On the interpretation of the operation of natural selection in class-structured populations

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Abstract

Biological adaptation is the outcome of allele-frequency change by natural selection. At the same time, populations are usually class structured as individuals occupy different states such as sex, stage or age. This is known to result in the differential transmission of alleles called class transmission, and thus also affects allele-frequency change even in the absence of selection. How does one then isolate the allele-frequency change due to selection from that owing to class transmission? We show how reproductive values can be used to decompose multigenerational arithmetic allele-frequency change between any two generations of the evolutionary process in terms of effects of selection and class transmission. This provides a missing relationship between allele-frequency change and the operation of selection. It allows to define an appropriate measure of fitness summarizing the effect of selection in a multigenerational process, which connects asymptotically to invasion fitness and quantitative trait evolution under weak selection.

Keywords: natural selection, class structure, reproductive values, allele-frequency change.

Introduction

Consider the following situation an evolutionary biologist may encounter. Suppose you observe the evolutionary process in a population between two distant points in time, and empirically measure at each census point the number of alleles at some locus of interest. Suppose further that one also measures the survival and number of descendants of the carriers of the alleles, and that these measurements can be subdivided into different reproductive classes of the alleles, such as the sex, age, stage or habitat of the individuals that carry them. The overall time of observation is moreover assumed short enough to neglect the appearance of new mutations and the population is large enough to neglect the effect of genetic drift. Then, any change in allele frequency must have occurred due to natural selection and/or

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the non-selective process of class transmission, i.e., the differential reproductive success of an individual owing to differential classes in which individuals reproduce and survive, also known to alter allele frequencies in class-structured populations. However, it is only natural selection that shapes biological adaptations [Barton et al., 2007, Fisher, 1930, Futuyama, 2017, Lynch and Walsh, 2018]. It is therefore natural to ask how much of the measured change in frequency is caused by natural selection, and how much of the overall change caused by selection can be attributed to a specific demographic time step. Surely, evolutionary theory should be able to answer such a basic question. Yet, despite a large and growing literature on the evolution in class-structured populations (e.g., Caswell, 2000, de Roos, 1997, Frank, 2008, Grafen, 2006, 2015, Leturque and Rousset, 2002, Lion, 2018, Priklopil and Lehmann, 2020, Rousset, 2004, Taylor, 1990), there is no clear answer to this question and thus no operational way to isolate the contribution of natural selection to allele-frequency change over an arbitrary number of time steps of the evolutionary process.

This paper aims to fill this gap by providing an operational decomposition of the contribution of natural selection and that of class transmission to allele-frequency change under an evolutionary process. In this decomposition, we consider a change over an arbitrary number of demographic time steps and allocate fractions of allele-frequency change to each step of this evolutionary process. Our analysis shows, perhaps counter-intuitively, that the allele-frequency change caused by selection during any demographic time step is tied to the entire evolutionary process of interest and hence cannot be studied in isolation. We also show how to correctly calculate the changes due to selection and class transmission by appropriately weighting the distribution of classes of individuals. In doing so, we provide a detailed and biologically meaningful definition of a reproductive value, which has been used before to describe weighted allele-frequency change, but that was generally not connected back to the (arithmetic) allele frequency observed in a population (e.g., Grafen, 2015, Lion, 2018, Priklopil and Lehmann, 2020, Rousset, 2004, Taylor, 1990). We then provide a representation of fitness summarizing the effect of selection in the multiple time-step evolutionary process, and suggest the following definition for the effect of selection attributed to a specific demographic time step of interest: *it is the frequency of alleles measured at the end of the observed evolutionary process that descend under the non-selective process of class transmission from all additional offspring produced over the time step of interest by parents having the allele in each class, as compared to the average parent within each class.*

Our analysis proceed in two main steps. In order to motivate the formalization of allele-frequency change over an evolutionary process spanning multiple demographic time steps, we first consider the homogeneous population case, which still widely serves as the baseline model to understand evolutionary concepts, e.g., the review of Queller [2017]. Second, we turn to the analysis of class-structured populations model, which forces us to reconsider some of the intuition gained from the homogeneous case. Here, we formalize the force of selection and class transmission as an allele-frequency change over a single and multiple time

steps. We show how to summarize the overall effect of selection and class transmission by way of a representation of geometric mean fitness. We then connect our results to earlier work on asymptotic evolutionary dynamics, in particular invasion fitness and quantitative trait evolution under weak selection.

Framing the Question

Homogeneous Population Model and Single Generation Change

Let us start by considering a spatially and physiologically homogeneous population of haploid individuals, each of which is characterized, at some locus of interest, by one of a finite number of alleles that segregate in the population. We assume that reproduction occurs at discrete demographic time steps, that there are no mutations, and that the population is large enough to ignore the effect of genetic drift. This is the baseline one-locus population genetic textbook model underlying the treatment of natural selection (e.g., Ewens, 2004, Gillespie, 1991, Nagylaki, 1992). The state of the population under this model is fully characterized by the vector $\mathbf{n}_t$ collecting the elements $n_t(i)$, which gives the number of individuals carrying allele i at time t. This number satisfies the recursion

$$n_{t+1}(i) = w_t(i)n_t(i), \tag{1}$$

where we use the shorthand notation $w_t(i) = w_t(i, \mathbf{n}_t)$ to represent the *individual fitness* of a carrier of allele i [Nagylaki, 1992, eq. 2.2]. Individual fitness $w_t(\cdot)$ is defined as the expected number of settled 'offspring' at $t+1$ produced by a single 'parent' at t including the surviving self (hence quotation marks), and thus gives the number of gene copies at time $t+1$ descending from that parent. Because individual fitness may depend in an arbitrary way on the population state $\mathbf{n}_t$, the model allows for arbitrarily complicated frequency- and density-dependent interactions between individuals and because it is indexed by t it allows for arbitrary extrinsic environmental fluctuations affecting survival and reproduction.

Since we are interested in changes in the relative number of alleles, we re-write eq. (1) by using the total population size $n_t = \sum_i n_t(i)$ and the frequency $p_t(i) = n_t(i)/n_t$ of allele i at time t. From this and eq. (1), the total population size satisfies the recursion $n_{t+1} = \bar{w}_t n_t$, where $\bar{w}_t = \sum_i w_t(i)p_t(i)$ is the average individual fitness (i.e., the fitness of an *average* individual where the average is taken over alleles it can carry) and the frequency of i satisfies the recursion $p_{t+1}(i) = p_t(i)w_t(i)/\bar{w}_t$ (Appendix A1). The change in frequency $\Delta p_t(i) = p_{t+1}(i) - p_t(i)$ over the single time step $[t, t+1]$, which we refer to as "generation" t, is then

$$\Delta p_t(i) = \frac{1}{n_{t+1}}\left(w_t(i) - \bar{w}_t\right) n_t(i) = \left(\frac{w_t(i) - \bar{w}_t}{\bar{w}_t}\right) p_t(i). \tag{2}$$

The first equality makes the interpretation of the cause of allele-frequency change in genera-

tion t explicit. Since $w_t(i) - \bar{w}_t$ gives the additional number of offspring descending from a single allele i carrier compared to an average individual from the population, the process is said to be selective. In homogeneous populations, natural selection acting on i allele is thus defined as being proportional to the difference between the total number $w_t(i)$ of gene copies descending from a single individual i and the number of gene copies $\bar{w}_t$ descending from that individual if it were assigned the population-wide average fitness $\bar{w}_t$. The change $\Delta p_t(i)$ is then the frequency of alleles measured at $t+1$ that descend from the additional individuals produced due to natural selection by all i carriers at generation t. We can thus say allele i is favored by selection in generation t whenever $w_t(i)/\bar{w}_t$ exceeds one, i.e., $w_t(i)/\bar{w}_t > 1$. If all individuals in the population were to be assigned fitness $\bar{w}_t$, then reproduction and survival would still unfold, but the evolutionary process is non-selective (neutral). The second equality in eq. (2) is the standard representation of allele-frequency change under this model (Gillespie, 1991, eq. 4.1, Nagylaki, 1992, eq. 2.8).

The Multigenerational Process and the Question

Let us now suppose that the evolutionary process runs over multiple generations between some initial time t_0 and final time t_f. We denote this time-interval with $\mathcal{T} = [t_0, t_\mathrm{f}]$, and suppose it contains the generation t discussed in eq. (2). Then, and as motivated in the section Introduction, the aim is to ascertain how much of the total allele-frequency change

$$\Delta p_{\mathcal{T}}(i) = p_{t_\mathrm{f}}(i) - p_{t_0}(i) \tag{3}$$

that has occurred during $\mathcal{T}$ is due to selection, and how much of the total change due to selection can be attributed to generation t. We denote the total change due to selection with $\Delta p^{\mathrm{sel}}_{\mathcal{T}}(i)$ and the change attributed to generation t with $\Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i)$ such that

$$\Delta p^{\mathrm{sel}}_{\mathcal{T}}(i) = \sum_{t=t_0}^{t_\mathrm{f}-1} \Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i). \tag{4}$$

Because this total change is necessarily assessed at the final time t_f, and the individuals observed at t_f must consist of descendants of the selected offspring in all previous generations, we define $\Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i)$ as the frequency of individuals measured at t_f that descend under a non-selective process from all the offspring measured at $t+1$ that were produced due to selection during $[t, t+1]$. In other words, $\Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i)$ is the fraction of the total frequency change due to natural selection that can be ascribed to the effect (force) of selection at generation t, conditional on the evolutionary process running over the entire time-interval $\mathcal{T}$. We confirm in section Selection and Class Transmission in a Multigenerational Process that this is indeed to correct way to think of the effect of selection in a multigenerational context.

In a homogeneous population finding $\Delta p^{\mathrm{sel}}_{\mathcal{T}}(i)$ in eq. (4) is straightforward because only selection alters allele frequencies (eq. 2), and hence the total measured change $\Delta p_{\mathcal{T}}(i)$ must

all be due to selection. That is, we have $\Delta p_{\mathcal{T}}(i) = \Delta p^{\text{sel}}_{\mathcal{T}}(i)$ and

$$\Delta p^{\text{sel}}_{t|\mathcal{T}}(i) = \left(\frac{w_t(i) - \bar{w}_t}{\bar{w}_t} \right) p_t(i). \tag{5}$$

It is thus useful to realize that the right hand side has two interpretations. First, as the *asymptotic contribution (or effect) of selection* in generation t, where asymptotic refers to the fact that this fraction is assessed at the final time t_{f} and as the *active contribution (or effect) of selection* in generation t as this is assessed as the evolutionary process unfolds at time $t+1$ (eq. 2; Figure 1A). In the homogeneous population model, the individuals assessed at time t_{f} thus descend under the non-selected process from individuals where all have fitness $\bar{w}_t$. The question is how does one calculate such contributions in the class-structured case? As it turns out, the answer is not straightforward.

Class-Structured Population Model

Let us now consider the situation where individuals are heterogeneous so that each individual belongs to one of a finite number of classes (e.g., age, stage) and can possibly transition between the classes, but hold all others assumptions of section Framing the Question the same. Then, the state of the population can be fully characterized by the vector $\mathbf{n}_t$ collecting elements of the form $n_t(a,i)$, which stands for the number of individuals in class a with allele i at time t. This number satisfies the recursion

$$n_{t+1}(a,i) = \sum_b w_t(a \leftarrow b, i) n_t(b,i), \tag{6}$$

where $w_t(a \leftarrow b, i) = w_t(a, b, i, \mathbf{n}_t)$ gives the expected number of offspring of class a produced over the time step $[t, t+1]$ by a single parent in class b carrying allele i. We sum over all classes in eq. (6) because parents in any class may possibly produce offspring of any other class either via reproduction or class transition, e.g., survival, maturation or physiological development.

We now extend the notations introduced for homogeneous populations to be able to consider change of allele frequency in a heterogeneous population (see Table for a summary of all notations). First, we denote by $n_t(i) = \sum_a n_t(a,i)$ the total number of individuals carrying allele i, by $n_t(a) = \sum_i n_t(a,i)$ the total number of individuals in class a and by $n_t = \sum_{a,i} n_t(a,i)$ the total number of individuals in the population. From these quantities, $p_t(i) = n_t(i)/n_t$ is the frequency of allele i, $p_t(a) = n_t(a)/n_t$ is the frequency of class a individuals, $p_t(a \mid i) = n_t(a,i)/n_t(i)$ is the frequency of class a individuals amongst those with allele i and $p_t(i \mid a) = n_t(a,i)/n_t(a)$ is the frequency of allele i within class a. As in the homogeneous population case, we have that $n_{t+1} = \bar{w}_t n_t$, where $\bar{w}_t = \sum_{a,b} \bar{w}_t(a \leftarrow b) p_t(b)$ is the average fitness, which is here expressed in terms of the class-specific average fitness $\bar{w}_t(a \leftarrow b) = \sum_i w_t(a \leftarrow b, i) p_t(i \mid b)$ over alleles. The average fitness of allele i itself is

$\bar{w}_t(i) = \sum_{a,b} w_t(a \leftarrow b, i) p_t(b \mid i)$ and the recursion for allele i is $p_{t+1}(i) = p_t(i)\bar{w}_t(i)/\bar{w}_t$. The recursions for total population size n_t and allele frequency $p_t(i)$ coupled with the recursion for genetic structure $p_t(a \mid i)$ are then equivalent to eq. (6) (Appendix A2).

Selection and Class Transmission in a Single Generation

Allele-frequency change $\Delta p_t(i)$ over a single time step $[t, t+1]$ in a class-structured population can be expressed analogously to the homogeneous population as in eq. (2), but where we need to substitute the fitness functions as defined above for class-structured populations, namely replace $w_t(i)$ by $\bar{w}_t(i)$ and redefine $\bar{w}_t$. Equation (2) then says that an increase in allele frequency occurs whenever $\bar{w}_t(i)/\bar{w}_t$ exceeds one, i.e., $\bar{w}_t(i)/\bar{w}_t > 1$. In contrast to the homogeneous population model, however, it would be wrong to conclude that for class-structured populations $\bar{w}_t(i)/\bar{w}_t > 1$ implies the allele i is favoured by natural selection. This can be understood by using the partitioning over $[t, t+1]$,

$$\Delta p_t(i) = \Delta p_t^{\text{sel}}(i) + \Delta p_t^{\text{ct}}(i), \tag{7a}$$

where

$$\Delta p_t^{\text{sel}}(i) = \frac{1}{n_{t+1}} \sum_a \sum_b \Big[w_t(a \leftarrow b, i) - \bar{w}_t(a \leftarrow b) \Big] p_t(b \mid i) n_t(i) = \left(\frac{\bar{w}_t(i) - \bar{\bar{w}}_t(i)}{\bar{w}_t} \right) p_t(i) \tag{7b}$$

and

$$\Delta p_t^{\text{ct}}(i) = \frac{1}{n_{t+1}} \sum_a \sum_b \Big[\bar{w}_t(a \leftarrow b) - \frac{1}{n_{\mathcal{C}}} \bar{w}_t \Big] p_t(b \mid i) n_t(i) = \left(\frac{\bar{\bar{w}}_t(i) - \bar{w}_t}{\bar{w}_t} \right) p_t(i), \tag{7c}$$

where $\bar{\bar{w}}_t(i) = \sum_{a,b} \bar{w}_t(a \leftarrow b) p_t(b \mid i)$ gives the average fitness of an i carrier if it were to survive and reproduce as an average individual in a class (Appendix A2.1). Because $w_t(a \leftarrow b, i) - \bar{w}_t(a \leftarrow b)$ in eq. (7b) gives the additional number of gene copies in class a at $t+1$ descending from a single individual of class b carrying allele i at t compared to the number of gene copies descending from an average individual in that class, $\Delta p_t^{\text{sel}}(i)$ gives the allele-frequency change caused by selection over the time step $[t, t+1]$ measured at $t+1$ (and conditioning on the state of the population at t). Because the average fitness $\bar{w}_t$ is always positive, we get from the second equality in eq. (7b) that selection favors an increase of allele i whenever $\bar{w}_t(i)/\bar{\bar{w}}_t(i)$ is greater than one, i.e., $\bar{w}_t(i)/\bar{\bar{w}}_t(i) > 1$. On the other hand, since $\bar{w}_t(a \leftarrow b) - \bar{w}_t/n_{\mathcal{C}}$ in eq. (7c) gives the additional number of gene copies in class a at $t+1$ descending from an average individual of class b as compared to an average individual in the population across classes and alleles, $\Delta p_t^{\text{ct}}(i)$ gives the allele-frequency change caused by class transmission over the time step $[t, t+1]$ measured at $t+1$ (and conditioning on the state of the population at t). The process of class transmission thus reflects the change in allele frequency due to differential reproduction caused by fitness differences between classes, and $\bar{\bar{w}}_t(i)/\bar{w}_t > 1$ implies a positive contribution of class transmission to allele-frequency change, which occurs regardless of whether individuals within classes differ and thus have

heritable differences in fitness. We can indeed confirm that whenever alleles do not cause any differences in fitness (alleles are neutral), that is, whenever $w_t(a \leftarrow b, i) = w_t(a \leftarrow b, j)$ for all i and j, then the term for selection (7b) is 0 and the process is said to be non-selective. Yet the term for class transmission (7c) can still alter allele allele frequency whenever $w_t(a \leftarrow b, i) \neq \bar{w}_t$ for at least some a, b. Note that a partitioning conceptually equivalent to eq. (7) for phenotypic change was derived by Lion [2018, eq. 2] from the Price equation.

Selection and Class Transmission in a Multigenerational Process

We just provided a single generation partitioning of allele-frequency change. Now, the aim is to find a partitioning for the evolutionary process running over multiple generations $\mathcal{T}$, and because both selection and class transmission alter allele frequencies, we write the partitioning as

$$\Delta p_{\mathcal{T}}(i) = \sum_{t=t_0}^{t_f-1} \Delta p_{t|\mathcal{T}}(i) \quad \text{with} \quad \Delta p_{t|\mathcal{T}}(i) = \Delta p^{\text{sel}}_{t|\mathcal{T}}(i) + \Delta p^{\text{ct}}_{t|\mathcal{T}}(i), \tag{8}$$

where $\Delta p^{\text{sel}}_{t|\mathcal{T}}(i)$ and $\Delta p^{\text{ct}}_{t|\mathcal{T}}(i)$ are, respectively, the fractions of the total allele-frequency change that are attributed to selection and class transmission occurring in generation t. Recall from the partitioning of the homogeneous population model (eq. 4) that the asymptotic effect of selection $\Delta p^{\text{sel}}_{t|\mathcal{T}}(i)$ was more precisely defined as the frequency of individuals measured at t_f that descend under a non-selective process from all the offspring measured at $t+1$ that were produced due to selection during $[t, t+1]$. In contrast to a homogeneous population, however, in a heterogeneous population the non-selective process includes class transmission that does alter allele frequencies (eq. 7). Therefore, the asymptotic $\Delta p^{\text{sel}}_{t|\mathcal{T}}(i)$ and the active $\Delta p^{\text{sel}}_{t}(i)$ effects can no longer be equal. Moreover, it is not immediately obvious how to define the asymptotic effect of class transmission $\Delta p^{\text{ct}}_{t|\mathcal{T}}(i)$. Equations (7) are thus not useful in the decomposition given in eq. (8), and we need to re-consider the change of allele frequency over multiple time steps.

Disentangling Selection from Class Transmission

Our objective here is to find an expression for the contribution $\Delta p^{\text{sel}}_{t|\mathcal{T}}(i)$ in eq. (8). For this, we need to introduce additional notation to be able to describe more explicitly the non-selective process already alluded to above and under which every allele in a class is assigned the class-specific fitness of an average individual (gene) in that class.

Non-selective process. To that end, we define $n^{\circ}_t(\cdot)$ and $p^{\circ}_t(\cdot)$ as the state variables at t that underwent the non-selective process from time t_0 onward. In particular, $n^{\circ}_t(a, i)$ is interpreted as the number of a, i individuals at time t when the population process is non-selective between

$[t_0, t]$. It satisfies the recursion

$$n^{\circ}_{t+1}(a,i) = \sum_b \bar{w}_t(b \leftarrow a) n^{\circ}_t(b,i), \tag{9}$$

with initial condition $n^{\circ}_{t_0}(a,i) = n_{t_0}(a,i)$ for all a and i. Formally, this is the adjoint equation to the backward in time process

$$v_t(a) = \sum_b v_{t+1}(b) \bar{w}_t(b \leftarrow a) \tag{10}$$

with the final condition $v_{t_\mathrm{f}}(a) = 1$ for all a (Box A). We can therefore interpret $v_t(a)$ as the *number of individuals alive at the final time t_f that under a non-selective process between $[t, t_f]$ descend from a single individual a alive at time t*. This interpretation is valid for any allele under consideration. We call $v_t(a)$ the reproductive value of an (average) individual of class a (average is taken over alleles) and it is a representation of the classic notion of individual reproductive value [Fisher, 1930, Grafen, 2006, Leslie, 1948, Lessard and Soares, 2018, Lion, 2018, Taylor, 1990, Tuljapurkar, 1989]. We denote by $\bar{v}_t(i) = \sum_a v_t(a) p_t(a \mid i)$ the average reproductive value of a carrier of allele i and also define a population-wide average reproductive value $\bar{v}_t$ from $\bar{v}_t = \bar{v}_{t+1}\bar{w}_t$ which is an adjoint equation to the population dynamic process $n_{t+1} = \bar{w}_t n_t$. The interpretation of $\bar{v}_t$ is then the number of individuals at t_f that descend under population dynamics from an average individual in the population at time t (from which one obtains the useful relation $\bar{v}_t = \prod_{t=t_0}^{t_\mathrm{f}-1} \bar{w}_t$).

Disentanglement. We can now use reproductive values to represent the contribution of selection attributed to generation t as

$$\Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i) = \frac{1}{n_{t_\mathrm{f}}} \sum_a \sum_b v_{t+1}(a) \Big[w_t(a \leftarrow b, i) - \bar{w}_t(a \leftarrow b) \Big] p_t(b \mid i) n_t(i) = \left(\frac{\bar{w}^{\mathrm{v}}_t(i) - \bar{v}_t(i)}{\bar{v}_t} \right) p_t(i), \tag{11}$$

where $\bar{w}^{\mathrm{v}}_t(i) = \sum_a \sum_b v_{t+1}(a) w_t(a \leftarrow b, i) p_t(b \mid i)$ is the *asymptotic (or reproductive-value weighted) average individual fitness* giving the number of individuals at t_f that descend under the non-selective processes from all the offspring produced by a single individual i at t (Appendix A2.2). Therefore, because $w_t(a \leftarrow b, i) - \bar{w}_t(a \leftarrow b)$ gives the number of individuals in class a at $t+1$ descending by selection from a single class b individual with allele i at t, each of which has $v_{t+1}(a)$ descendants at t_f under the non-selective process (eq. 10), the expression in the sum gives the frequency of individuals at t_f that descend under the non-selective process from all offspring a produced by a single parent b alive at t. And by summing over all classes of offspring and parents and by dividing by the total population size n_{t_f} we obtain the desired interpretation of $\Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i)$ required for the partitioning of total allele-frequency change (eq. 8). One can thus see $v_{t+1}(a)$ as a scaling factor that projects the event of selection during $[t, t+1]$ to the final time t_f under a non-selective process between $t+1$ and t_f (Figure 1B). Because $\bar{v}_t$ is always positive, selection favours allele i in a multigenerational process at t whenever

$\bar{w}_t^{\mathrm{v}}(i)/\bar{v}_t(i) > 1$, where $\bar{w}_t^{\mathrm{v}}(i)/\bar{v}_t(i)$ can be interpreted as the relative number of individuals at t_{f} that descend under the non-selective process from all offspring produced by a single individual i at t, relative to the number of individuals at time t_{f} that would descend under a non-selective process only (from a single i at t). The total allele-frequency change due to selection over $\mathcal{T}$ can then be expressed as $\Delta p_{\mathcal{T}}^{\mathrm{sel}}(i) = \sum_{t=t_0}^{t_{\mathrm{f}}-1} \Delta p_{t|\mathcal{T}}^{\mathrm{sel}}(i)$.

The next task is to find an expression for the contribution $\Delta p_{t|\mathcal{T}}^{\mathrm{ct}}(i)$ in eq. (8). Because $\Delta p_{t|\mathcal{T}}^{\mathrm{ct}}(i)$ must complement the change in frequency caused by selection $\Delta p_{t|\mathcal{T}}^{\mathrm{sel}}(i)$ as partitioned in eq. (8), we are only interested in parent individuals at t that themselves come from a lineage of non-selected individuals, otherwise the fraction $\Delta p_{t|\mathcal{T}}^{\mathrm{ct}}(i)$ would also count offspring produced by parents that were produced due to selection. The change due to class transmission that is attributed to the generation t is then

$$\Delta p_{t|\mathcal{T}}^{\mathrm{ct}}(i) = \frac{1}{n_{t+1}} \sum_a \sum_b \left[\bar{w}_t(a \leftarrow b) - \frac{1}{n_{\mathcal{C}}} \bar{w}_t \right] p_t^{\circ}(b \mid i) n_t^{\circ}(i) = \left(\frac{\bar{w}_t^{\circ}(i) - \bar{w}_t}{\bar{w}_t} \right) r_t^{\circ}(i) p_t(i), \quad (12)$$

where $\bar{w}_t^{\circ}(i) = \sum_{a,b} \bar{w}_t(a \leftarrow b) p_t^{\circ}(b \mid i)$ is the fitness of i if it were to reproduce as an average individual in the class at time t and where the parent i itself comes from a lineage of non-selected individuals during $[t_0, t]$, in which case we refer to it as the non-selected parent. Moreover, $p_t^{\circ}(b \mid i)$ satisfies $p_t^{\circ}(b \mid i) n_t^{\circ}(i) = n_t^{\circ}(b, i)$ and $r_t^{\circ}(i) = n_t^{\circ}(i)/n_t(i)$ is the fraction of individuals i that descend from a lineage of individuals that have undergone only a non-selective process between $[t_0, t]$, allowing us to condition on a randomly sampled allele i (whether selected or not) in the second equality in eq. (12) (Appendix A2.2). Indeed, because $\bar{w}_t^{\circ}(i) - \bar{w}_t$ gives the number of offspring at $t+1$ due to class transmission by a single individual at t that itself was produced under the non-selective process (compare with eq. 7c), then multiplying this with the number of non-selected parents $p_t^{\circ}(b \mid i) n_t^{\circ}(i)$ and divide by the total population size, we get $\Delta p_{t|\mathcal{T}}^{\mathrm{ct}}(i)$ required for the partitioning of total allele-frequency change (eq. 8). Note that we do not weight the offspring at $t+1$ with reproductive values because we would then also count events of class transmission at later generations and not only at t of interest. Now, because $\bar{w}_t$ is always positive, class transmission favours allele i in a multigenerational process in generation t whenever $\bar{w}_t^{\circ}(i)/\bar{w}_t > 1$, where $\bar{w}_t^{\circ}(i)/\bar{w}_t$ gives the number of offspring at $t+1$ produced due to the non-selective processes $\bar{w}_t^{\circ}(i)$ (see eq. 9) relative to the number of offspring produced due to the non-selective process of population dynamics only $\bar{w}_t$ by a single non-selected parent i at t. Because population dynamics does not alter allele frequencies, the above interpretation of eq. (12) is equal to the frequency of individuals measured at t_{f} that descend under the non-selective process of population dynamics from all offspring measured at $t+1$ that were produced due to class transmission during $[t, t+1]$ by a single non-selected parent i at t (Figure 1C). This is the *asymptotic* interpretation of class transmission that is attributed to a generation t in a multigenerational evolutionary process over $\mathcal{T}$.

To summarize, we have produced a recursion for allele-frequency change in a multigener-

ational process (eq. 8), where such change can be partitioned into generation specific contributions caused by natural selection (eq. 11) and class transmission (eq. 12). These calculations are consistent with the partitioning of the active effects of selection and class transmission (since the recursions in eq. 7 are recovered by setting $t = t_0$ and $t+1 = t_\mathrm{f}$ in eqs. 8 and 11-12). Note that the right-hand side of eq. (11) also gives the change in reproductive value weighted allele frequency (see eqs. (A17)–(A19)) and is therefore conceptually equivalent to eq. (7) of Lion [2018] for the phenotypic change in a panmictic population and to eq. (69) of Priklopil and Lehmann [2021] for allele-frequency change in a spatially structured population. At this stage, it seems natural to ask whether one can summarize the action of natural selection over the multigenerational process by a single number – a representation of mean fitness – that would predict whether the allele frequency increases or decreases as a result of selection?

Mean fitness in a multigenerational evolutionary process

Geometric mean fitness

The representation of mean fitness is well established for a homogeneous population (e.g., Gillespie, 1991) where the effect natural selection over $\mathcal{T}$ can be summarized by the geometric growth ratio defined as

$$\overline{W}_{\mathcal{T}}(i) = \left(\prod_{t=t_0}^{t_\mathrm{f}-1} W_{t|\mathcal{T}}(i)\right)^{1/(t_\mathrm{f}-t_0)} \quad \text{with} \quad W_{t|\mathcal{T}}(i) = \frac{\bar{w}_t(i)}{\bar{w}_t}, \tag{13}$$

where $W_{t|\mathcal{T}}(i)$ is the relative fitness attributed to selection in generation t (Appendix A3). Therefore $W_{t|\mathcal{T}}(i) > 1$ implies that selection favours allele i in generation t and $\overline{W}_{\mathcal{T}}(i) > 1$ implies that selection favours allele i over the entire interval $\mathcal{T}$.

While eq. (13) also does give the correct geometric growth ratio of allele i for class-structured populations, $W_{t|\mathcal{T}}(i)$ in eq. (13) is not the relative fitness attributed to generation t nor does eq. (13) summarize the effect of selection over $\mathcal{T}$. In order to correctly summarize this effect, the geometric mean needs to be written as $\overline{W}_{\mathcal{T}}(i) = \overline{W}^{\mathrm{sel}}_{\mathcal{T}}(i)\overline{W}^{\mathrm{ct}}_{\mathcal{T}}(i)$, where

$$\overline{W}^{\mathrm{sel}}_{\mathcal{T}}(i) = \left(\prod_{t=t_0}^{t_\mathrm{f}-1} W^{\mathrm{sel}}_{t|\mathcal{T}}(i)\right)^{1/(t_\mathrm{f}-t_0)} \quad \text{with} \quad W^{\mathrm{sel}}_{t|\mathcal{T}}(i) = \frac{\bar{w}^{\mathrm{y}}_t(i)}{\bar{v}_t(i)} \tag{14}$$

and

$$\overline{W}^{\mathrm{ct}}_{\mathcal{T}}(i) = \left(\prod_{t=t_0}^{t_\mathrm{f}-1} W^{\mathrm{ct}}_{t|\mathcal{T}}(i)\right)^{1/(t_\mathrm{f}-t_0)} \quad \text{with} \quad W^{\mathrm{ct}}_{t|\mathcal{T}}(i) = \frac{\bar{w}^{\circ}_t(i)}{\bar{w}_t} \tag{15}$$

(Appendix A3). Here, $W^{\mathrm{sel}}_{t|\mathcal{T}}(i)$ is the relative fitness of a randomly sampled allele i at t that is attributed to selection at t, and $W^{\mathrm{ct}}_{t|\mathcal{T}}(i)$ is the relative fitness of a randomly sampled non-selected i at t that is attributed to class transmission at t. Conditioning on a randomly sampled allele i at t (whether selected or not), this relative fitness is $W^{\mathrm{ct}}_{t|\mathcal{T}}(i)r^{\circ}_t(i)$ (Appendix A3, and

see also eq. 12). Whenever $W^{\text{sel}}_{t|\mathcal{T}}(i) > 1$, selection thus favours allele i in generation t and whenever $W^{\text{ct}}_{t|\mathcal{T}}(i) > 1$ class transmission favours allele i in generation t (see also section Disentangling Selection from Class Transmission). Over the entire time-interval $\mathcal{T}$, selection thus favours allele i whenever $\overline{W}^{\text{sel}}_{\mathcal{T}}(i) > 1$, while class transmission favours allele i whenever $\overline{W}^{\text{ct}}_{\mathcal{T}}(i) > 1$. Finally, note that one can express $W^{\text{sel}}_{\mathcal{T}}(i)$ also in terms of the $\bar{w}_t(i)$'s but then the generation specific partitioning is incorrect, see Appendix A3.2.

We have thus obtained a partitioning of the total geometric mean fitness into the means $\overline{W}^{\text{sel}}_{\mathcal{T}}(i)$ and $\overline{W}^{\text{ct}}_{\mathcal{T}}(i)$ summarizing the multigenerational contribution of selection and class transmission for allele-frequency change, respectively. Importantly, it is not a conclusion that if the allele is favored by evolution, $\overline{W}_{\mathcal{T}}(i) > 1$, it is also favored by selection, $\overline{W}^{\text{sel}}_{\mathcal{T}}(i) > 1$, nor vice versa. This suggests that one should worry about the effect of class transmission on the evolutionary process if one is interested in understanding the exact effect of natural selection in class-structured populations. Yet such worry is essentially absent in the theoretical literature, which routinely uses representations of mean fitness attributing such effects entirely to selection (i.e., much of the theoretical literature on adaptation).

Asymptotic Evolutionary Process

The partitioning of the recursion for a multigenerational process (eq. 8) as well as the partitioning of the geometric mean (eqs. 14-15) actually turn out to be fully consistent and supporting previous approaches on long-term (asymptotic) allele-frequency change. We now connect to this literature by discussing the invasion fitness of a rare allele and the fast-slow evolutionary trajectory of weak selection approximations for quantitative trait evolution.

Invasion Fitness. Recall that the invasion exponent of allele i is defined (under some technical conditions) as $\rho = \lim_{t_{\text{f}}\to\infty} 1/(t_{\text{f}} - t_0) \ln\left(n_{t_{\text{f}}}(i)/n_{t_0}(i)\right)$ giving the asymptotic exponential rate of growth of allele i, which has been widely used as a summary measure of selection since at least Fisher [1930] and is often called the Malthusian growth rate. Suppose that all alleles but i coexist at some asymptotically stable equilibrium, which we call the resident equilibrium (we hastily note that the assumption of an equilibrium is not necessary as the calculations of the invasion exponent carry over to more complex population dynamics e.g. Ferrière and Gatto, 1995, Metz et al., 1992). Then, the invasion fitness for allele i, defined as $\hat{\bar{W}}(i) = e^{\rho}$, and giving the expected number of offspring produced asymptotically per generation per parent i, can be expressed as

$$\hat{\bar{W}}(i) = \frac{\sum_{a,b} \hat{q}(a)\hat{w}(a \leftarrow b, i)\hat{p}(b \mid i)}{\sum_a \hat{q}(a)\hat{p}(a \mid i)} = \frac{\hat{\bar{w}}^q(i)}{\hat{\bar{q}}(i)} \tag{16}$$

(Appendix A4.1). Here, $\hat{q}(a)$ is an arbitrary weight of an individual in class a evaluated at the resident equilibrium (all hats hereafter indicate evaluation at an equilibrium), $\hat{\bar{w}}^q(i) = \sum_{a,b} \hat{q}(a)\hat{\bar{w}}(a \leftarrow b)\hat{p}(b \mid i)$ is an arbitrarily weighted fitness of i and $\hat{\bar{q}}(i) = \sum_a \hat{q}(a)\hat{p}(a \mid i)$.

The fact that eq. (16) is equal for arbitrary weights implies that only selection is in play in calculations of invasion fitness. Indeed, on one hand, by setting $\hat{q}(a) = \hat{v}(a)$ for all a, the invasion fitness can be represented as the asymptotic geometric mean for selection $\hat{\hat{W}}(i) = \lim_{t_f \to \infty} \overline{W}^{\text{sel}}_{\mathcal{T}}(i) = \hat{\hat{w}}^{\text{v}}(i)/\hat{\hat{v}}(i)$ (Appendix A4.1). On the other hand, by setting $\hat{q}(a) = 1$ for all a, the invasion fitness can be represented as the asymptotic geometric mean fitness $\hat{\hat{W}}(i) = \lim_{t_f \to \infty} \overline{W}_{\mathcal{T}}(i) = \hat{\hat{w}}(i)$ (Appendix A4.1). This confirms that the asymptotic evolutionary trajectory of a rare allele i is fully determined by a measure of fitness where only selection is in play. Or even more precisely, upon the introduction of the allele i the evolutionary trajectory is subject to both class transmission and selection but then converges to the leading eigenvector with elements $\hat{p}(a \mid i)$, along which class transmission vanishes and the rate of growth is given by the invasion fitness determined by selection only (Appendix A4.1). We note that the two representations of invasion fitness, $\hat{\hat{w}}(i)$ and $\hat{\hat{w}}^{\text{v}}(i)/\hat{\hat{v}}(i)$, extend to spatially structured populations and $\hat{\hat{w}}^{\text{v}}(i)/\hat{\hat{v}}(i)$ forms the basis of the inclusive fitness representation of invasion fitness [Lehmann and Rousset, 2020, Lehmann et al., 2016].

Quantitative Traits under Weak Selection. Consider now a population with two alleles only, say allele i and its ancestral allele j from which it was derived by mutation, and suppose that the corresponding locus controls the expression of some quantitative trait (the assumption of two alleles is not necessary). Suppose further that the phenotypic expression is class-specific so that the phenotypic profile of i can be written as $\mathbf{z}(i) = \mathbf{z}(j) + \delta\boldsymbol{\eta}$, where $\mathbf{z}(k)$ is the phenotypic profile of allele $k = i, j$, namely, the vector collecting elements of the form $z(a, k)$, which gives the phenotype of an individual of class a bearing allele k. The vector $\boldsymbol{\eta}$ collects the class specific deviations $\eta(a)$ and δ controls the magnitude of the effect of the mutation. Assuming the fitness functions to be continuous, a small parameter δ implies i and j having closely similar phenotypes, and hence having closely similar fitness functions, resulting in weak selection (so-called δ-weak selection Wild and Traulsen, 2007). This is the realm – more or less explicitly stated – of the vast literature on quantitative trait game theory, adaptive dynamics and kin selection (e.g. Geritz et al., 1998, Rousset, 2004, Taper and Case, 1992, Taylor and Frank, 1996) and for this case, the recursion for allele-frequency change in a multigenerational process can be written as

$$\Delta p_{t|\mathcal{T}}(i) = \Delta p^{\text{ct}}_{t|\mathcal{T}}(i)\Big|_{\delta=0} + \delta \frac{\mathrm{d}}{\mathrm{d}\delta} \Delta p^{\text{sel}}_{t|\mathcal{T}}(i)\Big|_{\delta=0} + \text{h.o.t.} \tag{17a}$$

where h.o.t. refers to terms of order δ^2 and where

$$\Delta p^{\text{ct}}_{t|\mathcal{T}}(i)\Big|_{\delta=0} = \frac{1}{n_{t+1}} \sum_a \sum_b w_t(a \leftarrow b, i \mid \delta = 0)\, [p^{\circ}_t(b \mid i) - p_t(b)]\, n^{\circ}_t(i), \tag{17b}$$

and

$$\frac{\mathrm{d}}{\mathrm{d}\delta} \Delta p^{\text{sel}}_{t|\mathcal{T}}(i)\Big|_{\delta=0} = (1 - p_t(i)) p_t(i) \sum_a \sum_b \hat{v}(a) \partial_{z(b,i)} \hat{w}(a \leftarrow b, i) \eta(b) \hat{p}(b) + \text{h.o.t.}. \tag{17c}$$

Here, $w_t(a \leftarrow b, i \mid \delta = 0)$ is the frequency-independent representation of class-specific fitness of an allele i in a population without selection ($\delta = 0$), and where the partial derivative is taken with respect to the trait expression of the parent individual b, i and evaluated at an equilibrium as calculated for $\delta = 0$ (see below for further explanation).

Equation (17) says that the generation specific change in the (arithmetic) average allele frequency over $\mathcal{T}$ can be partitioned into fast changes (eq. 17b) governed purely by class transmission and slow changes (eq. 17c) governed purely by selection. More precisely, a process starting at time t_0 initially alters the allele frequency due to class transmission only (eq. 17b), with selection being negligible on allele-frequency change, until the genetic structure converges close to its quasi-equilibrium in finite time, after which class transmission becomes negligible and the allele frequency is governed only by selection (eq. 17c). The expression for the genetic structure at the quasi-equilibrium is given in Appendix A4.2, and note that in eq. (17c) we can use the unweighted $p_t(i)$ because at the quasi-equilibrium every average frequency is equal. Timescale separation arguments guarantee that one can substitute this quasi-equilibrium into eq. (17c) and the entire approximation (eq. 17) is valid for small but non-zero δ [for details on such arguments see Priklopil and Lehmann [2020]]. In other words, $\Delta p_{t|\mathcal{T}}(i) \approx \delta \frac{\mathrm{d}}{\mathrm{d}\delta} \Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i) \Big|_{\delta=0}$. This in turn implies that asymptotically the allele frequency either increases or decreases until the allele i either fixes in the population or goes extinct and this invasion implies substitution process applies to spatially structured populations as well [Priklopil and Lehmann, 2021]. Finally, we note that if one were to use, for instance, the partitioning given in eq. (7), the slow dynamics would depend on both terms $\Delta p^{\mathrm{ct}}_t(i)$ and $\Delta p^{\mathrm{sel}}_t(i)$ and hence a perturbation of $\Delta p^{\mathrm{ct}}_t(i)$ and consequently the genetic structure $\hat{p}(a \mid i)$ would have to be taken into account (Appendix A4.2). Indeed, in a multigenerational process the term $\Delta p^{\mathrm{ct}}_t(i)$ conflates the effect of class transmission and selection because it conditions on the population state at time t and hence counts also individuals whose ancestors underwent selection in the past, and confirms that it is the partitioning in eqs. (8) and (11)-(12) that correctly describe selection and class transmission in a multigenerational process.

Conclusion

We analyzed allele-frequency change in a class-structured population with the aim to decompose multigenerational change into contributions caused by natural selection and the non-selective process of class transmission. Three main messages arise from our analysis.

First, while the active contributions of selection and class transmission in a single generation t correctly give the frequency of individuals produced due to selection and class transmission when the frequency measurements are taken at consecutive time steps t and $t+1$ (eqs. 7b–7c), they should not be used as contributions in a multigenerational context. This is so because, on one hand, the contribution of class transmission as given in eq. (7c) contains the contributions of selection in the past, and hence in a multigenerational context it conflates the effect of class transmission with past effects of selection. On the other hand, the contribution

of selection as given in eq. (7b) fails to take into account that the frequency of descendants of the selected offspring undergo class transmission in the future, and hence does not take into account that non-heritable survival and reproduction differences affect the evolutionary process in class-structured populations. Hence, the one-generational allele-frequency change that is still widely used to describe the essence of selection (e.g., the review of Queller, 2017 p. 347) does not generally capture the essence of selection in a multigenerational context, yet all change leading to adaptation is certainly multigenerational.

Second, we provided the expressions for the contribution of selection and class transmission attributed to generation t in a multigenerational process spanning between some initial time t_0 and final time t_f (eqs. 11–12). We showed that these contributions must be defined in the context of the entire span of the evolutionary process under focus and requires a careful account of the notion of reproductive value for which we provided a biological definition in the context of a finite-time process. Namely, the reproductive value of an individual in class a in generation t is the number of its descendants measured at t_f under the non-selective process. With this, the contribution of selection attributed to generation t is the frequency of individuals measured at t_f that descend under the non-selective process from all offspring that were produced due to selection in generation t. We called this the asymptotic contribution of selection as it is measured at t_f and thus differs from the active contribution of selection in generation t that is assessed at time $t+1$ (eq. 7b). It may therefore be the case that while the active effect of selection contributes negatively to allele-frequency change, the asymptotic effect may be positive and vice versa.

Finally, we summarized the contributions of selection and class transmission over the entire evolutionary process in terms of geometric mean fitnesses (eqs. 14-15). The representation of fitness that correctly summarizes the multigenerational effect of selection is the relative reproductive-value weighted average individual fitness (eq. 14), which gives the mean number of offspring measured at the end of the multigenerational process that descend under the non-selective process from all offspring produced by all parents throughout the entire evolutionary process. While this fitness is generally not sufficient to predict the direction of evolution, it should do so over long time scales ($t_\mathrm{f} \to \infty$) where the class-transmission often vanishes. In particular, this is the case and underlies the widespread use of invasion fitness as a representation of fitness summarizing the effect of selection only, as well as the use of weak selection approximation for quantitative trait evolution (section Asymptotic Evolutionary Process). Overall, we hope to have given a satisfactory answer to the question posed in the introduction and clarified the operation of natural selection in heterogeneous populations.

A1 Allele-Frequency Change in Homogeneous Populations

First, we represent the recursion in eq. (1) by using the total population size $n_t = \sum_i n_t(i)$ and the allele frequency $p_t(i) = n_t(i)/n_t$. The recursion for the total population size is

$$n_{t+1} = \sum_i n_{t+1}(i) = \sum_i w_t(i) n_t(i) = \bar{w}_t n_t, \tag{A1}$$

where we used eq. (1) and $p_t(i) = n_t(i)/n_t$ and recall that $\bar{w}_t = \sum_j w_t(j) p_t(j)$ is the individual fitness of an average allele in the population. The recursion for allele frequency is then

$$p_{t+1}(i) = \frac{n_{t+1}(i)}{n_{t+1}} = \frac{w_t(i)}{\bar{w}_t} p_t(i), \tag{A2}$$

where we used eqs. (1) and (A1). The coupled system in eqs. (A1)-(A2) is equivalent to eq. (1).

Second, we derive the change in allele frequency over a single time step given in eq. (2) and simultaneously show that only selection contributes to this change. Because selection is broadly defined as a process involving the differential success of alleles it is useful to use the following partitioning of fitness of a carrier of allele i:

$$w_t(i) = 1 + \underbrace{w_t(i) - \bar{w}_t}_{\text{selection}} + \underbrace{\bar{w}_t - 1}_{\text{pop growth}} . \tag{A3}$$

Because $w_t(i) - \bar{w}_t$ gives the total number of copies of alleles i produced by a single carrier of i compared to the number of allele copies produced by an average individual from the population, we say that $w_t(i) - \bar{w}_t$ is the number of i copies at $t+1$ that were produced due to selection by a single individual i alive at time t. Furthermore, because $\bar{w}_t - 1$ gives the additional number of allele copies resulting from population-size change, we say this is the number of alleles i at $t+1$ that were produced due to the process of 'population growth' by a single i at t. The total number of alleles i at time $t+1$ can thus be written as

$$n_{t+1}(i) = n_t(i) + \Delta n_t^{\text{sel}}(i) + \Delta n_t^{\text{pg}}(i), \tag{A4}$$

with

$$\begin{aligned} \Delta n_t^{\text{sel}}(i) &= \big(w_t(i) - \bar{w}_t\big) n_t(i) \\ \Delta n_t^{\text{pg}}(i) &= \big(\bar{w}_t - 1\big) n_t(i) \end{aligned} \tag{A5}$$

giving the total number of additional individuals (allele copies) produced by all carriers of allele i at t due to selection and the process of population growth, respectively. Now, noting that

$$\begin{aligned} \Delta p_t(i) = p_{t+1}(i) - p_t(i) &= \frac{n_{t+1}(i)}{n_{t+1}} - \frac{n_t(i)}{n_t} = \frac{n_{t+1}(i)}{n_{t+1}} - \frac{\bar{w}_t n_t(i)}{\bar{w}_t n_t} = \frac{n_{t+1}(i)}{n_{t+1}} - \frac{\bar{w}_t n_t(i)}{n_{t+1}} \\ &= \frac{1}{n_{t+1}} \left(n_{t+1}(i) - \bar{w}_t n_t(i) \right), \end{aligned} \tag{A6}$$

and substituting eqs. (A4)-(A5) into the last term and simplifying, the change in frequency of allele i in generation t can be written as

$$\Delta p_t(i) = \frac{1}{n_{t+1}} \Delta n_t^{\text{sel}}(i) = \frac{1}{n_{t+1}} \big(w_t(i) - \bar{w}_t\big) n_t(i) = \left(\frac{w_t(i) - \bar{w}_t}{\bar{w}_t} \right) p_t(i), \tag{A7}$$

which is entirely due to selection (compare eqs. A5 and A7). In particular, the process of population growth does not affect allele-frequency change in homogeneous populations, a well-known population-genetic fact [Ewens, 2004, Nagylaki, 1992].

Third, we calculate the total change (eq. 4) in allele-frequency over $\mathcal{T} = [t_0, t_{\text{f}}]$. For this, we use the identity

$$p_{t+1|\mathcal{T}}(i) = p_{t|\mathcal{T}}(i) + \Delta p_{t|\mathcal{T}}^{\text{sel}}(i), \tag{A8}$$

which is valid for all t because only selection alters allele frequencies. We can therefore substitute $t_{\text{f}} = t + 1$ and recursive substitution generates

$$p_{t_{\text{f}}|\mathcal{T}}(i) = p_{t_0|\mathcal{T}}(i) + \sum_{t=t_0}^{t=t_{\text{f}}-1} \Delta p_{t|\mathcal{T}}^{\text{sel}}(i), \tag{A9}$$

and because $p_{t_{\text{f}}}(i) = p_{t_{\text{f}}|\mathcal{T}}(i)$ and $p_{t_0}(i) = p_{t_0|\mathcal{T}}(i)$, re-arrangement yields eq. (4).

A2 Allele-Frequency Change in Class-Structured Populations

Because $n_t(a, i) = p_t(a \mid i) p_t(i) n_t$, we can equivalently represent the recursion in eq. (6) in terms of allele frequencies $p_t(i)$, total population size n_t and the within class genetic structure $p_t(a \mid i)$. In the main text we gave the recursions for $p_t(i)$ and n_t and so the remaining task is to provide the recursion for $p_t(a \mid i)$. Immediately from the definition we get

$$p_{t+1}(a \mid i) = \frac{n_{t+1}(a, i)}{n_{t+1}(i)} = \frac{1}{\bar{w}_t(i)} \sum_b w_t(a \leftarrow b, i) p_t(b \mid i), \tag{A10}$$

where in the second equality we used eq. (6) and the recursion $n_{t+1}(i) = \bar{w}_t(i) n_t(i)$.

A2.1 Single-Generation Change

We here derive eq. (7) using eq. (6), from which by summing over all classes we can write

$$n_{t+1}(i) = n_t(i) + \Delta n_t^{\text{sel}}(i) + \Delta n_t^{\text{ct}}(i) + \Delta n_t^{\text{pg}}(i), \tag{A11}$$

with

$$\begin{aligned}
\Delta n_t^{\text{sel}}(i) &= \sum_a \sum_b \Big[w_t(a \leftarrow b, i) - \bar{w}_t(a \leftarrow b) \Big] p_t(b \mid i) n_t(i) \\
\Delta n_t^{\text{ct}}(i) &= \sum_a \sum_b \Big[\bar{w}_t(a \leftarrow b) - \frac{1}{n_{\mathcal{C}}} \bar{w}_t \Big] p_t(b \mid i) n_t(i) \\
\Delta n_t^{\text{pg}}(i) &= \big(\bar{w}_t - 1\big) n_t(i).
\end{aligned} \tag{A12}$$

Thus, in class-structured populations, the non-selective processes that alter numbers of alleles are both class transmission and population growth. Substituting eqs. (A11)-(A12) into eq. (A6) produces the recursion

$$\Delta p_t(i) = \frac{1}{n_{t+1}} \left(n_{t+1}(i) - \bar{w}_t n_t(i) \right) = \frac{1}{n_{t+1}} \Big(\Delta n_t^{\text{sel}}(i) + \Delta n_t^{\text{ct}}(i) \Big) \tag{A13}$$

which together with eq. (A12) shows the first equality in eqs. (7b)-(7c) and upon applying $n_{t+1}(i) = \bar{w}_t(i) n_t(i)$ we obtain the second equality in eqs. (7b)-(7c). As in a homogeneous population, the process of population growth does not affect allele frequencies in class-structured populations over a single time step $[t, t+1]$.

A2.2 Multigenerational Change

We here derive eq. (8) with the per generation contributions $\Delta p_{t|\mathcal{T}}^{\text{sel}}(i)$ and $\Delta p_{t|\mathcal{T}}^{\text{ct}}(i)$ as given in eq. (11) and eq. (12), respectively. To that end, we define $n_{t|h}(\cdot)$ and $p_{t|h}(\cdot)$ as the state variables at t that underwent the full (selective and non-selective) evolutionary process between $[t_0, h]$ and that from time h onward have undergone the non-selective process. In the main text we use the short-hand notation $n_t^{\circ}(\cdot) = n_{t|t_0}(\cdot)$ and $p_t^{\circ}(\cdot) = p_{t|t_0}(\cdot)$ for variables that have undergone the non-selective process right from the onset (i.e., the initial time t_0), but we must define these more general state variables here in the appendix as we need them for the derivation of the results. We should immediately emphasise that these variables are theoretical constructs aiding our calculations and hence can not be measured *per se* (they must be calculated). Now, in particular, $n_{t|h}(a, i)$ gives the number of individuals a, i at time t that descend from a lineage of individuals that underwent the full evolutionary process between $[t_0, h]$ and a non-selective process between $[h, t]$. For $h \leq t < t_{\text{f}}$, this state variable thus satisfies the recursion

$$n_{t+1|h}(a, i) = \sum_b \bar{w}_t(a \leftarrow b) n_{t|h}(b, i) \tag{A14}$$

(compare with eq. 9 in the main text) with initial condition $n_{h|h}(a, i) = n_h(a, i)$, which is the final state of the state variable $n_t(a, i)$ that has undergone the full evolutionary process (eq. 6) between $[t_0, h]$. Next, we introduce the state variable

$$p_{t|h}(a, i) = \frac{n_{t|h}(a, i)}{n_t}, \tag{A15}$$

which gives the proportion of individuals in the population at time t that descend from a lineage of a, i individuals that underwent the full evolutionary process between $[t_0, h]$ and that from time h onward have undergone a non-selective process (and recall that $n_t = n_{t|t}$ and hence this proportion is relative to the total number of individuals under the full evolutionary process). Because the non-selective process of population dynamics where all individuals are assigned fitness $\bar{w}_t$ does not alter allele frequencies, we can equivalently interpret $p_{t|h}(a, i)$ as the frequency of a, i at the final time t_f that descend from a lineage of individuals that underwent selection and class transmission between $[t_0, h]$ and then only class transmission between $[h, t]$ (relative to the number of individuals that underwent the full evolutionary process from t_0 onward).

A2.2.1 Disentangling Selection from the Evolutionary Process

We are now ready to derive eq. (11). Using eq. (A15), we immediately observe that in a multigenerational process over $\mathcal{T}$ the effect of selection in generation t on allele frequency can be defined for all t as

$$\Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i) = p_{t_\mathrm{f}|t+1}(i) - p_{t_\mathrm{f}|t}(i). \tag{A16}$$

Indeed, the variable $p_{t_\mathrm{f}|t+1}(i)$ gives the frequency of individuals i at t_f that descend from individuals that underwent selection and class transmission until $t+1$ and then class transmission until t_f, and hence subtracting from this the allele frequency $p_{t_\mathrm{f}|t}(i)$ where selection acts only until time t, we isolate in eq. (A16) one iteration of selection $[t, t+1]$ from an otherwise class-transmission process during $[t, t_\mathrm{f}]$. Moreover, we have the identity

$$p_{t_\mathrm{f}|t}(i) = \frac{1}{n_{t_\mathrm{f}}} v_t(i) n_t(i), \tag{A17}$$

where we used the definition for reproductive values (eq. 10) and where

$$\bar{v}_t(i) = \sum_a v_t(a) p_t(a \mid i) \tag{A18}$$

is the average reproductive value of i at time t as defined in the main text. Notice that eq. (A17) is the reproductive value weighted allele frequency often used in the evolutionary analysis of class-structured populations [Lion, 2018, Rousset and Ronce, 2004, Taylor, 1990].

Now, the weighted allele frequency (eq. A17) satisfies

$$\begin{aligned}
p_{t_\mathrm{f}|t+1}(i) &= \frac{1}{n_{t_\mathrm{f}}} v_{t+1}(i) n_{t+1}(i) = \frac{1}{n_{t_\mathrm{f}}} \sum_a v_{t+1}(a) n_{t+1}(a,i) \\
&= \frac{1}{n_{t_\mathrm{f}}} \sum_a \sum_b v_{t+1}(a) \Big[w_t(a \leftarrow b, i) - \bar{w}_t(a \leftarrow b) \Big] p_t(b \mid i) n_t(i) + \\
&+ \frac{1}{n_{t_\mathrm{f}}} \sum_a \sum_b v_{t+1}(a) \bar{w}_t(a \leftarrow b) p_t(b \mid i) n_t(i) \\
&= p_{t_\mathrm{f}|t}(i) + \frac{1}{n_{t_\mathrm{f}}} \sum_a \sum_b v_{t+1}(a) \Big[w_t(a \leftarrow b, i) - \bar{w}_t(a \leftarrow b) \Big] p_t(b \mid i) n_t(i),
\end{aligned} \tag{A19}$$

where we applied eqs. (A11)-(A12) in the second equality, and eq. (10) and eq. (A17) in the third equality. From the definition in eq. (A16) this thus proves the first equality in eq. (11).

The second equality in eq. (11) can be obtained by noting that $n_{t_\mathrm{f}} = \bar{v}_t n_t$ where $\bar{v}_t = \prod_{h=t}^{h=t_\mathrm{f}-1} \bar{w}_h$ as defined in the main text, in which case we can write eq. (A17) equivalently as

$$p_{t_\mathrm{f}|t}(i) = \frac{\bar{v}_t(i)}{\bar{v}_t} p_t(i), \tag{A20}$$

and hence

$$\begin{aligned}
\Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i) &= \frac{1}{\bar{v}_t} \sum_a \sum_b v_{t+1}(a) \Big[w_t(a \leftarrow b, i) - \bar{w}_t(a \leftarrow b) \Big] p_t(b \mid i) p_t(i) \\
&= \frac{1}{\bar{v}_t} \Big[\sum_a \sum_b v_{t+1}(a) w_t(a \leftarrow b, i) p_t(b \mid i) - \sum_a \sum_b v_{t+1}(a) \bar{w}_t(a \leftarrow b) p_t(b \mid i) \Big] p_t(i) \\
&= \frac{1}{\bar{v}_t} \Big[\sum_a \sum_b v_{t+1}(a) w_t(a \leftarrow b, i) p_t(b \mid i) - \sum_b v_t(b) p_t(b \mid i) \Big] p_t(i) \\
&= \left(\frac{\bar{w}^{\mathrm{v}}_t(i) - \bar{v}_t(i)}{\bar{v}_t} \right) p_t(i)
\end{aligned} \tag{A21}$$

where in the third equality we applied eq. (10) and in the fourth equality the definition of $\bar{v}_t(i)$ and

$$\bar{w}^{\mathrm{v}}_t(i) = \sum_a \sum_b v_{t+1}(a) w_t(a \leftarrow b, i) p_t(b \mid i). \tag{A22}$$

The sum that appears in eq. (8) is obtained by applying eq. (A16) recursively

$$p_{t_\mathrm{f}|t_\mathrm{f}}(i) = \sum_{t=t_0}^{t_\mathrm{f}-1} \Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i) + p_{t_\mathrm{f}|t_0}(i). \tag{A23}$$

Then, by using the consistency relation $p_{t_\mathrm{f}|t_\mathrm{f}}(i) = p_{t_\mathrm{f}}(i)$ and by reorganizing the terms gives

$$p_{t_\mathrm{f}}(i) - p_{t_\mathrm{f}|t_0}(i) = \sum_{t=t_0}^{t_\mathrm{f}-1} \Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i). \tag{A24}$$

Because $p_{t_\mathrm{f}|t_0}(i)$ is the frequency of i at time t_f if only class transmission was in play over the entire $\mathcal{T}$ (and $p_{t_\mathrm{f}}(i) = p_{t_\mathrm{f}|t_\mathrm{f}}(i)$ if both selection and class transmission was in play), we

have obtained that $\Delta p^{\text{sel}}_{\mathcal{T}}(i) = p_{t_\text{f}}(i) - p_{t_\text{f}|t_0}(i)$ and hence eq. (A24) indeed gives the fraction of the total allele-frequency change that is due to selection with $\Delta p^{\text{sel}}_{t|\mathcal{T}}(i)$ as the contribution of selection in generation t.

A2.2.2 Disentangling Class Transmission from the Evolutionary Process

We here derive eq. (12). We immediately observe that in a multigenerational process over $\mathcal{T}$ the effect of class transmission in generation t on allele frequency can be defined for all t as

$$\Delta p^{\text{ct}}_{t|\mathcal{T}}(i) = p_{t+1|t_0}(i) - p_{t|t_0}(i). \tag{A25}$$

Indeed, $p_{t+1|t_0}(i)$ gives the frequency of i individuals that underwent class transmission until $t+1$, and hence by subtracting from this the frequency $p_{t|t_0}(i)$ of i individuals that underwent class transmission until t, we isolate one iteration of class transmission during $[t, t+1]$. Because the process of population dynamics does not alter allele frequencies, $\Delta p^{\text{ct}}_{t|\mathcal{T}}(i)$ is also the desired frequency of individuals at t_f that descend under population dynamics from offspring produced due to class transmission during $[t, t+1]$ thus in a multigenerational context giving the effect of class transmission in generation t. Using eq. (A15), we can write the recursion

$$\begin{aligned} p_{t+1|t_0}(i) &= \frac{n_{t+1|t_0}(i)}{n_{t+1}} = \frac{1}{n_{t+1}} \sum_a n_{t+1|t_0}(a,i) \\ &= \frac{1}{n_{t+1}} \sum_a \sum_b \left[\bar{w}_t(a \leftarrow b) - \frac{1}{n_{\mathcal{C}}} \bar{w}_t \right] n_{t|t_0}(b,i) + \frac{1}{n_{t+1}} \bar{w}_t n_{t|t_0}(i) \\ &= \frac{1}{n_{t+1}} \sum_a \sum_b \left[\bar{w}_t(a \leftarrow b) - \frac{1}{n_{\mathcal{C}}} \bar{w}_t \right] n_{t|t_0}(b,i) + p_{t|t_0}(i), \end{aligned} \tag{A26}$$

where in the third equality we used eq. (A14) (eq. 9 in the main text) and in the fourth equality $n_{t+1} = \bar{w}_t n_t$ and eq. (A15). Reorganization and using $r^\circ_t(i)$ as defined in the main text as well as recalling the shortcut notation $n_{t|t_0}(\cdot) = n^\circ_t(\cdot)$ and $p_{t|t_0}(\cdot) = p^\circ_t(\cdot)$ yields eq. (12).

The sum that appears in eq. (8) is obtained from

$$p_{t_\text{f}|t_0}(i) = \Delta p^{\text{ct}}_{t_\text{f}|\mathcal{T}}(i) + p_{t_\text{f}-1|t_0}(i) \tag{A27}$$

and a recursive substitution produces

$$p_{t_\text{f}|t_\text{f}}(i) = \sum_{t=t_0}^{t_\text{f}-1} \Delta p^{\text{ct}}_{t|\mathcal{T}}(i) + p_{t_0|t_0}(i). \tag{A28}$$

Then, by noting that $p_{t_0|t_0}(i) = p_{t_0}(i)$ and by reorganizing the terms gives

$$p_{t_\text{f}|t_0}(i) - p_{t_0}(i) = \sum_{t_0}^{t=t_\text{f}-1} \Delta p^{\text{ct}}_{t|\mathcal{T}}(i). \tag{A29}$$

Because $p_{t_\text{f}|t_0}(i)$ is the frequency of i at time t_f if only class transmission was in play over the

entire time-interval $\mathcal{T}$, we have obtained that the total change in allele frequency due to class transmission is $\Delta p^{\mathrm{ct}}_{\mathcal{T}}(i) = p^{\circ}_{t_{\mathrm{f}}|t_0}(i) - p_{t_0}(i)$ and $\Delta p^{\mathrm{ct}}_{t|\mathcal{T}}(i)$ is the contribution of class transmission in generation t.

A3 Geometric Mean Fitness

A3.1 Geometric Mean Effects of Selection and Class Transmission

We here derive eq. (13) and eqs. (14)-(15). First, consider the recursion $p_{t+1}(i) = p_t(i)\bar{w}_t(i)/\bar{w}_t$, which describes both homogeneous and class-structured populations depending on the definition of fitness functions (recall eq. 2 and eq. 7). Setting $t+1 = t_{\mathrm{f}}$ on the left hand side and iterating backward in time yields

$$p_{t_{\mathrm{f}}}(i) = \prod_{t=t_0}^{t_{\mathrm{f}}-1} \frac{\bar{w}_t(i)}{\bar{w}_t} p_{t_0}(i), \tag{A30}$$

which shows the validity of the eq. (13).

Second, we derive eqs. (14)-(15). Using eq. (A15) we obtain the recursion

$$\begin{aligned} p_{t_{\mathrm{f}}|t+1}(i) = \frac{1}{n_{t_{\mathrm{f}}}} v_{t+1}(i) n_{t+1}(i) &= \frac{1}{n_{t_{\mathrm{f}}}} \sum_a v_{t+1}(a) n_{t+1}(a,i) \\ &= \frac{1}{n_{t_{\mathrm{f}}}} \sum_a \sum_b v_{t+1}(a) w_t(a \leftarrow b, i) p_t(b \mid i) n_t(i) \\ &= \frac{1}{\bar{v}_t(i)} \sum_a \sum_b v_{t+1}(a) w_t(a \leftarrow b, i) p_t(b \mid i) p_{t_{\mathrm{f}}|t}(i), \end{aligned} \tag{A31}$$

where in the third equality we used eq. (6) and in the final equality we used the relation $n_t(i) = p_{t_{\mathrm{f}}|t}(i) n_{t_{\mathrm{f}}}/\bar{v}_t(i)$, which was obtained from $p_{t_{\mathrm{f}}|t}(i) = n_{t_{\mathrm{f}}|t}(i)/n_{t_{\mathrm{f}}}$ (using eq. A15) and the identity $n_{t_{\mathrm{f}}|t}(i) = \bar{v}_t(i) n_t(i)$. Then, using the definition of $\bar{w}^{\mathrm{v}}_t(i)$ produces

$$p_{t_{\mathrm{f}}|t+1}(i) = \frac{\bar{w}^{\mathrm{v}}_t(i)}{\bar{v}_t(i)} p_{t_{\mathrm{f}}|t}(i), \tag{A32}$$

and setting $t+1 = t_{\mathrm{f}}$ on the left hand side and iterating backward in time yields

$$p_{t_{\mathrm{f}}|t_{\mathrm{f}}}(i) = \prod_{t=t_0}^{t_{\mathrm{f}}-1} \frac{\bar{w}^{\mathrm{v}}_t(i)}{\bar{v}_t(i)} p_{t_{\mathrm{f}}|t_0}(i). \tag{A33}$$

Because $p_{t_{\mathrm{f}}|t_0}(i)$ is the allele frequency at time t_{f} in a process without selection and $p_{t_{\mathrm{f}}|t_{\mathrm{f}}}(i) = p_{t_{\mathrm{f}}}(i)$ is the frequency at t_{f} with selection, the product in eq. (A33) summarizes the fitness excess over $\mathcal{T}$ caused by selection only with $\bar{w}^{\mathrm{v}}_t(i)/\bar{v}_t(i)$ giving the relative fitness attributed to selection in generation t.

Next, consider the recursion

$$
\begin{aligned}
p_{t+1|t_0}(i) = \frac{n_{t+1|t_0}(i)}{n_{t+1}} &= \frac{1}{n_{t+1}} \sum_a n_{t+1|t_0}(a,i) \\
&= \frac{1}{n_{t+1}} \sum_a \sum_b \bar{w}_t(a \leftarrow b) n_{t|t_0}(b,i) \\
&= \sum_a \sum_b \frac{\bar{w}_t(a \leftarrow b) p_{t|t_0}(b \mid i)}{\bar{w}_t} p_{t|t_0}(i) \\
&= \frac{\bar{w}_{t|t_0}(i)}{\bar{w}_t} p_{t|t_0}(i),
\end{aligned}
\tag{A34}
$$

where we applied eq. (A14) (eq. 9 in the main text) and where $\bar{w}_{t|t_0}(i) = \sum_{a,b} \bar{w}_t(a \leftarrow b) p_{t|t_0}(b \mid i)$ is the fitness of a single i at t coming from a lineage of non-selected individuals, and note that in the main text we used the shorthand notation $\bar{w}_t^{\circ}(i) = \bar{w}_{t|t_0}(i)$. Setting $t+1 = t_{\mathrm{f}}$ on the left hand side in eq. (A34) and iterating backwards in time yields

$$
p_{t_{\mathrm{f}}|t_0}(i) = \prod_{t=t_0}^{t_{\mathrm{f}}-1} \frac{\bar{w}_{t|t_0}(i)}{\bar{w}_t} p_{t_0|t_0}(i). \tag{A35}
$$

Because $p_{t_0|t_0}(i) = p_{t_0}(i)$ is the initial allele frequency at t_0 and $p_{t_{\mathrm{f}}|t_0}(i)$ is the final frequency under class transmission only, the product in eq. (A35) summarizes the fitness excess over $\mathcal{T}$ caused by class transmission (see below further discussion on the relative fitness attributed to class transmission in generation t). Substituting eq. (A35) into eq. (A33) we get

$$
\begin{aligned}
p_{t_{\mathrm{f}}|t_{\mathrm{f}}}(i) &= \prod_{t=t_0}^{t_{\mathrm{f}}-1} \frac{\bar{w}_t^{\mathrm{v}}(i)}{\bar{v}_t(i)} \prod_{t=t_0}^{t_{\mathrm{f}}-1} \frac{\bar{w}_{t|t_0}(i)}{\bar{w}_t} p_{t_0|t_0}(i) \\
&= \prod_{t=t_0}^{t_{\mathrm{f}}-1} \frac{\bar{w}_t^{\mathrm{v}}(i)}{\bar{v}_t(i)} \frac{\bar{w}_{t|t_0}(i)}{\bar{w}_t} p_{t_0|t_0}(i)
\end{aligned}
\tag{A36}
$$

and since $p_{t_{\mathrm{f}}|t_{\mathrm{f}}}(i) = p_{t_{\mathrm{f}}}(i)$ and $p_{t_0|t_0}(i) = p_{t_0}(i)$, we obtain the expression in eqs. (14)-(15).

Note that $W^{\mathrm{ct}}_{t|\mathcal{T}}(i) = \bar{w}_t^{\mathrm{v}}(i)/\bar{v}_t(i)$ in eq. (A36) is the (asymptotic) relative fitness for class transmission of a single i individual at t in a multigenerational process over $\mathcal{T}$, given we have sampled an individual at t who is itself a product of class transmission. If we want to condition on the realized population state at t, we can use the fact that

$$
p_{t|t_0}(i) = \prod_{h=t_0}^{t_{\mathrm{f}}-1} W^{\mathrm{ct}}_{h|\mathcal{T}}(i) p_{t_0}(i) \tag{A37}
$$

and substituting this into (A36) we have

$$p_{t_\mathrm{f}}(i) = \left(\prod_{t=t_0}^{t_\mathrm{f}-1} W^{\mathrm{sel}}_{t|\mathcal{T}}(i) \prod_{t=h}^{t_\mathrm{f}-1} W^{\mathrm{ct}}_{t|\mathcal{T}}(i)\right) \prod_{t=t_0}^{h-1} W^{\mathrm{ct}}_{t|\mathcal{T}}(i) p_{t_0}(i) \tag{A38}$$

$$= \left(\prod_{t=t_0}^{t_\mathrm{f}-1} W^{\mathrm{sel}}_{t|\mathcal{T}}(i) \prod_{t=h}^{t_\mathrm{f}-1} W^{\mathrm{ct}}_{t|\mathcal{T}}(i)\right) p_{h|t_0}(i) \tag{A39}$$

and using the identity $p_{h|t_0}(i) = r^\circ_h(i) p_h(i)$ we get

$$p_{t_\mathrm{f}}(i) = \left(\prod_{t=t_0}^{t_\mathrm{f}-1} W^{\mathrm{sel}}_{t|\mathcal{T}}(i) \prod_{t=h}^{t_\mathrm{f}-1} W^{\mathrm{ct}}_{t|\mathcal{T}}(i)\right) r^\circ_h(i) p_h(i) \tag{A40}$$

$$= \left(\prod_{t=t_0}^{t_\mathrm{f}-1} W^{\mathrm{sel}}_{t|\mathcal{T}}(i) \prod_{t=h+1}^{t_\mathrm{f}-1} W^{\mathrm{ct}}_{t|\mathcal{T}}(i)\right) W^{\mathrm{ct}}_{h|\mathcal{T}}(i) r^\circ_h(i) p_h(i). \tag{A41}$$

We have obtained that $W^{\mathrm{ct}}_{h|\mathcal{T}}(i) r^\circ_h(i)$ is the (asymptotic) relative fitness for class transmission of a single randomly sampled i individual in generation h.

A3.2 Alternative Representation of Geometric Mean for Selection

Here we show that one can write the geometric mean for selection (eq. 14) also in terms of individual fitness functions as

$$\overline{W}^{\mathrm{sel}}_{\mathcal{T}}(i) = \left(\prod_{t=t_0}^{t=t_\mathrm{f}-1} \frac{\bar{w}_t(i)}{\bar{w}^\circ_{t|t_0}(i)}\right)^{1/(t_\mathrm{f}-t_0)}. \tag{A42}$$

To do this, we first derive a recursion for $p_{h|t}(a \mid i)$ over $[t, t_\mathrm{f}]$ as

$$p_{h+1|t}(a \mid i) = \frac{n_{h+1|t}(a,i)}{n_{h+1|t}(i)} = \frac{1}{\bar{w}_{h|t}(i)} \sum_b \bar{w}_t(a \leftarrow b) p_{h|t}(b \mid i), \tag{A43}$$

where we applied eq. (A14) (eq. 9 in the main text) and $n_{h+1|t}(i) = \bar{w}_{h|t}(i) n_{h|t}(i)$ with $\bar{w}_{h|t}(i) = \sum_{a,b} \bar{w}_t(a \leftarrow b) p_{h|t}(b \mid i)$, and where the initial condition satisfies $p_{t|t}(a \mid i) = p_t(a \mid i)$. Then, we produce

$$\begin{aligned} \bar{v}_t(i) &= \sum_a v_t(a) p_{t|t}(a \mid i) \\ &= \sum_a \sum_b v_{t+1}(b) \bar{w}_t(b \leftarrow a) p_{t|t}(a \mid i) \\ &= \sum_b v_{t+1}(b) p_{t+1|t}(a \mid i) \bar{w}_{t|t}(i), \end{aligned} \tag{A44}$$

where the first equality follows from the definition of $\bar{v}_t(i)$, and in the second equality we used eq. (10) and in the third equality we used the relation $p_{h+1|t}(a \mid i) \bar{w}_{h|t}(i) = \sum_b \bar{w}_t(a \leftarrow$

$b)p_{h|t}(b \mid i)$ obtained from eq. (A43). Applying the logic in eq. (A44) recursively we get

$$\bar{v}_t(i) = \prod_{h=t}^{t_\mathrm{f}-1} \bar{w}_{h|t}(i) \sum_a v_{t_\mathrm{f}}(a) p_{t_\mathrm{f}|t}(a \mid i), \tag{A45}$$

and by noting that $v_{t_\mathrm{f}}(a) = 1$ for all a and $1 = \sum_a p_{t_\mathrm{f}|t}(a \mid i)$ produces

$$\bar{v}_t(i) = \prod_{h=t}^{h=t_\mathrm{f}-1} \bar{w}^{\circ}_{h|t}(i). \tag{A46}$$

We can then write

$$\begin{aligned} \bar{w}^{\mathrm{v}}_t(i) n_t(i) &= \sum_a \sum_b v_{t+1}(a) w_t(a \leftarrow b, i) n_t(b, i) \\ &= \sum_a v_{t+1}(a) n_{t+1}(a, i) \\ &= \sum_a v_{t+1}(a) p_{t+1}(a \mid i) n_{t+1}(i) \\ &= \bar{v}_{t+1}(i) \bar{w}_t(i) n_t(i) \end{aligned} \tag{A47}$$

where the first equality follows from the definition of $\bar{w}^{\mathrm{v}}_t(i)$, and in the second equality we used eq. (6) and in the final equality we applied the definition of $\bar{v}_t(i)$ and $n_{t+1}(i) = \bar{w}_t(i) n_t(i)$. We have thus produced the identity

$$\bar{w}^{\mathrm{v}}_t(i) = \bar{v}_{t+1}(i) \bar{w}_t(i). \tag{A48}$$

Substituting this into

$$\begin{aligned} \prod_{t=t_0}^{t_\mathrm{f}-1} \frac{\bar{w}^{\mathrm{v}}_t(i)}{\bar{v}_t(i)} &= \prod_{t=t_0}^{t_\mathrm{f}-1} \frac{\bar{v}_{t+1}(i) \bar{w}_t(i)}{\bar{v}_t(i)} \\ &= \prod_{t=t_0}^{t_\mathrm{f}-1} \frac{\bar{w}_t(i)}{\bar{v}_{t_0}(i)}, \end{aligned} \tag{A49}$$

where we used $\bar{v}_{t_\mathrm{f}}(i) = 1$ ($= \sum_a v_{t_\mathrm{f}}(a) p_{t_\mathrm{f}}(a \mid i) = \sum_a p_{t_\mathrm{f}}(a \mid i)$ by assumption), and by applying eq. (A46) and eq. (14) finally produces eq. (A42). We also note that we can write

$$\begin{aligned} p_{t_\mathrm{f}}(i) = \prod_{t=t_0}^{t_\mathrm{f}-1} \frac{\bar{w}^{\mathrm{v}}_t(i)}{\bar{v}_t(i)} \frac{\bar{w}_{t|t_0}(i)}{\bar{w}_t} p_{t_0}(i) &= \prod_{t=t_0}^{t_\mathrm{f}-1} \frac{\bar{w}_t(i)}{\bar{v}_{t_0}(i)} \frac{\bar{w}_{t|t_0}(i)}{\bar{w}_t} p_{t_0}(i) \\ &= \prod_{t=t_0}^{t_\mathrm{f}-1} \frac{\bar{w}_t(i)}{\bar{w}_t} p_{t_0}(i) \end{aligned} \tag{A50}$$

where in the second equality we used eq. (A49) and in the third equality eq. (A46). This calculation shows the relationship between eq. (13) and eq. (14).

A4 Asymptotic Evolutionary Process

A4.1 Invasion Fitness as a Measure of Selection

Recall the definition of the invasion exponent of allele i when the initial number of such alleles is $n_{t_0}(i)$:

$$\rho = \lim_{t_\mathrm{f}\to\infty} \frac{1}{t_\mathrm{f} - t_0} \ln \frac{n_{t_\mathrm{f}}(i)}{n_{t_0}(i)} \tag{A51}$$

(e.g., Ferrière and Gatto, 1995, Metz et al., 1992, Tuljapurkar, 1989). Since we are interested in the growth of i when rare, we suppose that the model contains an equilibrium $\hat{\mathbf{n}}_0 = (\hat{n}_0(a,j))_{a,j}$ where $\hat{n}_0(a,i) = 0$ for all a and $\hat{n}_0(a,j) > 0$ for all $j \neq i$ and all a, and that $\hat{\mathbf{n}}_0$ is asymptotically stable along the invariant (multidimensional) axis where allele i is absent (i.e., where $\hat{n}_0(a,i) = 0$ for all a). More specifically, we have $0 = \hat{n}(a,i) = \hat{p}(a \mid i)\hat{n}(i)$ for all a implying that $\hat{n}(i) = 0$ but not necessarily that $\hat{p}(a \mid i) = 0$.

We now calculate eq. (A51). First, from eq. (A36) we get

$$p_{t_\mathrm{f}}(i) = \left(\prod_{t=t_0}^{t_\mathrm{f}-1} \frac{\bar{w}_t^\mathrm{v}(i)}{\bar{v}_t(i)} \frac{\bar{w}_{t|t_0}(i)}{\bar{w}_t} \right) p_{t_0}(i), \tag{A52}$$

and by multiplying both sides by $n_{t_\mathrm{f}} = \prod_{t=t_0}^{t_\mathrm{f}-1} \bar{w}_t n_{t_0}$ we obtain

$$n_{t_\mathrm{f}}(i) = \left(\prod_{t=t_0}^{t_\mathrm{f}-1} \frac{\bar{w}_t^\mathrm{v}(i)}{\bar{v}_t(i)} \frac{\bar{w}_{t|t_0}(i)}{\bar{w}_t} \frac{\bar{w}_t}{1} \right) n_{t_0}(i), \tag{A53}$$

where the final term in the brackets $\bar{w}_t/1$ gives the expected number of offspring produced due to the non-selective process of population growth (as compared to constant dynamics where each parent produces exactly one offspring, see also eq. A12). We then divide both sides by $n_{t_0}(i)$ and Taylor expand the function $n_{t_\mathrm{f}}(i)/n_{t_0}(i)$ about the steady state $\hat{\mathbf{n}}_0$ (we need to expand the whole trajectory of vectors $\mathbf{n}_{t_0}, \ldots, \mathbf{n}_{t_\mathrm{f}-1}$), which results in the linearized equation

$$\frac{n_{t_\mathrm{f}}(i)}{n_{t_0}(i)} = \prod_{t=t_0}^{t_\mathrm{f}-1} \frac{\hat{\bar{w}}^\mathrm{v}(i)}{\hat{\bar{v}}(i)} + \text{h.o.t.} = \left(\frac{\hat{\bar{w}}^\mathrm{v}(i)}{\hat{\bar{v}}(i)} \right)^{t_\mathrm{f}-t_0} + \text{h.o.t.} \tag{A54}$$

where the h.o.t. refers to terms of order $|\mathbf{n}_t - \hat{\mathbf{n}}_0|$ for all $t \in \mathcal{T}$. Here and henceforth the hat above variables and functions indicate that they are evaluated at the equilibrium and the h.o.t. refers to higher order terms depending on the context. The first equality in eq. (A54) follows from evaluating $\bar{w}_t$ and $\bar{w}_{t|t_0}(i)$ at $\hat{\mathbf{n}}_0$: $\hat{\bar{w}} = 1$ follows from the definition of an equilibrium (i.e., $\hat{n} = \hat{\bar{w}}\hat{n}$ implies $\hat{\bar{w}} = 1$), and where $1 = \hat{\bar{w}} = \sum_{a,b} \hat{\bar{w}}(a \leftarrow b)\hat{p}(b) = \sum_{a,b} \hat{\bar{w}}(a \leftarrow b)\hat{p}(b \mid i) = \hat{\bar{w}}^\circ(i)$ follows from the fact that at the equilibrium $\hat{\mathbf{n}}_0$ the identity $\hat{p}^\circ(a \mid i) = \hat{p}(a)$ holds for all a. One can see this immediately by comparing the recursion in eq. (A43) and $p_{t+1}(a) = \sum_b \bar{w}_t(a \leftarrow b)p_t(b)/\bar{w}_t$, but we ought to emphasise that the identity $\hat{p}^\circ(a \mid i) = \hat{p}(a)$

holds only for allele i and only at the equilibrium $\hat{\mathbf{n}}_0$ where allele i is absent. Furthermore, in the expressions $\hat{\bar{w}}^{\mathrm{v}}(i) = \sum_{a,b} \hat{v}(a)\hat{\bar{w}}(a \leftarrow b, i)\hat{p}(b \mid i)$ and $\hat{\bar{v}}(i) = \sum_a \hat{v}(a)\hat{p}(a \mid i)$ the vector $\hat{\mathbf{v}}$ is calculated from eq. (10) and evaluated at $\hat{\mathbf{n}}_0$ and the vector $\hat{\mathbf{p}}(i)$ with elements $\hat{p}(a \mid i)$ is calculated from eq. (A10) and evaluated at $\hat{\mathbf{n}}_0$. Notice that whereas $\hat{\mathbf{p}}^{\circ}(i)$ is calculated under a non-selective process from (A43), the vector $\hat{\mathbf{p}}(i)$ is calculated under the full evolutionary process with selection (eq. A10), and hence in general $\hat{\mathbf{p}}^{\circ}(i) \neq \hat{\mathbf{p}}(i)$. Now, we can substitute eq. (A54) into eq. (A51) which leads to

$$\rho = \ln \frac{\hat{\bar{w}}^{\mathrm{v}}(i)}{\hat{\bar{v}}(i)}. \tag{A55}$$

In this final step we used the fact that as $t_{\mathrm{f}} \to \infty$ the h.o.t. present in eq. (A54) converge to 0. Moreover, $\exp \rho$ can be shown to be the leading eigenvalue of the fitness matrix with elements $\hat{w}(a \leftarrow b, i)$ and that its corresponding eigenvector is $\hat{\mathbf{p}}(i)$. These are standard results and have been proved elsewhere (e.g., Caswell, 2000, Tuljapurkar, 1989).

Finally, we show that any arbitrarily weighted fitness function could be used in eq. (A55). To this end, define an arbitrarily weighted fitness function

$$\bar{w}_t^q(i) = \sum_a \sum_a q_{t+1}(a) w_t(a \leftarrow b, i) p_t(b \mid i) \tag{A56}$$

with arbitrary weights $q_t(a)$ that follow some arbitrary system of recursions. Then, we produce an analogues identity to eq. (A48), which reads as

$$\bar{w}_t^q(i) = \bar{q}_{t+1}(i)\bar{w}_t(i), \tag{A57}$$

where $q_{t+1}(i) = \sum_a q_{t+1}(a) p_{t+1}(a \mid i)$. At the resident equilibrium we hence necessarily have that

$$\frac{\hat{\bar{w}}^q(i)}{\hat{\bar{q}}(i)} = \frac{\hat{\bar{q}}(i)\hat{\bar{w}}(i)}{\hat{\bar{q}}(i)} = \hat{\bar{w}}(i), \tag{A58}$$

thus proving eq. (16).

A4.2 Evolutionary Dynamics under Weak Selection

Here we consider a situation where one of the alleles, say allele i, is derived by mutation from another allele, say j. We further suppose that the effect of the mutation on the phenotypic expression of some trait is class-specific so that the phenotypic profile of i can be written as $\mathbf{z}(i) = \mathbf{z}(j) + \delta\boldsymbol{\eta}$, where $\mathbf{z}(k)$, with elements $z(a,k)$, is the phenotypic profile of allele k such that when the allele is in class a it expresses phenotype $z(a,k)$ and where $\boldsymbol{\eta}$ gives the direction of the effect of the mutation, with the effect in class a being $\eta(a)$. Assuming the fitness functions to be continuous, a small parameter δ implies i and j having closely similar phenotypes, and hence having closely similar fitness functions, leading to weak selection. As this model

is a discrete-time special case of previous models where the evolutionary dynamics under phenotypic similarity (weak selection) has been analysed in detail [Priklopil and Lehmann, 2020, 2021], we refer the reader to this earlier literature for further discussion.

Now, consider the evolutionary process over some arbitrary $\mathcal{T}$, and consider the change in allele frequency over a single generation as prescribed in the main text

$$\begin{aligned}\Delta p_{t|\mathcal{T}}(i) &= \Delta p^{\text{sel}}_{t|\mathcal{T}}(i) + \Delta p^{\text{ct}}_{t|\mathcal{T}}(i) \\ &= \frac{1}{n_{t_{\text{f}}}} \sum_a \sum_b v_{t+1}(a) \Big[w_t(a \leftarrow b, i) - \bar{w}_t(a \leftarrow b) \Big] n_t(b,i) + \\ &\quad + \frac{1}{n_{t+1}} \sum_a \sum_b \bar{w}_t(a \leftarrow b) \left[p_{t|t_0}(b \mid i) - p_t(b) \right] n_{t|t_0}(i),\end{aligned} \tag{A59}$$

where the second equality follows from rearrangement using the definition of individual fitness functions. As we are interested in the dynamics for small values of δ we Taylor expand eq. (A59) about $\delta = 0$ and we get

$$\Delta p_{t|\mathcal{T}}(i) = \Delta p^{\text{ct}}_{t|\mathcal{T}}(i)\Big|_{\delta=0} + \delta \frac{\text{d}}{\text{d}\delta} \Delta p^{\text{sel}}_{t|\mathcal{T}}(i)\Big|_{\delta=0} + \text{h.o.t.} \tag{A60}$$

where h.o.t. refers to terms of order δ^2 and where

$$\begin{aligned}\Delta p^{\text{ct}}_{t|\mathcal{T}}(i)\Big|_{\delta=0} &= \left(\frac{1}{n_{t+1}} \sum_a \sum_b \bar{w}_t(a \leftarrow b) \left[p_{t|t_0}(b \mid i) - p_t(b) \right] n_{t|t_0}(i) \right)_{\delta=0} \\ &= \frac{1}{n_{t+1}} \sum_a \sum_b w_t(a \leftarrow b, i \mid \delta = 0) \left[p_{t|t_0}(b \mid i) - p_t(b) \right] n_{t|t_0}(i)\end{aligned} \tag{A61}$$

and

$$\begin{aligned}\frac{\text{d}}{\text{d}\delta} \Delta p^{\text{sel}}_{t|\mathcal{T}}(i)\Big|_{\delta=0} &= \frac{n_t}{n_{t_{\text{f}}}} \sum_a \sum_b v_{t+1}(a) \frac{\text{d}}{\text{d}\delta} \Big[w_t(a \leftarrow b, i) - w_t(a \leftarrow b, j) \Big]_{\delta=0} p_t(b)(1 - p_t(i \mid b)) p_t(i \mid b) \\ &= \frac{n_t}{n_{t_{\text{f}}}} \sum_a \sum_b v_{t+1}(a) \partial_{z(b,i)} w_t(a \leftarrow b, i)\Big|_{\delta=0} \eta(b) p_t(b)(1 - p_t(i \mid b)) p_t(i \mid b).\end{aligned} \tag{A62}$$

In the second equality in eq. (A61) we used

$$\bar{w}_t(a \leftarrow b)\big|_{\delta=0} = \sum_j w_t(a \leftarrow b, j)\big|_{\delta=0} p_t(j \mid b) = w_t(a \leftarrow b, i \mid \delta = 0), \tag{A63}$$

with $w_t(a \leftarrow b, i \mid \delta = 0) = w_t(a \leftarrow b, i)\big|_{\delta=0}$, which follows from the consistency relation

$$w_t(a \leftarrow b, i \mid \delta = 0) = w_t(a \leftarrow b, j \mid \delta = 0) \quad \text{for all} \quad i, j, \tag{A64}$$

saying that the class-specific individual fitness in a population without selection ($\delta = 0$) is equal for all i. The consistency relation (eq. A64) also explains why in the first equality in eq. (A62) the only derivative present is taken with respect to the fitness difference because all the other derivatives are multiplied by the fitness difference evaluated at $\delta = 0$ and thus

vanish. The notation $\partial_{z(b,i)}$ refers to a partial derivative with respect to the phenotypic expression of the focal individual whose fitness function it is (note that one also takes a derivative with respect to the phenotypic expression of other 'non-focal' individuals but this cancels in eq. (A62) because in a well-mixed population each individual irrespective of its allele i or j is surrounded by the same distribution of alleles and hence those partial derivatives of $w_t(a \leftarrow b, i)$ and $w_t(a \leftarrow b, j)$ are equal). Notice in eq. (A60) that the zero order term is fully determined by class transmission because the selection-term is 0 due to the consistency relation in eq. (A64). In contrast, the first order term in eq. (A60) is fully determined by selection because both variables $p_{t|t_0}(b \mid i)$ and $p_t(b)$ in the expression for class transmission in eq. (A60) follow the exact same recursion

$$y_{t+1}(b) = \frac{1}{\sum_{a,b} \bar{w}_t(a \leftarrow b) y_t(b)} \sum_b \bar{w}_t(a \leftarrow b) y_t(b), \tag{A65}$$

where $y_t(b) = p_{t|t_0}(b \mid i)$ or $y_t(b) = p_t(b)$, and hence their derivatives are also equal and the entire derivative of class transmission $\frac{\mathrm{d}}{\mathrm{d}\delta} \Delta p^{\mathrm{ct}}_{t|\mathcal{T}}(i)|_{\delta=0}$ is 0.

Now, timescale separation arguments applied to class-structured populations [Priklopil and Lehmann, 2020, 2021] tell us that the change in allele frequency (eq. A60) is first governed by class transmission according to eq. (A61) until the genetic structure converges to the neighborhood of its (quasi-)steady state where, in particular, $\hat{p}^{\circ}(a \mid i) = \hat{p}(a)$ and $\hat{p}(i \mid a) = \hat{p}(i \mid b)$ for all a, b (but note that $\hat{p}(a \mid i) = p_t(i)$ for all a and that the allele frequency changes also in slower timescale, see below). The steady state for $\hat{p}^{\circ}(a \mid i)$ can be calculated from eq. (A43) (or eq. A65) and the steady state for $\hat{p}(i \mid a)$ can be calculated from the recursion

$$p_{t+1}(i \mid a) = \frac{n_{t+1}(a,i)}{n_{t+1}(a)} = \frac{1}{\sum_b w_t(a \leftarrow b, i \mid \delta = 0) n_t(b)} \sum_b w_t(a \leftarrow b, i \mid \delta = 0) n_t(b,i), \tag{A66}$$

where we used the consistency relation in eq. (A64). After the initial convergence to this quasi-steady state, class transmission is no longer in play and the allele-frequency change (eq. A60) is solely affected by selection (eq. A62). The slow dynamics governed by eq. (A62) can still be simplified because the above quasi-steady state can be substituted into the expression and we obtain

$$\frac{\mathrm{d}}{\mathrm{d}\delta} \Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i)\Big|_{\delta=0} = (1 - p_t(i)) p_t(i) \sum_a \sum_b \hat{v}(a) \partial_{z(b,i)} \hat{w}(a \leftarrow b, i) \eta(b) \hat{p}(b). \tag{A67}$$

We have thus shown that eqs. (A59), (A60) and (A67) prove eq. (17) from the main text.

Finally, we note that if one were to use other weights than reproductive values, as e.g. in the single time-step allele-frequency change as given in eq. (7), the allele-frequency change for small δ would read as

$$\Delta p_t(i) = \Delta p^{\mathrm{ct}}_t(i)\Big|_{\delta=0} + \delta \frac{\mathrm{d}}{\mathrm{d}\delta} \left(\Delta p^{\mathrm{ct}}_t(i) + \Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i) \right)_{\delta=0} + \text{h.o.t.} \tag{A68}$$

where

$$\Delta p_t^{\mathrm{ct}}(i)\Big|_{\delta=0} = \frac{1}{n_{t+1}} \sum_a \sum_b w_t(a \leftarrow b, i \mid \delta = 0) \left[p_t(b \mid i) - p_t(b)\right] n_t(i) \tag{A69}$$

and

$$\begin{aligned}\left(\Delta p_t^{\mathrm{ct}}(i) + \Delta p_t^{\mathrm{sel}}(i)\right)\Big|_{\delta=0} = \frac{1}{n_{t+1}} \sum_a \sum_b w_t(a \leftarrow b, i \mid \delta = 0) \frac{\mathrm{d}}{\mathrm{d}\delta} \left[p_t(b \mid i) - p_t(b)\right]_{\delta=0} n_t(i) + \\ + (1 - p_t(i)) p_t(i) \sum_a \sum_b \partial_{z(b,i)} \hat{\bar{w}}(a \leftarrow b, i) \eta(b) \hat{p}(b).\end{aligned} \tag{A70}$$

This 'partitioning' indicates that the slow dynamics depends on the perturbation of the genetic structure (first term in eq. A70) and it confirms that the active effect of class transmission $\Delta p_t^{\mathrm{ct}}(i)$ is not governed by class transmission only in the context of a multigenerational process over $\mathcal{T}$: in the above partitioning one conditions on the state at time t and hence counts also the ancestors of individuals at t that underwent selection in the past $[t_0, t]$. Therefore, the expressions $\Delta p_t^{\mathrm{ct}}(i)$ and $\Delta p_t^{\mathrm{sel}}(i)$ in eq. (7) do not give the correct contributions of class transmission and selection in a multigenerational evolutionary process.

Symbol	Definition
$n_t(a,i)$	Number of individuals in class a carrying allele i at time t
$n_t(i) = \sum_a n_t(a,i)$	Total number of individuals carrying allele i at time t
$n_t(a) = \sum_i n_t(a,i)$	Total number of individuals in class a at time t
$p_t(i) = n_t(i)/n_t$	Frequency of individuals in the population carrying allele i at time t
$p_t(a \mid i) = n_t(a,i)/n_t(i)$	Frequency of individuals in class a amongst all the individuals that carry allele i in the population at time t
$p_t(i \mid a) = n_t(a,i)/n_t(i)$	Frequency of individuals carrying allele i amongst all the individuals in class a at time t
$w_t(a \leftarrow b, i)$	Expected number of offspring of class a produced over the time step $[t, t+1]$ by a single parent in class b carrying allele i
$\bar{w}_t(a \leftarrow b) = \sum_i w_t(a \leftarrow b, i) p_t(i \mid b)$	Expected number of offspring of class a produced over the time step $[t, t+1]$ by a single average parent in class b
$\bar{w}_t(i) = \sum_{a,b} w_t(a \leftarrow b, i) p_t(b \mid i)$	Expected number of offspring produced over the time step $[t, t+1]$ by a single average parent i in the population
$\bar{w}_t = \sum_{a,b} \bar{w}_t(a \leftarrow b) p_t(b)$	Expected number of offspring produced over the time step $[t, t+1]$ by a single average parent in the population
$v_t(a)$	Reproductive value of an individual a at time t in a multigenerational process over $\mathcal{T}$, defined as the expected number of individuals at time t_f that descend under the non-selective process from that individual
$\bar{v}_t(i) = \sum_a v_t(a) p_t(a \mid i)$	Reproductive value of an average i at time t in a multigenerational process over $\mathcal{T}$
$\bar{v}_t = \sum_i \bar{v}_t(i) p_t(i)$	Reproductive value of an average individual in the population at time t in a multigenerational process over $\mathcal{T}$
$\bar{\bar{w}}(i) = \sum_{a,b} \bar{w}_t(a \leftarrow b) p_t(b \mid i)$	Expected number of offspring produced over the time step $[t, t+1]$ by a single i at time t if it were to survive and reproduce as an average individual in the class
$n_t^\circ(a,i)$	Total number of individuals i in class a at time t in a non-selective process where all individuals between $[t_0, t]$ survive and reproduce as average individuals of their class
$n_t^\circ(i)$	Total number of individuals i at time t in a non-selective process where all individuals between $[t_0, t]$ survive and reproduce as average individuals in the class
$p_t^\circ(a \mid i)$	Frequency of a at t amongst all the individuals that carry allele i in a non-selective process that started at time t_0
$\bar{w}_t^\circ(i) = \sum_{a,b} \bar{w}_t(a \leftarrow b) p_t^\circ(b \mid i)$	Expected number of offspring produced over the time step $[t, t+1]$ by a single i if it were to reproduce as an average individual in the class and that comes from a lineage of non-selected individuals between $[t_0, t]$
$\bar{w}_t^\mathrm{v}(i) = \sum_{a,b} v_t(a) w_t(a \leftarrow b, i) p_{t+1}(b \mid i)$	Expected number of individuals at time t_f that descend under a non-selective process from all offspring produced during $[t, t+1]$ by a single i carrier

Symbol	Definition
$r^{\circ}(i) = n_t^{\circ}(i)/n_t(i)$	Fraction of i at t that come from a lineage of non-selected individuals during $[t_0, t]$
$q_t(a)$	Arbitrary weight of individuals in class a at time t
$q_t(i) = \sum_a q_t(a) p_t(a \mid i)$	Arbitrary weight of an average individual i in the population at time t
$\bar{w}^q(i) = \sum_{a,b} q_{t+1}(a) w_t(a \leftarrow b, i) p_{t+1}(b \mid i)$	Expected number of offspring produced during $[t, t+1]$ by a single i when each offspring in each class is weighted by an arbitrary weight $q_{t+1}(a)$

Table 1: Definitions of the variables and main quantities. See main text for further explanations.

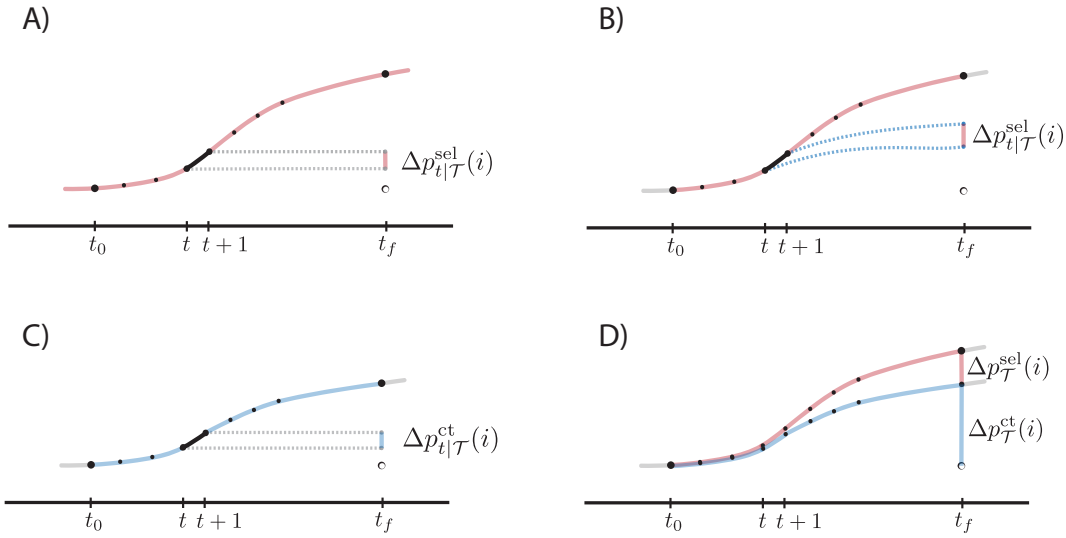

Figure 1: **Panel A)** Multigenerational allele-frequency change over $\mathcal{T} = [t_0, t_\mathrm{f}]$ in a homogeneous population. The black dots along the red curve indicate the observed allele frequencies in different generations. Gray dashed lines indicate the fraction $\Delta p^{\mathrm{sel}}_{t|\mathcal{T}}(i)$ of individuals at time t_f (indicated by the short vertical red line) that descend through the non-selective process of population dynamics from all offspring at $t+1$ that were produced due to selection during $[t, t+1]$. These gray lines are horizontal because population dynamics by itself does not alter allele frequencies. **Panel B)** multigenerational allele-frequency change over $\mathcal{T}$ due to selection in a heterogeneous population. The explanation is identical to panel A, except that in a heterogeneous population the non-selective process of class transmission does alter allele frequencies, indicated by the blue dashed curve. **Panel C)** Multigenerational allele-frequency change over $\mathcal{T}$ due to class transmission in a heterogeneous population. The fraction $\Delta p^{\mathrm{ct}}_{t|\mathcal{T}}(i)$ of individuals descend under the process of population dynamics from all offspring at $t+1$ that were produced due to class transmission during $[t, t+1]$. **Panel D)** The total multigenerational change in allele frequency over $\mathcal{T}$ caused by selection $\Delta p^{\mathrm{sel}}_{\mathcal{T}}(i)$ and class transmission $\Delta p^{\mathrm{ct}}_{\mathcal{T}}(i)$ in a heterogeneous population.

BOX A. Adjoint system

Consider an arbitrary population process during $\mathcal{T}$,

$$x_{t+1}(a) = \sum_b f_t(a \leftarrow b) x_t(b), \tag{A.1}$$

where $f_t(a \leftarrow b)$ gives the number of a produced by a single b at time t and $x_t(b)$ specifies the number of individuals b at time t under this process. In particular, this process may or may not include selection. The so-called adjoint system (e.g., Athans and Falb, 2007, p. 147) of eq. (A.1) can then be expressed as

$$y_t(a) = \sum_b y_{t+1}(b) f_t(b \leftarrow a), \tag{A.2}$$

where $\mathbf{y}_t = (y_t(a))$ is called an adjoint variable (associated to the vector $\mathbf{x}_t = (x_t(a))$). A useful property of adjoint systems is that $\sum_a x_t(a) y_t(a)$ is constant and equal for all t, and the exact value depends on the initial and final conditions $\mathbf{x}_{t_0}$ and $\mathbf{y}_{t_\mathrm{f}}$. In fact, the specification of the final condition also suggests a biological interpretation for the adjoint variable $\mathbf{y}_t$. For instance, suppose that the final condition satisfies $y_{t_\mathrm{f}}(a) = 1$ for all a. Then, we have $\sum_a x_t(a) y_t(a) = x_{t_\mathrm{f}}$ for all t where $x_{t_\mathrm{f}} = \sum_a x_{t_\mathrm{f}}(a)$ is the total population size at the final time t_f under this arbitrary population process. The adjoint variable can be interpreted, under this arbitrary process, as the *number of individuals alive at time t_f that are the descendants of a single individual a alive at time t*. Indeed, this definition follows from the recursion: the number of individuals at t_f that descend from a single individual a at t – the left hand-side of eq. (A.2) – is equal to the number $f_t(b \leftarrow a)$ of offspring-individuals b that this parent individual a produces under this process and where each offspring-individual at $t+1$ is multiplied by the number $y_{t+1}(b)$ of its descendants alive at t_f, and then we sum over all classes of offspring. Note that the final condition $y_{t_\mathrm{f}}(a) = 1$ is consistent with this interpretation because the 'descendant' alive at t_f and its 'ancestor' alive at t_f must be one and the same individual, and hence the number of individuals at t_f that 'descend' from an individual alive at t_f must be 1.

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