete time. This extends previous works by Day and Gandon (2006) and Gandon and Day (2007) and gives an ecological underpinning to some results of Grafen (2015*b*). I then show, using only minimal ecological assumptions, that the purely demographic effect of class dynamics can be removed from the dynamics of the trait mean if one weights the trait mean 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 stable population 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 and Ronce 2004; Barton and Etheridge 2011), but to my knowledge their implications for the Price equation under general ecological scenarios have not been discussed.

The structure of this article should provide two levels of reading. I first introduce a general model for the dynamics of a class-structured population. An evolutionary analysis is then grafted onto this ecological model, leading to the derivation of two kinds of Price equation and to the definition of reproductive values as time-dependent weights computed in polymorphic populations. The section Reproductive Values for Retrospective Data Analyses illustrates how these reproductive values can be used to analyze selection in time series using simulated data. Readers unfamiliar with the mathematical details behind the concept of reproductive value are encouraged to read up to here. The following sections go deeper into the technical details and connections with previous studies and can be skipped at first read by nontheoreticians. The section The Interplay of Demography and Se-

lection discusses the conceptual implication of the results and their connection with the standard usages of reproductive values. The section Reproductive Values for Predictive Theoretical Analyses shows that, under weak selection, approximations for the selection gradient can be derived from the reproductive value-weighted Price equation for non-equilibrium and polymorphic populations. The discussion should be readable by both categories of readers.

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 a large population, such that demographic stochasticity can be ignored. The population consists of M clon-

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
$f_i^k = n_i^k/n^k$	Frequency of i individuals within class k
$f^k = n^k/n$	Frequency of individuals in class k (with respect to the total population)
$f_i = \sum_k n_i^k/n = \sum_k f_i^k f^k$	Frequency of type i (with respect to the total population)
z_i	Value of the trait for individuals of type i
$\bar{z}^k = \sum_i z_i f_i^k$	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^{kj}	Per capita rate at which type- i individuals in class j produce type- i individuals in class k
$\bar{r}^{kj} = \sum_i r_i^{kj} f_i^j$	Average per capita rate at which individuals in class j produce individuals in class k
$\bar{r}^k = \sum_j \bar{r}^{kj} \frac{f_j^j}{f^j} = d \ln(n^k)/dt$	Average per capita rate at which individuals in class k are produced
$\bar{r} = \sum_k \bar{r}^k n^k = d \ln(n)/dt$	Average per capita growth rate of the total population

ally reproducing types. A type may represent an allele 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 density of individuals in class k as n^k and the density of type- i individuals in class k as n_i^k (the term “density” must be understood in the usual ecological sense, as number of individuals per surface area). These densities are collected in the vectors $\mathbf{n}_i = (n_i^1 \dots n_i^K)^\top$ and $\mathbf{n} = (n^1 \dots n^K)^\top$.

Apart from clonal reproduction and large population densities, I will make only minimal ecological assumptions. The results are expressed only in terms of the transition rates r_i^{kj} of i individuals from class j to class k . These transitions can be due to reproduction, mortality, maturation, or dispersal depending on the biological context. For instance, the production of class- j offspring by type- i parents in class k will contribute positively to the rate r_i^{jk} , while the death of type- i individuals in class k will contribute negatively to r_i^{jk} . Similarly, the movement of type- i individuals from class k to class j (due to maturation, dispersal, infection, etc.) will add to r_i^{jk} and subtract from r_i^{kk} . In general, the rates r_i^{jk} will depend on the vital rates of the focal type (fecundity, mortality, migration, infection, etc.) but also on the vital rates of the other types. Most importantly, the rates r_i^{jk} also depend on the environment $\mathbf{E}(t)$. The environment is defined from an individual-centered perspective (Metz et al. 1992; Mylius and Diekmann 1995; Lion 2018) 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. For spatially structured populations, other variables summarizing the spatial distribution of types and individuals can also be added to the environment.

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

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

The matrix \mathbf{R} has element \bar{r}^{kj} on the k th line and j th 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 often 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.

Dynamics of a Phenotypic Trait

The aim of this section is to build on the ecological model to derive a description of evolutionary dynamics. This is done by deriving two Price equations to describe the dynamics of the trait mean in the population. One considers a simple arithmetic average, the other a weighted average, where each class is given a class-specific and genotype-independent but time-dependent weight. The key result is that if we use the class reproductive values at time t as the weights, the Price equation takes a particularly simple form where fluctuations in the trait mean that are not due to selection have been eliminated.

Trait and Averages

Consider a focal trait z . Individuals with type i have trait value z_i . For simplicity, the trait is assumed to be fully heritable, measurable in each class, and nonplastic, so that a type- i individual has the same trait value in all classes (but see Discussion for how to deal with plastic traits). To study evolutionary change, I will focus on the change in the average of the focal trait, \bar{z} . This average can be calculated in two equivalent ways, either directly as $\bar{z} = \sum_i z_i f_i$, where f_i represents the frequency of type i in the population, or as a weighted sum of class means, $\bar{z} = \sum_k f^k \bar{z}^k$, where \bar{z}^k is the trait mean in class k and f^k is the frequency of class k . The 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. The within-class average \bar{z}^k can be calculated as $\bar{z}^k = \sum_i z_i f_i^k$, where $f_i^k = n_i^k / n^k$ is the frequency of type i within class k . Throughout the article, an overbar with a superscript represents an average using the within-class frequencies f_i^k (as in \bar{z}^k), and an overbar without a superscript represents an average using the population frequencies f_i (as in \bar{z}).

The Class-Structured Price Equation

In appendix A, I show that the dynamics of \bar{z} are given by the following differential equation:

$$\frac{d\bar{z}}{dt} = \sum_k f^k \text{cov}_k(z_i, r_i^{*k}) + \sum_k (\bar{z}^k - \bar{z}) \bar{r}^{*k} f^k + \text{mutation term}. \quad (2)$$

Equation (2) is the class-structured version of the Price equation and shows that the change in trait mean can be partitioned into three components. The first term is the weighted average of the within-class covariances between the trait and the rate at which each individual of type i in class k produces individuals in any class, $r_i^{*k} = \sum_j r_i^{jk}$, which is a measure of fitness of type- i individuals in class k . By definition, $\text{cov}_k(z_i, r_i^{*k}) = \sum_i (z_i - \bar{z}^k)(r_i^{*k} - \bar{r}^{*k}) f_i^k$. The second term is the between-class covariance between the trait mean in a class and the average

rate at which an individual in class k produces individuals in any class, $\bar{r}^{*k} = \sum_j \bar{r}^{jk}$. This term depends on the phenotypic differentiation between a given class and the total population, $\bar{z}^k - \bar{z}$. Hence, equation (2) partitions the change in trait mean 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 trait mean, but a more complete description of the mutation term can be found in appendix A.

Now let us assume that the per capita growth rates r_i^{jk} are independent of the type (i.e., $r_i^{jk} = r_i^{kj}$ for all i). Intuitively, we should not observe any selection in such a population. Indeed, equation (2) tells us that the covariances in the first term are 0. However, one might still observe directional change in the trait mean due to the second term, which depends on the average rates \bar{r}^{jk} and not on the correlation between the trait and the type-specific transition rates. Following Grafen (2015b), I will refer to this effect as the “passive changes in trait mean.”

Passive changes in trait mean obviously disappear if the class means exactly coincide with the population average. The mechanisms causing the buildup of between-class differentiation can be elucidated by writing the equation giving the dynamics of the trait mean in class k , \bar{z}^k (app. A). Dropping the mutation term for simplicity, this gives

$$\frac{d\bar{z}^k}{dt} = \sum_j \text{cov}_j(z_i, r_i^{kj}) \frac{f^j}{f^k} + \sum_j (\bar{z}^j - \bar{z}^k) \bar{r}^{kj} \frac{f^j}{f^k}. \quad (3)$$

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 0, the trait mean within class k can still change due to between-class demographic transitions between class k and the other classes. This can lead to changes in the phenotypic differentiation 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 (through the covariance term in eq. [3]) and of other ecological or genetical mechanisms causing phenotypic differentiation between classes.

The Class-Structured Price Equation for a Weighted Average

Equation (2) is derived by giving each individual a weight of unity. In contrast, a common approach in the literature has been to assign a class-specific weight to each individual to extract the signal of natural selection from the change in trait mean (Fisher 1930; Crow 1979; Taylor 1990; Taylor and

Frank 1996; Leturque and Rousset 2002; Rousset 2004; Rousset and Ronce 2004; Engen et al. 2014; Grafen 2015b). Here, I follow this approach and consider the dynamics of a weighted average of the focal trait. In contrast with the standard practice, however, I consider that the individual weights are not constant through time. I therefore give each individual in class k at time t a weight of $v^k(t)$. A weighted average for the focal trait can then be calculated at time t as

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

where the weight $c^k(t) = v^k(t) f^k(t)$ is assigned to class k at t and scaled such that $\sum_k c^k(t) = 1$. When all v^k values are set to the constant value 1, we recover the results of the previous paragraph. With these assumptions, the change in the weighted trait mean takes the following simple form:

$$\frac{d\tilde{z}}{dt} = \sum_k f^k \text{cov}_k \left(z_i, \sum_j v^j r_i^{jk} \right), \quad (5)$$

if the weights $c^k(t)$ satisfy a particular dynamical equation (app. A). Hence, for a well-chosen set of weights, we can write the change in trait mean 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 0. Comparing the covariance term in equation (5) to the covariance term in equation (2), we note that the only difference is that the sum $r_i^{*k} = \sum_j r_i^{jk}$ is replaced with the weighted sum $\sum_j v^j r_i^{jk}$.

For equation (5) to hold, the c^k values must satisfy the following system of differential equations:

$$\frac{dc^k}{dt} = c^k \sum_j \bar{r}^{kj} \frac{f^j}{f^k} - \sum_j c^j \bar{r}^{jk} \frac{f^k}{f^j}. \quad (6)$$

This equation takes the form of a master equation describing the time evolution of a vector of probabilities. An interpretation of this equation will be given in the next section. Note that equation (6) depends only on the average transition rates and makes no assumption on the strength of selection of the trait distribution.

Discrete-Time Dynamics. For comparison with other works, it is useful to consider the discrete-time version of this result. In appendix C.1 (app. C is available online), I show that the change in weighted trait mean can be written in discrete time as

$$\tilde{z}(t+1) - \tilde{z}(t) = \sum_k f^k(t) \text{cov}_k \left(z_i, \sum_j v^j(t+1) \frac{w_i^{jk}(t)}{w(t)} \right). \quad (7)$$

Compared to equation (5), 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 and the class weights satisfy the following recursion:

$$c^k(t) = \sum_j c^j(t+1) \frac{\bar{w}^{jk}(t)n^k(t)}{n^j(t+1)}, \quad (8)$$

which is a discrete-time analog of equation (6).

Biological Interpretation of the Weighted Average

So far, the validity of the results does not hinge on a particular biological interpretation of the weights used to compute the average \bar{z} . However, it turns out that the weights $v^j(t)$ that appear in equation (5) are the individual reproductive values in each class at time t and that the weights $c^j(t)$ are the class reproductive values at time t (Taylor 1990; Rousset 2004).

Indeed, 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 discrete time, this probability will satisfy the following recursion:

$$c^k(t) = \sum_j c^j(t+1)p(k, t|j, t+1), \quad (9)$$

where $p(k, t|j, t+1)$ is the probability that the lineage was in class k at t given that it is in class j at $t+1$ (see, e.g., Rousset 2004, eq. [9.21]). This probability is the fraction of class- j offspring produced by class- k individuals at time t , which is simply the number of class- j offspring produced by class- k parents, $\bar{w}^{jk}(t)n^k(t)$, divided by the total number of class- j offspring, $n^j(t+1)$. Hence, equation (9) is exactly equation (8).

A perhaps more intuitive but equivalent interpretation of $c^k(t)$ can be given as the (relative) number of descendants left by genes present in class k at time t , from t onward (Tuljapurkar 1989; Caswell 2001; Rousset 2004; Barton and Etheridge 2011), which 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]). The connection with previous definitions of reproductive values will be explored in more detail in *The Interplay of Demography and Selection*.

The previous analysis thus shows that the individual reproductive values can be used as time-dependent individual weights that guarantee the elimination of the passive changes in trait mean at any time. The discrete-time formulation (eq. [8]) more clearly shows that the reproductive-value weighting needs to be applied to the offspring generation: an offspring in class j (at generation $t+1$) is valued by its current contribution to the future of the population, $v^j(t+1)$.

In continuous time, the distinction between parent and offspring generations is blurred, but equation (6) can still

be interpreted in a similar way. Indeed, because the terms for $j = k$ cancel out, the first term on the right-hand side is $v^k \sum_{j \neq k} \bar{r}^{kj} f^j$. This tells us that the probability for a gene lineage to be in class k at time t will increase due to the creation of new class- k individuals, with reproductive value v^k , from individuals belonging to all the other classes. The second term is $-\sum_{j \neq k} v^j \bar{r}^{jk} f^k$ and shows that the probability for a gene lineage to be in class k at time t will decrease due to the creation of new class- j individuals, with reproductive value v^j , from class- k individuals. It can be shown that the master equation (6) is the continuous-time limit of the discrete-time backward recursion (8).

Choice of a Final Condition

Importantly, the elimination of passive changes holds if the class reproductive values satisfy equations (6) and (8), irrespective of initial or final conditions. As a result, the vector of weights that allow the passive changes to be eliminated is not unique and depends on the choice of an appropriate final condition. A possible choice is to set all the v^k values to 1 at a given time T in the future (Barton and Etheridge 2011), in which case the class weights at T are simply the class frequencies at time T . In other words, this is equivalent to setting the relative contribution at time T of each individual to its own generation to 1. This approach will be used in the next section, where I apply reproductive-value weighting to a retrospective analysis of simulated time series. In contrast, for typical predictive analyses, the choice of the final condition is irrelevant because reproductive values are computed on a population dynamical attractor, so that only the large-time behavior of equations (6) and (8) matters (see *Reproductive Values for Predictive Theoretical Analyses*).

Reproductive Values for Retrospective Data Analyses

Suppose I am an empirical evolutionary ecologist. How can I eliminate passive changes to estimate selection on a given trait of interest? The previous section suggests that I should weight the trait mean in each class by time-dependent reproductive values computed from the aggregate demographic dynamics. No information is required about the underlying genetic variation of my study population.

The aim of this section is to present a numerical illustration of this approach. As a proof of concept, I consider a discrete-time three-class model, with class densities n_1^t , n_2^t , and n_3^t . The transition matrix for type i at time t is given by

$$\mathbf{W}_i(t) = \begin{pmatrix} 0 & 0 & \phi_3 F_3(\mathbf{E}_t, t) \\ s_1 + \omega \frac{z_i}{1 + \kappa z_i} & 0 & 0 \\ 0 & s_2 S_2(\mathbf{E}_t, t) & s_3 \end{pmatrix}. \quad (10)$$

The elements of \mathbf{W}_i are the w_i^{jk} of equation (7). The model is a variation on the classical larva-pupae-adult (LPA) model for the dynamics of *Tribolium* populations (Dennis et al. 1995). The reproduction and survival of stages 2 (pupae) and 3 (adults) depend on the environmental dynamics through the fecundity function $F_3(\mathbf{E}_t, t)$ and the survival function $S_2(\mathbf{E}_t, t)$, for which I make the following assumptions:

$$F_3(\mathbf{E}_t, t) = e^{-c_{el}n_1^1 - c_{ea}n_1^3}, \quad (11a)$$

$$S_2(\mathbf{E}_t, t) = e^{-c_{pa}n_1^3}. \quad (11b)$$

Following traditional notation, c_{el} (alternately, c_{ea} and c_{pa}) reflects the intensity of cannibalism of eggs by larvae (alternately, eggs by adults and pupae by adults). Individuals are characterized by a trait z , which is a property of the type. I assume that the only effect of the trait is to confer a nonlinear survival advantage to the first stage. The parameter ω measures the strength of selection.

General Method

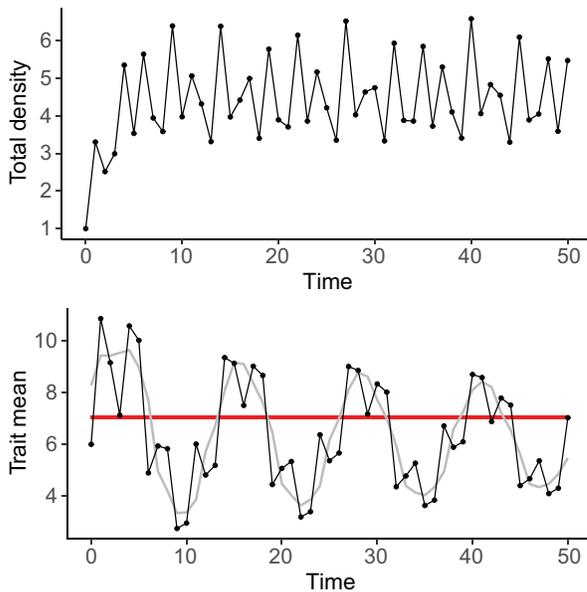
Starting from some initial conditions, the model can be run forward in time from time 0 to time T to provide a sequence

of data. The details of the model are irrelevant, but what matters in the end is that we get a time series for the trait means in each class, $\bar{z}^k(t)$, for the class densities $n^k(t)$, 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 (8) 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 trait means $\bar{z}^k(t)$ at each time step. I will first present two illustrating examples before discussing the choice of the final condition.

Example 1

Figure 1A shows that, even for a neutral trait ($\omega = 0$), the model exhibits sustained fluctuations in the trait mean. A naive observer may interpret these fluctuations as caused by selection, but in fact this is due only to demographic transitions between classes. The absence of selection is revealed by plotting the dynamics of the weighted trait mean, using the class reproductive values computed from equation (8) as weights. Doing so gives a flat line (in red), which reveals that the fluctuations are not caused by selection. For comparison,

A Neutral model ($\omega = 0$)



B Model with selection ($\omega = 0.05$)

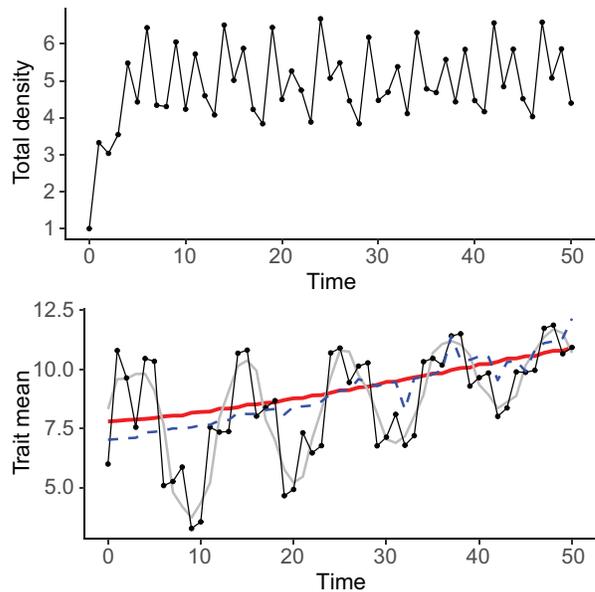


Figure 1: Dynamics of total population density and trait mean shown for model 1 at neutrality (A) and in the presence of selection (B). The dynamics of the model are given by the equation $\mathbf{n}_i(t + 1) = \mathbf{W}_i(t)\mathbf{n}_i(t)$, where the transition matrix is defined in equations (10) and (11). 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 trait mean using constant reproductive values computed from the average matrix over time (gray line). In B, the blue dashed line shows the dynamics of the weighted trait mean using the reproductive values computed in the neutral model of A. The initial densities for each class are $n_1(0) = 0.3$, $n_2(0) = 0.3$, and $n_3(0) = 0.4$. The initial distribution of the types is Poisson 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 $z_i = i$ for $0 \leq i \leq 49$. Parameters: $\phi_3 = 10$; $s_1 = 0.6$; $s_2 = 1$; $s_3 = 0.05$; $c_{ea} = 0.5$; $c_{pa} = 1$; $c_{el} = 0.4$; $\kappa = 0.2$.

the lower panels of figure 1 also show the dynamics of the trait mean weighted with constant reproductive values calculated from the time-averaged projection matrix (gray line). This weighting does not completely remove the passive changes in trait mean. In the model with selection (fig. 1B), the trait mean appears to fluctuate around an increasing trend. Applying our reproductive-value weighting irons out the fluctuations due to the passive changes in trait mean and yields a smooth trajectory that reveals the part of the change in trait mean that is actually due to selection. Again, using constant reproductive values calculated from the time-averaged projection matrix does not eliminate the passive changes in trait mean (gray line). Using the time-dependent neutral reproductive values from figure 1A as weights (blue dashed line) also imperfectly removes the passive changes, even though selection is assumed to be weak in the model.

Example 2

I now assume that fecundity in stage 3 is further affected by environmental stochasticity, through a stochastic multiplicative factor ρ_t . Figure 2 shows that, even with environmental stochasticity, reproductive-value weighting can eliminate the transient passive changes in trait mean. Note that with environmental stochasticity the transient fluctuations decay rap-

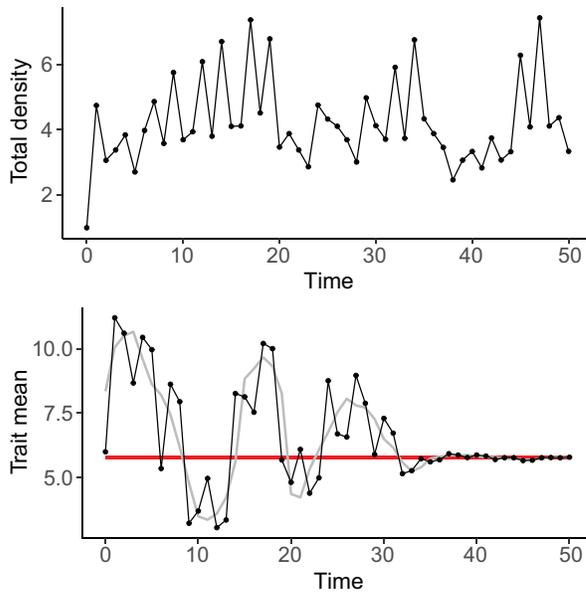
idly, and eventually the weighted and unweighted averages of the trait coincide.

Choice of the Final Condition

As noted above, the choice of the final condition is irrelevant when deriving equations (5) and (7). In fact, for a neutral trait, the dynamics of the weighted trait mean 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 trait mean at each time. The choice of this particular final condition is equivalent to setting the relative contribution of each individual to the present generation to 1 (Barton and Etheridge 2011) but also guarantees that the trajectory of the weighted trait mean 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 trait mean in an ideal population where the passive changes have been removed.

A further motivation for choosing this final condition comes from the consideration of the limiting regime where selection is weak. The influence of the passive changes in trait

A Neutral model ($\omega = 0$)



B Model with selection ($\omega = 0.05$)

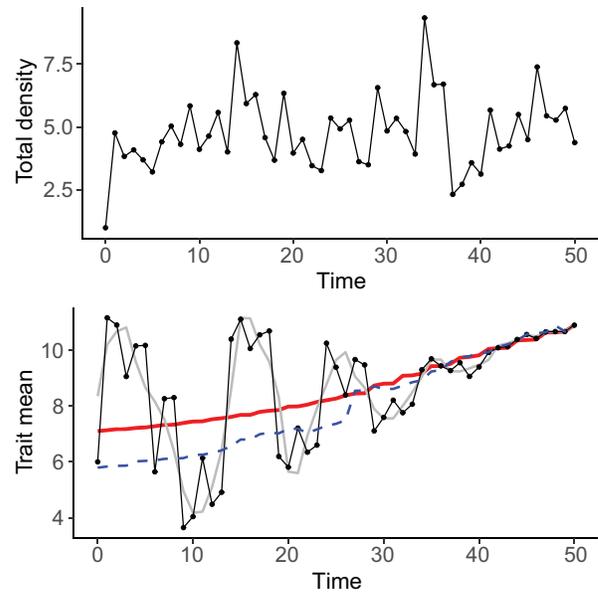


Figure 2: Dynamics of total population density and trait mean shown for model 2 at neutrality (A) and in the presence of selection (B). Compared with model 1 and figure 1B, the only change is that the fecundity $F_3(\mathbf{E}_t, t)$ in the matrix $\mathbf{W}_i(t)$ is multiplied by a stochastic factor ρ_t , modeled as a uniformly distributed random variable between 0.5 and 1.5. To allow for comparison, the same sequence of random numbers is used in A and B.

mean 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 trait mean, as in figure 2B.

The Interplay of Demography and Selection

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, equation (5), which can also be written in matrix form as follows:

$$\frac{d\bar{z}}{dt} = \mathbf{v}^\top \mathbf{C} \mathbf{f}, \tag{12}$$

where \mathbf{C} is the matrix of covariances with components $C_{jk} = \text{cov}_k(z_i, r_i^{jk})$, \mathbf{v} is the vector of individual reproductive value $v^k(t)$, and \mathbf{f} is the vector of class frequencies $f^k(t)$. In the remainder of the article, the notation \top represents the transpose operation, that is, \mathbf{v}^\top is a row vector.

Dynamical Equations for the Demographic Process

The vectors of reproductive values and class frequencies follow coupled dynamical equations that generalize the classical interpretation in terms of eigenvectors. For class reproductive values, equation (6) may be written compactly in matrix form as

$$\frac{d\mathbf{c}^\top}{dt} = -\mathbf{c}^\top \mathbf{Q}(\mathbf{E}(t)), \tag{13}$$

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 $q_{kk} = -\sum_{j \neq k} q_{kj}$ (app. B).

Similarly, the vectors \mathbf{v}^\top and \mathbf{f} in equation (12) satisfy the following equations (app. B):

$$\frac{d\mathbf{v}^\top}{dt} = -\mathbf{v}^\top \mathbf{R}(\mathbf{E}(t)) + \bar{r}(t) \mathbf{v}^\top, \tag{14a}$$

$$\frac{d\mathbf{f}}{dt} = \mathbf{R}(\mathbf{E}(t)) \mathbf{f} - \bar{r}(t) \mathbf{f}, \tag{14b}$$

where $\bar{r}(t) = (1/n)dn/dt$ is the average growth rate of the total population. Note the similarity between these two equations. The individual reproductive values and class frequencies are both calculated using the matrix $\mathbf{R}(\mathbf{E}(t))$, which collects the average transition rates, $\bar{r}^{kj}(\mathbf{E}(t))$, and the per capita growth rate of the total population size, $\bar{r}(t)$. However, while equations (14a) and (14b) use the same input, they have different interpretations: using equation (14b), the future class frequencies can be calculated from an initial condition,

whereas the adjoint equation (14a) works backward in time to compute past reproductive values from a final condition.

Equations (14a) and (14b) can be combined to recover an important property of the individual reproductive values already noted by Fisher (1930) for linear models. If we evaluate the population size not by a head count but by weighting each individual by its reproductive value, the weighted population size, $\tilde{n}(t) = \sum_k v^k(t) n^k(t)$, satisfies the following equation:

$$\frac{d\tilde{n}}{dt} = \bar{r}(t) \tilde{n}. \tag{15}$$

Hence, the reproductive value-weighted population size always grows as the unweighted population size, even for out-of-equilibrium, nonlinear ecological dynamics.

Note that it is also possible to derive similar equations for populations with continuous structure. I give an illustration in box 1 using a model with continuous age structure that allows Fisher’s original definition of reproductive value to be recovered.

Discrete-Time Dynamics. Equations (13) and (14) have discrete-time counterparts. In appendix C.1, I show that the class reproductive values satisfy the following recursion:

$$\mathbf{c}^\top(t) = \mathbf{c}^\top(t+1) \mathbf{P}(\mathbf{E}(t)), \tag{16}$$

where \mathbf{P} is the matrix with elements $p_{k,j} = \bar{w}^{kj}(t) n^j(t) / n^k(t+1)$. Similarly, the individual reproductive values and class frequencies satisfy the recursions

$$\bar{w}(t) \mathbf{v}^\top(t) = \mathbf{v}^\top(t+1) \mathbf{W}(\mathbf{E}(t)), \tag{17a}$$

$$\bar{w}(t) \mathbf{f}(t+1) = \mathbf{W}(\mathbf{E}(t)) \mathbf{f}(t), \tag{17b}$$

where $\mathbf{W}(\mathbf{E}(t))$ is the matrix with elements \bar{w}^{kj} . Again, the two equations use the same input but represent different processes. As already noted by Tuljapurkar (1989), the matrix \mathbf{W} acts to propagate \mathbf{f} forward in time and \mathbf{v}^\top backward in time. In Tuljapurkar’s words, the vector of class frequencies at each time is an “accumulation of the past,” while the vector of reproductive values at each time is a “summation of the future.”

Selection and Demography

Equation (12) provides a simple partition of the change in the weighted mean phenotype into selective and demographic components. While the matrix of covariances \mathbf{C} captures the relative performances of the different types for each between-class transition, the vectors \mathbf{v}^\top and \mathbf{f} solely depend on the average rates at the population level and are therefore purely demographic properties of the system. Indeed, a naive ecologist oblivious to the underlying genetic diversity of her study population would still be able to calculate the reproductive

Box 1: Continuous age structure and Fisher's original concept of reproductive value

Fisher (1930) originally defined the concept of reproductive value in a model with continuous age structure, whereas the results in the main text are derived using a discrete class structure. However, the elimination of passive changes through reproductive-value weighting also extends to models with continuous structure. Defining the reproductive value of individuals with age a at time t as $v(a, t)$, it is possible to derive the dynamics of a weighted average trait, $\bar{z} = \sum_i z_i v(a, t) f_i(a, t) / \sum_i v(a, t) f_i(a, t)$, where $f_i(a, t)$ is the fraction of type- i individuals among individuals with age a at t and $f(a, t)$ is the fraction of individuals with age a at time t . In appendix C.3, it is shown that the change in trait mean then takes the following form:

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

This is the continuous-age equivalent of equation (12). Here, $b_i(a, t)$ and $d_i(a, t)$ are the birth and death rates of individuals with age a at time t . The covariances between the trait z and the vital rates are taken over all individuals with age a and time t . The contribution of the reproduction of individuals with age a to selection is weighted by their frequency $f(a, t)$ and by the reproductive value $v(0, t)$ of their newborn offspring. In contrast, the contribution of death events to selection is weighted by the reproductive value of the age group, $v(a, t)$.

Equation (a) holds only if the reproductive values $v(a, t)$ satisfy the following partial differential equation:

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

Again, this is the continuous analog of equation (14a). The reproductive values depend on the average birth and death rates $\bar{b}(a, t)$ and $\bar{d}(a, t)$ and on the growth rate of the total population $\bar{r}(t)$. Bacaër and Abdurahman (2008) derived a similar equation in a monomorphic epidemiological model structured with infectious age.

To fully connect these results to Fisher's (1930) original definition of reproductive values, one needs to assume time-independent birth and death rates that depend only on age. With these assumptions, the population will be characterized by a stable growth rate r , a stable age structure $f(a)$, and a stable distribution of reproductive values $v(a)$. From equation (b), we then have the following expression:

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

where $\ell(s) = \exp(-\int_0^s \bar{d}(x) dx)$ is the probability of surviving up to age s . Expression (c) is Fisher's original expression of reproductive value (Fisher 1930; Charlesworth 1994), but it explicitly takes into account genetic polymorphism in the population by using the average birth and death rates.

values and class frequencies from the aggregate response of the population. This is potentially valuable for data analysis, as we have seen in the previous section.

This demographic definition of reproductive values has its roots in Fisher's (1930) original exposition of the concept and provides a conceptually clear connection to the usage of reproductive values in other fields, such as human demography, where details about the genetic composition of the population are typically averaged out. Importantly, the dynamical definition of reproductive values used here holds for a broad class of models, irrespective of the genetic composition of the population, the trait distribution, and the underlying population and environmental dynamics. In particular, the reproductive values are calculated neither in a neutral or monomorphic population nor under any limiting assumption of mutant rarity, as typically assumed in evolutionary

game theory. The next paragraph clarifies the connection with these previous usages of reproductive values.

Connection with Classical Asymptotic Results

Although most works directly compute reproductive values as a left eigenvector, some authors have proposed the computation of reproductive values from dynamical equations. To my knowledge, a dynamical equation was first proposed by Crow (1979) for allele-specific reproductive values and by Tuljapurkar (1989) at the population level (see also Barton and Etheridge 2011). Dynamical equations for the class reproductive values in monomorphic populations have also been used in inclusive fitness theory (e.g., Rousset 2004, eq. [9.21]; Lehmann 2014, eq. [6]). However, while Tuljapurkar (1989) explicitly defined reproductive values as a

function of time, usage in evolutionary theory has typically reserved the term “reproductive value” for the asymptotic behavior of the dynamical equations, yielding a time-independent definition (Charlesworth 1994; Rousset 2004; Barton and Etheridge 2011; Lehmann 2014). The validity of this asymptotic definition of reproductive values hinges on additional demographic or genetic assumptions, such as exponential growth or weak selection, although it has been noted that reproductive values could in principle be defined as time-dependent weights, as I do here (see Lehmann and Rousset 2014, note 3). In this section, I discuss how previous definitions of reproductive values can be recovered from the above dynamical equations under additional assumptions.

Exponential Growth. The easiest way to recover the standard asymptotic definition of reproductive values is to assume that the matrix \mathbf{R} is approximately constant.¹ This way it is well known that in the long run the population growth rate \bar{r} is constant and equal to the dominant eigenvalue of \mathbf{R} . The population then grows exponentially with a stable class structure given by the right eigenvector of matrix \mathbf{R} associated with \bar{r} . The corresponding left eigenvector collects the individual reproductive values (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.

Equations (14) allow us to recover this result by assuming that the reproductive values and class frequencies stabilize in the long run. Setting the time derivatives to 0 then yields

$$\mathbf{v}^T \mathbf{R} = \bar{r} \mathbf{v}^T, \tag{18a}$$

$$\mathbf{R} \mathbf{f} = \bar{r} \mathbf{f}. \tag{18b}$$

The analogous discrete-time result follows from setting $\mathbf{v}(t + 1) = \mathbf{v}(t)$ and $\mathbf{f}(t + 1) = \mathbf{f}(t)$ in equation (17), which gives

$$\mathbf{v}^T \mathbf{W} = \bar{w} \mathbf{v}^T, \tag{19a}$$

$$\mathbf{W} \mathbf{f} = \bar{w} \mathbf{f}. \tag{19b}$$

The latter equations are, respectively, the left- and right-eigenvector results of Taylor (1990, eqq. [7] and [5]), but they do not rely on the assumption that the population is monomorphic. Rather, they explicitly take into account polymorphic populations with arbitrary trait distribution. The key to this generalization is to use the matrix of average transition rates.

Density-Dependent Populations at Equilibrium. Another frequent assumption in the literature is that the population is at

a stable demographic equilibrium. This way, the dynamics of reproductive values also depend on constant projection matrices $\hat{\mathbf{Q}} = \mathbf{Q}(\hat{\mathbf{E}})$ and $\hat{\mathbf{R}} = \mathbf{R}(\hat{\mathbf{E}})$, where the environmental vector $\hat{\mathbf{E}}$ is calculated at equilibrium. Because $\bar{r} = 0$ at equilibrium, it follows from equation (13) that the vector \mathbf{c} is a left eigenvector of the matrix $\hat{\mathbf{Q}}$ associated with eigenvalue 0, where $\hat{\mathbf{Q}}$ has elements $\bar{r}^{jk} f^k / f^j$. Similarly, equations (14) show that the individual reproductive values are proportional to a left eigenvector of $\hat{\mathbf{R}}$ associated with eigenvalue 0 and the class frequencies are proportional to a right eigenvector.

A similar result holds in discrete time. From equation (16), we see that at equilibrium when $\mathbf{c}(t + 1) = \mathbf{c}(t)$ and $\mathbf{E}(t) = \hat{\mathbf{E}}$, the vector \mathbf{c} is a left eigenvector of the matrix $\hat{\mathbf{P}} = \mathbf{P}(\hat{\mathbf{E}})$ associated with eigenvalue 1. For the individual reproductive values, we have $\bar{w} = 1$ at equilibrium, and therefore \mathbf{v} is a left eigenvector of the matrix $\hat{\mathbf{W}}$ associated with eigenvalue 1. These two results extend a widely used result in evolutionary game theory and inclusive fitness theory (Taylor 1990; Rousset 1999, 2004). Once again, in contrast to these previous studies, the reproductive values and class frequencies are defined in a polymorphic population with arbitrary trait distribution instead of being calculated in a monomorphic population. However, it is straightforward to recover the standard monomorphic case from the polymorphic population under the assumption that all types are identical.

Reproductive Values for Predictive Theoretical Analyses

In this section, equation (12) is used as a starting point to derive approximations for the change in trait mean following the introduction of a mutation with small phenotypic effect. The aim is now to make some predictions about the change in the trait, and for this I return to the standard weak selection assumption of evolutionary game theory. The classical expression of the selection gradient for a mutant arising in a monomorphic resident population at equilibrium is first recovered, but I then relax two assumptions. First, I show that the above definition of reproductive values can be used to describe the invasion of a mutant arising in a polymorphic resident population with arbitrary trait distribution. Second, I show that the time-dependent reproductive values can be used to describe potential variations in reproductive values for nonequilibrium ecological attractors, such as cycling populations.

Separation of Timescales

By construction, reproductive values quantify class contributions to the future demography of the population. Equations (13), (14a), (16), and (17a) show that they can be calculated from backward dynamical equations. As a result, equation (12) appears to have little predictive power, as the change in the trait mean at a given time depends on the whole

1. More generally, the matrix \mathbf{R} can depend on a density-independent ergodic environment (Tuljapurkar 1989).

future we are precisely trying to predict. However, this problem can be solved if we are interested only in long-term evolution and assume a separation of timescales between evolutionary and ecological timescales, as is typical when computing invasion fitness (Metz et al. 1992; Geritz et al. 1998; Lehmann and Rousset 2014; Van Cleve 2015). If evolution is slow compared to the demography of the population, we only need to evaluate equation (12) 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 analyze long-term evolution.

Monomorphic Resident Populations at Equilibrium

I will first recall a classical result of evolutionary game theory obtained under the assumption of a vanishingly small trait 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. For small values of ε , the following approximation for the change in weighted trait mean can be derived (app. C.2; Taylor 1990; Taylor and Frank 1996; Rousset 2004):

$$\frac{d\bar{z}}{dt} = \sigma_{zz} \hat{\mathbf{v}}^T \frac{d\mathbf{R}_m}{d\varepsilon} \hat{\mathbf{f}} + O(\varepsilon^3), \quad (20)$$

where σ_{zz} is the trait variance, the vectors $\hat{\mathbf{v}}$ and $\hat{\mathbf{f}}$ are the equilibrium values of \mathbf{v} and \mathbf{f} computed in the monomorphic resident population, and the matrix $d\mathbf{R}_m/d\varepsilon$ is the perturbation of the matrix of the mutant per capita growth rates r_m^{jk} (see app. C.2 for more details). Note that $\bar{z} = z_w + \varepsilon \tilde{f}_m$, where \tilde{f}_m is the average frequency of the mutant type, calculated using class reproductive values as weights (as defined in app. A.3), so that tracking the average phenotype is equivalent to tracking the frequency of the mutant allele.

Equations (12) and (20) have the same form, but the second is valid only as an approximation under weak selection. Expanding the matrix product in equation (20) 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, 2004):

$$S = \sum_k \sum_j \hat{f}^k \hat{v}^j \frac{dr_m^{jk}}{d\varepsilon}. \quad (21)$$

Selection gradients of this form are frequently encountered in the literature, when quasi-monomorphic populations are considered. 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 se-

lection). Under these assumptions, the effect of a mutation on the demography of the population can be neglected compared to the effect of the mutation on the covariance matrix (app. C.2).

Polymorphic Resident Populations at Equilibrium

Although standard models tend to focus on monomorphic resident populations, many natural populations will typically display a nonnegligible amount of standing variation, with potentially multimodal trait distributions. Because equation (12) is still valid under these assumptions, it can be used as a starting point to derive approximations of the selection gradient. As in the monomorphic case, the idea is to calculate perturbations of equation (12) resulting from a slight change in the trait distribution. For instance, if we have a stable coalition of M types, we may consider that a fraction p of the individuals of type M mutates to trait value $z_M + \varepsilon$. As before, the limit $\varepsilon = 0$ corresponds to the resident population at equilibrium. 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 (12) as

$$\frac{d\bar{z}}{dt} \approx \hat{\mathbf{v}}^T \frac{d\mathbf{C}}{d\varepsilon} \hat{\mathbf{f}}. \quad (22)$$

As in equation (20), the vectors $\hat{\mathbf{v}}$ and $\hat{\mathbf{f}}$ are computed at equilibrium for $\varepsilon = 0$. However, equation (22) 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 article. In particular, because in the resident polymorphic population the covariance matrix \mathbf{C} is not null, it may not always be possible to neglect the effect of the mutation on the demographic variables \mathbf{v} and \mathbf{f} (app. C.2). However, the present considerations shed light on the potential utility of equation (12) for deriving analytical expressions for long-term measures of selection in polymorphic class-structured populations, while keeping the central concept of reproductive value on board.

Periodic Ecological Attractor

Another potential extension of standard theory attainable from equation (12) is to consider nonequilibrium ecological attractors, such as limit cycles. Limit cycles can be thought of as a continuous-time description of periodic environments, as needed, for instance, for taking into account seasonality.

Consider a monomorphic population that has settled on a limit cycle with period T . Assuming, as in the equilibrium case, that selection is weak, the average change in the trait mean over one period is approximately proportional to (app. C.2)

$$S = \sum_k \sum_j \int_0^T \hat{f}^k(t) \hat{v}^j(t) \frac{dr_m^{jk}(t)}{d\varepsilon} dt. \quad (23)$$

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 rates r_m^{jk} are also calculated on the resident environment, which is indicated by the dependency on t . The use of time-dependent reproductive values for periodic models has been suggested before (Brommer et al. 2000; Caswell 2001; Bacaër and Abdurahman 2008), but to my knowledge equation (23) has not been previously derived. Compared to earlier approaches that have dealt with complex demographics by incorporating the demographic states into the class structure (Brommer et al. 2000; Rousset and Ronce 2004; Lehmann et al. 2016), equation (23) provides a lower-dimensional invasion criterion in which classes are defined using biological considerations of the life cycle, instead of the behavior of the 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 analyze the different regions of parameter space. Although a full analysis of the connections between this result and previous characterizations of invasion fitness in periodic environments (Tuljapurkar 1985; Ferrière and Gatto 1995) is beyond the scope of this article, this preliminary attempt suggests that equation (12) could be used to provide potentially useful approximations for the change in trait mean also in nonstationary ecological systems.

Discussion

In class-structured populations, changes in gene frequencies or mean phenotypes can be brought about through three distinct routes. First, natural selection can 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 trait mean can occur due to the dynamics of between-class differentiation, as measured by the difference between the trait mean in a class and the trait mean in the total population. The dynamics of between-class differentiation is itself the resultant of natural selection and “passive changes” due to transitions between classes. These passive changes can be observed even in the absence of natural selection, either transiently or on longer timescales, depending on genetic con-

straints and environmental feedback. Third, mutation or recombination may introduce some directional change in the trait mean, 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 through the dynamics of the vector $\mathbf{E}(t)$.

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 characterized 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 with this long-term growth rate, even before the stable class structure has been reached. Furthermore, these constant weights can be used to cancel out the passive changes in the trait mean and therefore extract the signal of natural selection from the purely demographic consequences of class dynamics (Engen et al. 2014; Grafen 2015*b*).

This article provides a general extension of this result using a dynamical and demographic definition of reproductive values. 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, nonequilibrium population dynamics, and environmental fluctuations. In addition, although I have focused on discrete trait and state distributions, the derivation of appendix A carries out unchanged if the trait averages are computed over a continuous trait distribution. This provides a direct connection with previous quantitative genetics models of age- and stage-structured populations (Lande 1982*a*; Barfield et al. 2011). Furthermore, the result also extends to populations structured by continuous states, such as age-structured (box 1; app. C.3) or size-structured populations studied by integral projection models (Rees and 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 article departs from the classical usage in two ways. First, class reproductive values are defined not 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 emphasize a purely demographic notion of reproductive value: the weight we need to give to each individual does not depend on its type but only on its class. This class-specific weight is simply 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, where genotype-dependent reproductive values are defined) but appears to match the definition attributed to Fisher (1930) by Grafen (2015a, 2015b). Defining reproductive values at a demographic level allows one 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. This procedure does not require any a priori knowledge of the underlying genetic variation in the population. Note that the standard calculation of reproductive values in a monomorphic population is a special case obtained when only one type is present.

The Different Usages of Reproductive Values

An important question to ask is whether the properties of reproductive values discussed here are of relevance for practical studies of natural selection. The usefulness of reproductive value clearly depends on the biological question. First, one might be interested in detecting patterns of natural selection in demographic and genetic data, as collected, for instance, in field or controlled experimental studies. It is then 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 a constant eigenvector. In this article, I present an illustration of this approach 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 trait mean resulting from class dynamics. Note that although these passive changes are expected to 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 timescales, at least long enough for these fluctuations to become relevant for empirical or experimental studies. An example is given in figure 1, based on the classical LPA model for *Tribolium* dynamics. Haplodiploid systems of inheritance provide another example of this phenomenon (Gardner 2015).

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 new medical treatment in a population, the transient dynamics are of direct relevance to identify 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 be computed only 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 question, 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 populations. For example, when studying the evolution of virulence during spatial epidemics on networks, Lion and Gandon (2016) found that the change in mean virulence depends on the buildup of a difference between the (local) virulence measured in hosts that have at least one susceptible neighbor 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 on additional assumptions. For instance, if ecological dynamics takes place on a fast timescale compared to evolutionary dynamics, the effect of transient ecological dynamics can 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 (12) gives a general description of the dynamics of a weighted trait mean that can be combined with other genetic or ecological assumptions to derive expressions for the selection gradient. This suggests perspectives for analyzing selection in polymorphic resident populations with arbitrary trait distributions. In addition, because most ecological models can be expected to be nonstationary (Chesson 2017), a time-dependent concept of reproductive values may allow consideration of more complex and realistic population dynamics.

Neutrality, Demography, and Selection

A key insight of equation (12) is that the effects of selection are captured by the covariance matrix C and weighted by

the individual reproductive values \mathbf{v} and the class frequencies \mathbf{f} , which are purely demographic quantities computed using the average transition matrix \mathbf{R} . In many problems in evolutionary game theory, the selection gradient is calculated by evaluating the change in mean phenotype due to a perturbation of a monomorphic population at equilibrium. The perturbation is caused by a new mutation, which is typically assumed to be rare or to have a small effect on the phenotype (weak selection). Under these assumptions, the reproductive values and class frequencies in equation (12) can be approximated by those calculated in the resident monomorphic population, and this resident population, being monomorphic, may be thought of as “neutral.” However, real populations will often be polymorphic and characterized by a possibly multimodal trait distribution. In this case, it is still possible to ask how a mutation of small effect will affect the mean phenotype, but it is not immediately clear how the concept of a neutral reproductive value will be helpful. The results of this article suggest that for polymorphic populations with arbitrary trait distribution, the reproductive values and class frequencies in equation (12) should be approximated using the mean demographic matrix of the resident population. The reproductive values calculated in this way are still neutral because they are calculated in the resident population where the change in trait mean is assumed to be 0. However, they are not calculated under the assumption that the variance in the trait is vanishingly small. Instead, the nonzero standing genetic variation is handled by averaging over all types. Importantly, although the reproductive values do depend on the trait distribution of the resident population, they are not “selective reproductive values” because they are calculated from the average transition rates, so that information about the relative fitness of the different types is not used.

Possible Generalizations

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 straightforward. 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 2. 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 valid only 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 and 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.

Taking into account stochasticity is particularly important to fully extend the results of this article to spatially structured populations. Many results on evolution in class-structured populations have been derived using an inclusive fitness formalism in subdivided populations (Taylor 1990; Rousset 2004; Lehmann and Rousset 2014; Lehmann et al. 2016). In this approach, spatial structure is modeled using a demstructured population, and the local fluctuations in allele frequencies are taken into account through measures of population structure. It would be interesting to analyze how local stochasticity affects the definition and properties of reproductive values discussed here. However, if the total population size is sufficiently large, the spatial dynamics will follow approximately deterministic equations given by spatial moment equations (Lion 2016; Lion and Gandon 2016). The per capita growth rates r_i^{kj} will then depend on the dynamics of higher-order spatial moments, and the equations for the trait mean and reproductive values will represent only the first in a hierarchy of dynamical equations. However, the key result of this article on the weighted Price equation would still be valid because it does not depend on any assumption on the functional form of the r_i^{kj} values.

Finally, I have assumed throughout that the trait under consideration can be measured in each class. This has clear limitations, because, for example, wing length cannot be used as a trait in the above formalism if we are studying an insect species with both alate and wingless classes. This difficulty may be avoided by tracking the change in the frequencies of types rather than the change in mean phenotype. Appendix A presents equations for the dynamics of the unweighted and weighted frequencies of type i in the population, with similar interpretations regarding the use of reproductive-value weighting. Working with frequencies should also be more appropriate to study a plastic trait that takes different values depending on the class in which it is expressed.

Connection with Other Usages of Reproductive Values

Historically, the use of reproductive values has also been advocated in two ways. In demography, reproductive values

are often characterized 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 and Smith 1972; Samuelson 1977; Crow 1979; Charlesworth 1994). The generality of this result has been debated, as this property of reproductive values seems tied to linear models (Samuelson 1977; see also Bacaër and Abdurahman 2008 for an extension to periodic environments). However, the dynamical definition of reproductive values used here guarantees that the reproductive-valued population size has the same growth rate as the nonweighted population size.

Alternatively, in evolutionary theory, reproductive values have been discussed in relation to Fisher's fundamental theorem of natural selection (FTNS; Crow 1979; Grafen 2015a, 2015b; Lessard and 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 and Day 2009). However, these Price equations are derived for constant traits, whereas the growth rate r_i is a function of the environment $E(t)$ 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 and Slatkin 1992; Gandon and Day 2009; Lion 2018). Hence, as has long been recognized, the FTNS captures only a partial change in mean fitness, with or without reproductive-value weighting.

Summary

The results of this article confirm that reproductive values are best viewed as weights that can be used to decouple the changes due to selection from the passive changes due to demographic class dynamics. This allows one to measure selection in distinct classes with potentially different evolutionary values using a single, time-dependent currency. The practical interest 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 trait mean 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 trait mean 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

$$\frac{df_i^k}{dt} = f_i^k (r_i^k - \bar{r}^k),$$

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

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

and the average per capita growth rate of individuals in class k , averaged over all types, is

$$\bar{r}^k = \sum_i r_i^k f_i^k = \sum_j \bar{r}^{kj} \frac{f^j}{f^k},$$

where $\bar{r}^{kj} = \sum_i f_i^{kj} f_i^j$ is the average transition rate from class j to class k . It is straightforward to verify that $dn^k/dt = \bar{r}^k n^k = \sum_j \bar{r}^{kj} n^j$ as expected.

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

$$\begin{aligned} \frac{df_i}{dt} &= \sum_k f^k \frac{df_i^k}{dt} + \sum_k f_i^k \frac{df^k}{dt} \\ &= \sum_k f^k f_i^k (r_i^k - \bar{r}^k) + \sum_k f_i^k \left(\sum_j \bar{r}^{kj} f^j - f^k \frac{1}{n} \frac{dn}{dt} \right) \\ &= \sum_k f^k f_i^k \sum_j r_i^{kj} \frac{f_i^j f^j}{f_i^k f^k} - \sum_k f^k f_i^k \sum_j \bar{r}^{kj} \frac{f^j}{f^k} \\ &\quad + \sum_k f_i^k \sum_j \bar{r}^{kj} f^j - f_i \sum_k \sum_j \bar{r}^{kj} f^j \\ &= \sum_k \sum_j r_i^{kj} f_i^j f^j - f_i \sum_k \sum_j \bar{r}^{kj} f^j \\ &= \sum_k \sum_j (r_i^{kj} - \bar{r}^{kj}) f_i^j f^j + \sum_k \sum_j (f_i^j - f_i) \bar{r}^{kj} f^j. \end{aligned}$$

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

$$\frac{d\bar{z}}{dt} = \sum_j \text{cov}_j \left(z_i, \sum_k r_i^{kj} \right) f^j + \sum_j (\bar{z}^j - \bar{z}) \sum_k \bar{r}^{kj} f^j. \quad (\text{A1})$$

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

$$\begin{aligned} \frac{d\bar{z}^k}{dt} &= \text{cov}_k(z_i, r_i^k) = \sum_i \sum_j (z_i - \bar{z}^k) r_i^{kj} f_i^j \frac{f^j}{f^k} \\ &= \sum_j \sum_i (z_i - \bar{z}^j) r_i^{kj} f_i^j \frac{f^j}{f^k} + \sum_j (\bar{z}^j - \bar{z}^k) \sum_i r_i^{kj} f_i^j \frac{f^j}{f^k} \\ &= \sum_j \text{cov}_j(z_i, r_i^{kj}) \frac{f^j}{f^k} + \sum_j (\bar{z}^j - \bar{z}^k) \bar{r}^{kj} \frac{f^j}{f^k} \\ &= \sum_j \text{cov}_j(z_i, r_i^{kj}) \frac{f^j}{f^k} + \sum_j (\bar{z}^j - \bar{z}) \bar{r}^{kj} \frac{f^j}{f^k} \\ &\quad - (\bar{z}^k - \bar{z}) \frac{\sum_j \bar{r}^{kj} f^j}{f^k}. \end{aligned} \tag{A2}$$

From equations (A1) and (A2), we can also derive the dynamics of $\bar{z}^k - \bar{z}$, which gives

$$\begin{aligned} \frac{d}{dt}(\bar{z}^k - \bar{z}) &= \sum_j \text{cov}_j \left(z_i, \frac{r_i^{kj}}{f^k} - \sum_k r_i^k \right) f^j \\ &\quad + \sum_j (\bar{z}^j - \bar{z}) \left(\bar{r}^{kj} \frac{f^j}{f^k} - \sum_k \bar{r}^{kj} f^j \right) \\ &\quad - (\bar{z}^k - \bar{z}) \frac{\sum_j \bar{r}^{kj} f^j}{f^k}. \end{aligned} \tag{A3}$$

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 give birth to an offspring of type ℓ , conditional on mutation. Assuming that the per capita rate r_i^k can be decoupled into birth and death contributions as $b_i^k - d_i^k$, the change in the density n_i^k can then be written as

$$\begin{aligned} \frac{dn_i^k}{dt} &= -d_i^k n_i^k + (1 - \mu) b_i^k n_i^k + \mu \sum_{\ell} m_{\ell i} b_{\ell}^k n_{\ell}^k \\ &= r_i^k n_i^k + \mu \left(\sum_{\ell} m_{\ell i} b_{\ell}^k n_{\ell}^k - b_i^k n_i^k \right). \end{aligned}$$

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

$$\frac{d\bar{z}^k}{dt} = \text{cov}_k(z_i, r_i^k) + \mu \sum_i z_i \left(\sum_{\ell} m_{\ell i} b_{\ell}^k f_{\ell}^k - b_i^k f_i^k \right),$$

which can be rewritten as

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

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

$$\frac{d\bar{z}}{dt} = \text{RHS of (A1)} + \mu \sum_i \left(\sum_{\ell} z_{\ell} m_{\ell i} - z_i \right) b_i f_i, \tag{A4}$$

where $b_i = \sum_k b_i^k n_i^k / n$ is the average birth 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.

Noting $\delta_i = \sum_{\ell} z_{\ell} m_{\ell i} - z_i$ the deviation between parent and offspring trait, the second term of equation (A4) can be further split into two components, as follows:

$$\sum_i \left(\sum_{\ell} z_{\ell} m_{\ell i} - z_i \right) b_i f_i = \text{cov}(\delta_i, b_i) + \bar{\delta} \bar{b},$$

where $\bar{\delta} = \sum_i \delta_i f_i$ is the mean deviation over all types, \bar{b} is the mean birth rate, and $\text{cov}(\delta_i, b_i) = \sum_i \delta_i b_i f_i - \bar{\delta} \bar{b}$ is the covariance between the trait difference and the birth rate. This is the continuous-time version of equation (12) in Barfield et al. (2011).

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

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

If the c^k values satisfy the system

$$\frac{dc^k}{dt} = - \sum_j c^j \bar{r}^{jk} \frac{f^k}{f^j} + c^k \sum_j \bar{r}^{kj} \frac{f^j}{f^k}, \tag{A5}$$

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

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

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

$$\frac{d\tilde{z}}{dt} = \sum_j \text{cov}_j \left(z_i, \sum_k v^k r_i^{kj} \right) f^j, \quad (\text{A6})$$

or in matrix form:

$$\frac{d\tilde{z}}{dt} = \mathbf{v}^\top \mathbf{C} \mathbf{f}, \quad (\text{A7})$$

where \mathbf{C} is the matrix of covariances with elements $C_{kj} = \text{cov}(z_i, r_i^{kj})$. Taking into account mutation would contribute only an additional term, which is simply the second term of equation (A4) with \tilde{b}_i and \tilde{f}_i substituted for b_i and f_i .

APPENDIX B

Reproductive Values

Equation (A5) can be rewritten in matrix form as

$$\frac{d\mathbf{c}^\top}{dt} = -\mathbf{c}^\top \mathbf{Q}, \quad (\text{B1})$$

where the matrix \mathbf{Q} has elements

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

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

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

$$\begin{aligned} \frac{dv^k}{dt} f^k &= \frac{dc^k}{dt} - v^k \frac{df^k}{dt} \\ &= -\sum_j c^j \bar{r}^{jk} \frac{f^k}{f^j} + c^k \sum_j \bar{r}^{kj} \frac{f^j}{f^k} - v^k \left(\sum_j \bar{r}^{kj} f^j - \bar{r} f^k \right) \\ &= -\sum_j v^j \bar{r}^{kj} f^k + v^k f^k \bar{r}, \end{aligned}$$

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

$$\frac{d\mathbf{v}^\top}{dt} = -\mathbf{v}^\top \mathbf{R} + \bar{r} \mathbf{v}^\top. \quad (\text{B2})$$

Equations (B1) and (B2) show that the vector \mathbf{c} (alternately, \mathbf{v}) can be calculated at equilibrium as the left eigenvector of the matrix \mathbf{Q} (alternately, \mathbf{R}), associated with eigenvalue 0.

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“*Dasyurus ursinus*, Tasmanian devil.” From the review of *The Standard Natural History* by Elliott Coues and J. S. Kingsley (*The American Naturalist*, 1884, 18:166–168).