



Definitions of fitness in age-structured populations: Comparison in the haploid case



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HIGHLIGHTS

- A generalized growth-rate theorem holds with the Malthusian parameter as fitness.
- Mean fitness based on vital rates and age-specific reproductive values may decrease.
- The two definitions of fitness agree in the limit of weak selection.

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ABSTRACT

Fisher's (1930) Fundamental Theorem of Natural Selection (FTNS), and in particular the development of an explicit age-structured version of the theorem, is of everlasting interest. In a recent paper, Grafen (2015a) argues that Fisher regarded his theorem as justifying individual rather than population fitness maximization. The argument relies on a new definition of fitness in age-structured populations in terms of individual birth and death rates and age-specific reproductive values in agreement with a principle of neutrality. The latter are frequency-dependent and defined without reference to genetic variation. In the same paper, it is shown that the rate of increase in the mean of the breeding values of fitness weighted by the reproductive values, but keeping the breeding values constant as in Price (1972) is equal to the additive genetic variance in fitness. Therefore, this partial change is obtained by keeping constant not only the genotypic birth and death rates but also the mean age-specific birth and death rates from which the age-specific reproductive values are defined. In this paper we reaffirm that the Malthusian parameter which measures the relative rate of increase or decrease in reproductive value of each genotype in a continuous-time age-structured population is the definition of fitness used in Fisher's (1930) FTNS. This is shown by considering an age-structured asexual haploid population with constant age-specific birth and death (or survival) parameters for each type. Although the original statement of the FTNS is for a diploid population, this simplified haploid model allows us to address the definition of fitness meant in this theorem without the complexities and effects of a changing genic environment. In this simplified framework, the rate of change in mean fitness in continuous time is expected to be exactly equal to the genetic variance in fitness (or to the genetic variance in fitness divided by the mean fitness in discrete time), which can be seen as a generalized growth-rate theorem. This theorem is shown to hold with the Malthusian parameter used as the definition of fitness. Moreover, in the same framework, it is shown that a discrete-time version of Grafen's definition may lead to a decrease in mean fitness. In the limit of weak selection with the unit of time proportional to the inverse of the intensity of selection, however, this definition predicts the right population dynamics in agreement with the growth-rate theorem. This clarifies the domain of application of the new definition, at least as far as population dynamics is concerned, and reconciles the new definition with the original one.

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1. Introduction

In an infinite population of asexual haploid individuals in which each individual independent of all others reproduces at fixed rate b and dies at fixed rate μ , the population size grows at relative rate $m = b - \mu$. If $c(t)$ represents the population size at time

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$t \geq 0$, then $bc(t) dt$ and $\mu c(t) dt$ are the expected numbers of births and deaths, respectively, in the infinitesimal time interval $[t, t+dt]$, so that the expected change in the population size in the same time interval is

$$dc(t) = (b - \mu)c(t) dt = mc(t) dt, \quad (1)$$

from which

$$c(t) = c(0)e^{mt}. \quad (2)$$

With n types of individuals having fixed relative growth rates m_i and present in the population in numbers $c_i(t)$ at time $t \geq 0$ for $i = 1, \dots, n$, the mean relative growth rate at this time is given by

$$\bar{m}(t) = \sum_{i=1}^n m_i p_i(t), \quad (3)$$

where

$$p_i(t) = \frac{c_i(t)}{\sum_{j=1}^n c_j(t)} \quad (4)$$

is the frequency of type $i = 1, \dots, n$ at time $t \geq 0$. Differentiating this frequency with respect to time yields

$$\frac{dp_i(t)}{dt} = m_i p_i(t) - p_i(t) \sum_{j=1}^n m_j p_j(t), \quad (5)$$

from which

$$\frac{d\bar{m}(t)}{dt} = \sum_{i=1}^n m_i^2 p_i(t) - \bar{m}(t)^2. \quad (6)$$

This can be found in many textbooks (see, e.g., Crow and Kimura, 1970, p. 10). It was called the *growth-rate theorem* by Edwards (1994) who stated it as follows: *In a subdivided population the rate of change in the overall growth-rate is proportional to the variance in growth rates.*

As still recently stated (Ewens and Lessard, 2015), the aim of Fisher (1930, 1958) was likely to find a more subtle statement for genes that takes into account the complexities of the diploid Mendelian hereditary system as well as those for variable birth and death rates of genotypes. This theorem, known as the Fundamental Theorem of Natural Selection (FTNS), states that: *The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time.* This is the rate of change, however, obtained by keeping fixed the environment including the genic environment (Fisher, 1941, p. 56). This means that genotypic fitnesses are kept constant and only changes in genotypic frequencies ascribable to changes in gene frequencies are considered. These correspond to relative changes in genotypic frequencies as best predicted from the genes present (see Lessard, 1997; Edwards, 2002, for more details). Therefore, the rate of increase in fitness meant in the FTNS is actually a partial rate of change. Moreover, the genetic variance in the FTNS is known today as the additive genetic variance.

Note that the partial rate of change can alternatively be obtained by substituting the fitness of each genotype with its additive genetic value or its breeding value, which is given by the sum of the average allelic effects, and by keeping this value fixed (Price, 1972; see Ewens, 1989, for the corresponding partial change in discrete time without age structure). This interpretation, however, cannot be found in Fisher's (1930, 1941, 1958) writings.

Note also that, in the special case of a constant environment including a constant genic environment, the partial rate of change meant in the FTNS should give the total rate of change as in the growth-rate theorem.

For convenience, a rate of change in continuous time is sometimes simply called a change as in discrete time.

It remains to define fitness. In an age-structured population in continuous time, if $l(x)$ is the probability at conception that an individual will survive to age x and $b(x) dx$ is the expected number of offspring that an individual will produce from age x to age $x+dx$, then the *Malthusian parameter* of the population m is defined by Lotka's (1922) equation

$$\int_0^{\infty} e^{-mx} l(x) b(x) dx = 1. \quad (7)$$

The Malthusian parameter *measures the relative rate of increase or decrease of a population when in the steady state* (Fisher, 1958, p. 26). Moreover, if the *reproductive value* of an individual at age x is defined as

$$v(x) = v(0) \frac{e^{mx}}{l(x)} \int_x^{\infty} e^{-my} l(y) b(y) dy, \quad (8)$$

then *whatever may be the age constitution of a population, its total reproductive value will increase or decrease according to the correct Malthusian rate* (Fisher, 1958, p. 29). Here, the reproductive value of an individual is interpreted as the present value of all offspring expected to be produced by the individual in the future. Differentiating the above equation with respect to x yields (Fisher, 1958, p. 30)

$$mv(x) = \frac{dv(x)}{dx} + b(x)v(0) - \mu(x)v(x), \quad (9)$$

where $b(x)$ and

$$\mu(x) = -\frac{1}{l(x)} \frac{dl(x)}{dx} \quad (10)$$

are the birth and death rates, respectively, of an individual of age x .

The Malthusian parameter *implicit in any given system of rates of death and reproduction [...] measures fitness by the objective fact of representation in future generations [and ...] will in general be different for each different genotype* (Fisher, 1958, p. 26, 37, 50, respectively). This leaves little doubt that this is the definition of fitness meant in the FTNS. If individuals of genotype i at age x have birth and death rates $b_i(x)$ and $\mu_i(x)$, respectively, and reproductive value given by $v_i(x)$, then the Malthusian parameter of individuals of genotype i , denoted by m_i , satisfies

$$m_i v_i(x) = \frac{dv_i(x)}{dx} + b_i(x)v_i(0) - \mu_i(x)v_i(x). \quad (11)$$

In this equation, birth and death rates and reproductive values are averaged over all individuals with the same age for each genotype, while a Malthusian parameter defines fitness for each genotype irrespective of age. This is the classical definition of fitness for a genotype in a continuous-time age-structured population (see, e.g., Crow and Kimura, 1970; Crow, 1979; Charlesworth, 1980, 1994). This is the definition that was used in Lessard (1997) to interpret Fisher's (1930) FTNS as a partial change in fitness, actually in the mean fitness obtained by weighting each individual with its reproductive value as suggested in Fisher (1958, p. 38).

Grafen (2015a) proposes to define the fitness $m_i(x)$ of an individual of genotype i and age x having birth and death rates $b_i(x)$ and $\mu_i(x)$, respectively, and reproductive value given by $v(x)$, such that

$$m_i(x)v(x) = \frac{dv(x)}{dx} + b_i(x)v(0) - \mu_i(x)v(x). \quad (12)$$

Here, the birth and death rates take genotype- and age-specific values as previously, while the reproductive values are age-specific but not genotype-specific. This means that the reproductive values satisfy Eq. (9) where $b(x)$ and $\mu(x)$ are birth and death rates, respectively, averaged over all individuals of age x , and m is the Malthusian parameter for the whole population associated with these rates. Note, however, that this parameter as well as the

reproductive values change over time since this is the case for the average age-specific birth and death rates.

Fitness defined by Eq. (12) differs from fitness defined by Eq. (11) by the use of reproductive values that are the same for all individuals of the same age irrespective of their genotype. Using the former definition and keeping the breeding values fixed as in Price (1972), which implies here keeping the age-specific reproductive values fixed, Grafen (2015a) shows that the rate of change in the mean of the breeding values weighted by the reproductive values is equal to the additive genetic variance in fitness. Moreover, it is claimed that this is the first satisfactory proof of Fisher's (1930) FTNS.

The main question is: which of the definitions of fitness, that in Eq. (11) or (12), is the one that Fisher (1930) meant in the statement of the FTNS? An ancillary question is: under what conditions both definitions agree?

In order to answer these questions, we will consider the simplest possible age-structured population, namely an asexual haploid population with constant demographic vital parameters for each type. It will also be useful to consider discrete-time models since the concepts of Malthusian parameter and reproductive value are best understood in their discrete-time versions.

With time and age measured in number of time intervals of length Δt , let $c(k, \tau)$ be the number of individuals of age $k = 0, 1, \dots, \omega - 1$ at time step $\tau \geq 0$. Moreover, from one time step to the next, such an individual survives with probability $s(k)$ and produces an expected number $f(k)$ of offspring of age 0. Note that an individual must survive in order to produce offspring. Assuming $s(k) > 0$ for $k = 0, 1, \dots, \omega - 1$ and $s(\omega) = 0$ with $f(\omega - 1) > 0$ so that $\omega - 1$ is the maximum age of reproduction, the population state at time step $\tau \geq 0$ is represented by $\mathbf{c}(\tau) = (c(0, \tau), c(1, \tau), \dots, c(\omega - 1, \tau))^T$ (with T denoting transpose), and satisfies

$$\mathbf{c}(\tau + 1) = \mathbf{A}\mathbf{c}(\tau), \tag{13}$$

where

$$\mathbf{A} = \begin{pmatrix} f(0) & f(1) & \dots & f(\omega - 2) & f(\omega - 1) \\ s(0) & 0 & \dots & 0 & 0 \\ 0 & s(1) & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s(\omega - 2) & 0 \end{pmatrix} \tag{14}$$

is a Leslie matrix (Leslie, 1945). Under the additional assumption that $f(\omega - 2) > 0$ so that the matrix \mathbf{A} is necessarily irreducible and aperiodic, the Perron-Frobenius theory for non-negative matrices (see, e.g., Karlin and Taylor, 1975) guarantees that the leading eigenvalue λ is positive, simple and associated with positive left and right eigenvectors $\mathbf{v} = (v(0), v(1), \dots, v(\omega - 1))^T$ and $\mathbf{u} = (u(0), u(1), \dots, u(\omega - 1))^T$, respectively, which are unique under the conditions $\sum_{k=0}^{\omega-1} u(k) = 1$ and $\sum_{k=0}^{\omega-1} v(k)u(k) = 1$. The equations

$$\mathbf{v}^T \mathbf{A} = \lambda \mathbf{v}^T \quad \text{and} \quad \mathbf{A} \mathbf{u} = \lambda \mathbf{u}, \tag{15}$$

respectively, imply that $\mathbf{v}^T \mathbf{c}(\tau + 1) = \lambda \mathbf{v}^T \mathbf{c}(\tau)$ whatever $\mathbf{c}(\tau)$ may be, and $\mathbf{c}(\tau + 1) = \lambda \mathbf{c}(\tau)$ if $\mathbf{c}(\tau) = c \mathbf{u}$ for some constant $c > 0$. This means that \mathbf{u} is a stationary age distribution. On the other hand, it can be checked that

$$\sum_{k=0}^{\omega-1} \frac{l(k)f(k)}{\lambda^{k+1}} = 1 \tag{16}$$

and

$$\lambda v(k) = v(0) \frac{\lambda^k}{l(k)} \sum_{j=k}^{\omega-1} \frac{l(j)f(j)}{\lambda^j} = v(0)f(k) + v(k+1)s(k), \tag{17}$$

with $l(0) = 1$, $v(\omega) = 0$ and $l(k) = s(0) \dots s(k - 1)$, for $k = 1, \dots, \omega - 1$. The components of the vector \mathbf{v} are the reproductive values

associated with the different ages, while λ is the geometric rate of increase or decrease in the total reproductive value of the population: this rate defines its fitness.

The above quantities in the discrete-time model can be obtained for each genotype i to which corresponds a set of age-specific survival probabilities $s_i(k)$ and fecundities $f_i(k)$, for $k = 0, 1, \dots, \omega - 1$. Note that Eqs. (7)–(9) for each genotype i in the continuous-time model are retrieved by setting

$$\begin{aligned} \lambda_i &= 1 + m_i \Delta t + o(\Delta t), & f_i(k) &= b_i(k \Delta t) \Delta t + o(\Delta t), \\ s_i(k) &= 1 - \mu_i(k \Delta t) \Delta t + o(\Delta t), \end{aligned} \tag{18}$$

in the limit $k \Delta t \rightarrow x$ as $\Delta t \rightarrow 0$ (see, e.g., Lessard, 1997). On the other hand, Eq. (12) defining fitness in Grafen's sense in continuous time becomes

$$\lambda_i(k)v(k) = v(0)f_i(k) + v(k+1)s_i(k) \tag{19}$$

in discrete time for individuals of genotype i and age $k \geq 0$ with $v(k)$ satisfying (17) for average age-specific survival probabilities and fecundities. The discrete-time version in Grafen (2015a), namely

$$m_i(k)v(k) = v(k+1) - v(k) + v(0)b_i(k) - v(k+1)\mu_i(k), \tag{20}$$

can be recovered, for instance, by plugging (18) with $\Delta t = 1$ into (19) and ignoring terms of order $o(\Delta t)$.

In this paper, we consider a multi-type age-structured asexual haploid population with constant age-specific birth and death (or survival) parameters for each type. These assumptions are expected to guarantee a constant environment, including a constant genic environment, so that in continuous time the actual rate of increase in mean fitness should be equal to the variance in fitness. This corresponds to a generalized growth-rate theorem that can be viewed as a simplified haploid version of Fisher's (1930) FTNS. Discrete-time versions for which the actual increase in fitness should be equal to the variance in fitness divided by the mean fitness are also considered. These predictions are checked with the Malthusian parameter as definition of fitness and then Grafen's (2015a) definition, first without further assumptions on the birth and death (or survival) parameters and second, in the limit of weak selection as differences in these parameters become infinitesimally small.

2. Increase of mean fitness in discrete time

In a discrete-time age-structured asexual haploid population, let

$$V_i(\tau) = \mathbf{v}_i^T \mathbf{c}_i(\tau) = \sum_{k=0}^{\omega-1} v_i(k)c_i(k, \tau) \tag{21}$$

be the total reproductive value of haplotype i represented in number $c_i(k, \tau)$ in age class $k = 0, 1, \dots, \omega - 1$ at time step $\tau \geq 0$ with survival probabilities and fecundities given by the entries of the Leslie matrix

$$\mathbf{A}_i = \begin{pmatrix} f_i(0) & f_i(1) & \dots & f_i(\omega - 2) & f_i(\omega - 1) \\ s_i(0) & 0 & \dots & 0 & 0 \\ 0 & s_i(1) & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s_i(\omega - 2) & 0 \end{pmatrix}, \tag{22}$$

which satisfies

$$\mathbf{v}_i^T \mathbf{A}_i = \lambda_i \mathbf{v}_i^T = \lambda_i (v_i(0), v_i(1), \dots, v_i(\omega - 1)), \tag{23}$$

where $\lambda_i > 0$ and $v_i(k) > 0$ for $k = 0, 1, \dots, \omega - 1$, for $i = 1, \dots, n$. Then we have

$$V_i(\tau + 1) = \mathbf{v}_i^T \mathbf{c}_i(\tau + 1) = \mathbf{v}_i^T \mathbf{A}_i \mathbf{c}_i(\tau) = \lambda_i \mathbf{v}_i^T \mathbf{c}_i(\tau) = \lambda_i V_i(\tau), \tag{24}$$

which means that λ_i is the geometric rate of increase or decrease in the total reproductive value of haplotype i , for $i = 1, \dots, n$.

Note that the reproductive values associated with the different age classes of each haplotype are frequency-independent. Moreover, they can be multiplied by any positive constant. Since we will be concerned in the following with the changes in the total reproductive values, the scaling does not matter. A standard scaling is to assume $v_i(0) = 1$. Here, for convenience (mainly in view of Section 5), it is assumed that $\mathbf{v}_i^T \mathbf{u}_i = 1$, where \mathbf{u}_i is an ω -dimensional vector with all positive components that sum up to 1, which satisfies $A_i \mathbf{u}_i = \lambda_i \mathbf{u}_i$ as in Eq. (15).

Let

$$\bar{\lambda}(\tau) = \sum_{i=1}^n \lambda_i p_i(\tau), \tag{25}$$

for $\tau \geq 0$, where

$$p_i(\tau) = \frac{V_i(\tau)}{\sum_{j=1}^n V_j(\tau)}, \tag{26}$$

for $i = 1, \dots, n$. At the next time step, we have

$$\begin{aligned} \bar{\lambda}(\tau+1) &= \sum_{i=1}^n \lambda_i p_i(\tau+1) = \frac{\sum_{i=1}^n \lambda_i V_i(\tau+1)}{\sum_{i=1}^n V_i(\tau+1)} \\ &= \frac{\sum_{i=1}^n \lambda_i^2 V_i(\tau)}{\sum_{i=1}^n \lambda_i V_i(\tau)} = \frac{\sum_{i=1}^n \lambda_i^2 p_i(\tau)}{\sum_{i=1}^n \lambda_i p_i(\tau)}, \end{aligned} \tag{27}$$

from which

$$\Delta \bar{\lambda}(\tau) = \bar{\lambda}(\tau+1) - \bar{\lambda}(\tau) = \frac{\sum_{i=1}^n \lambda_i^2 p_i(\tau) - \bar{\lambda}(\tau)^2}{\bar{\lambda}(\tau)}. \tag{28}$$

Therefore, with fitness defined as the geometric rate of change in total reproductive value, the change in mean fitness with respect to frequencies in reproductive value is equal to the variance in fitness divided by the mean fitness. This extends the growth-rate theorem to discrete-time age-structured populations.

3. Increase of mean fitness in continuous time

For asexual haploid individuals of type i surviving to age x with probability $l_i(x)$ and reproducing at rate $b_i(x)$ at that age, let

$$V_i(t) = \int_0^\infty v_i(x) c_i(x, t) dx, \tag{29}$$

where $v_i(x)$ is the reproductive value of an individual of type i of age x defined by

$$v_i(x) = v_i(0) \frac{e^{m_i x}}{l_i(x)} \int_x^\infty e^{-m_i y} l_i(y) b_i(y) dy \tag{30}$$

with $v_i(0) = 1$ and

$$\int_0^\infty e^{-m_i x} l_i(x) b_i(x) dx = 1, \tag{31}$$

while $c_i(x, t)$ is the density of individuals of type i with respect to x at time t . Therefore, $V_i(t)$ represents the total reproductive value of all individuals of type i in the population.

With n types of individuals in the whole population, let

$$p_i(t) = \frac{V_i(t)}{\sum_{j=1}^n V_j(t)} \tag{32}$$

be the proportion of reproductive value of all individuals of type i at time t , for $i = 1, \dots, n$. We will show that

$$\frac{d\bar{m}(t)}{dt} = \sum_{i=1}^n m_i^2 p_i(t) - \bar{m}(t)^2, \tag{33}$$

as stated, and partially proved, in Charlesworth (1980, pp. 67–68),

where m_i is the Malthusian parameter of type i whose mean at time t is

$$\bar{m}(t) = \sum_{i=1}^n m_i p_i(t), \tag{34}$$

with respect to the frequencies of types as defined above. This is the mean Malthusian parameter when individuals are weighted by their reproductive value according to their type and age. In this context, Eq. (33) can be seen as a generalized growth-rate theorem.

As in the growth-rate theorem, it is enough to show that

$$\frac{dp_i(t)}{dt} = m_i p_i(t) - p_i(t) \bar{m}(t), \tag{35}$$

which is the case if

$$\frac{dV_i(t)}{dt} = m_i V_i(t), \tag{36}$$

for $i = 1, \dots, n$. This means that the Malthusian parameter is the relative rate of increase or decrease of the total reproductive value. Since this result does not depend on the type of the individuals, the index i is dropped in the rest of this section to simplify the notation.

First, note that

$$c(x, t) = B(t-x)l(x), \tag{37}$$

where

$$B(t) = \int_0^\infty c(y, t)b(y) dy \tag{38}$$

if $x < t$, while

$$c(x, t) = c(x-t, 0) \frac{l(x)}{l(x-t)} \tag{39}$$

if $x > t$. Therefore, we have

$$\begin{aligned} V(t) &= \int_0^\infty v(x)c(x, t) dx = \int_0^t v(x)B(t-x)l(x) dx \\ &\quad + \int_t^\infty v(x)c(x-t, 0) \frac{l(x)}{l(x-t)} dx = \int_0^t v(t-y)B(y)l(t-y) dy \\ &\quad + \int_0^\infty v(t+y)c(y, 0) \frac{l(t+y)}{l(y)} dy. \end{aligned} \tag{40}$$

Differentiating with respect to t gives

$$\begin{aligned} \frac{dV(t)}{dt} &= v(0)B(t)l(0) + \int_0^t B(y) \left\{ l(t-y) \frac{dv(t-y)}{dt} \right. \\ &\quad \left. + v(t-y) \frac{dl(t-y)}{dt} \right\} dy + \int_0^\infty \frac{c(y, 0)}{l(y)} \left\{ l(t+y) \frac{dv(t+y)}{dt} \right. \\ &\quad \left. + v(t+y) \frac{dl(t+y)}{dt} \right\} dy. \end{aligned} \tag{41}$$

Using Eqs. (9) and (10) with the equality $l(0) = 1$ leads to

$$\begin{aligned} \frac{dV(t)}{dt} &= v(0)B(t) + \int_0^t B(y) \{ mv(t-y) - b(t-y)v(0) \} l(t-y) dy \\ &\quad + \int_0^\infty \frac{c(y, 0)}{l(y)} \{ mv(t+y) - b(t+y)v(0) \} l(t+y) dy = v(0)B(t) \\ &\quad + \int_0^t B(t-x) \{ mv(x) - b(x)v(0) \} l(x) dx + \int_t^\infty \frac{c(x-t, 0)}{l(x-t)} \{ mv(x) \\ &\quad - b(x)v(0) \} l(x) dx = v(0)B(t) + \int_0^\infty c(x, t) \{ mv(x) - b(x)v(0) \} dx \\ &= v(0)B(t) + m \int_0^\infty c(x, t)v(x) dx - v(0) \int_0^\infty c(x, t)b(x) dx \\ &= v(0)B(t) + mV(t) - v(0)B(t) = mV(t). \end{aligned} \tag{42}$$

This result is stated, and a verbal argument given, in Crow and Kimura (1970, p. 22). It is derived from a first-order approximation

of the change in the total reproductive value from time t to time $t + \Delta t$ in Grafen (2015a, Eq. (10)).

4. Mean fitness in Grafen's sense

In the framework of Section 2, the fitness of an individual of haplotype $i = 1, \dots, n$ in age class $k = 0, 1, \dots, \omega - 1$ at time step $\tau \geq 0$ according to Grafen (2015a), denoted by $\lambda_i(k, \tau)$, is defined by the equation

$$\lambda_i(k, \tau)v(k, \tau) = v(0, \tau)f_i(k) + v(k+1, \tau)s_i(k), \tag{43}$$

where $v(\omega, \tau) = 0$ and $v(k, \tau)$ is the reproductive value of an individual in age class $k = 0, 1, \dots, \omega - 1$ at time step $\tau \geq 0$. In other words, $(v(0, \tau), v(1, \tau), \dots, v(\omega - 1, \tau))^T$ is a positive leading left eigenvector of the Leslie matrix

$$\bar{A}(\tau) = \begin{pmatrix} \bar{f}(0, \tau) & \bar{f}(1, \tau) & \dots & \bar{f}(\omega - 2, \tau) & \bar{f}(\omega - 1, \tau) \\ \bar{s}(0, \tau) & 0 & \dots & 0 & 0 \\ 0 & \bar{s}(1, \tau) & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & \bar{s}(\omega - 2, \tau) & 0 \end{pmatrix}, \tag{44}$$

with

$$\bar{f}(k, \tau) = \frac{\sum_{i=1}^n f_i(k)c_i(k, \tau)}{\sum_{i=1}^n c_i(k, \tau)}, \tag{45}$$

for $k = 0, 1, \dots, \omega - 1$, and

$$\bar{s}(k, \tau) = \frac{\sum_{i=1}^n s_i(k)c_i(k, \tau)}{\sum_{i=1}^n c_i(k, \tau)}, \tag{46}$$

for $k = 0, 1, \dots, \omega - 2$. Therefore,

$$\lambda(\tau)v(k, \tau) = v(0, \tau)\bar{f}(k, \tau) + v(k+1, \tau)\bar{s}(k, \tau), \tag{47}$$

for $k = 0, 1, \dots, \omega - 1$ with $v(\omega, \tau) = 0$, where $\lambda(\tau)$ is the positive leading eigenvalue of $\bar{A}(\tau)$.

Note that the mean fitness at time step $\tau \geq 0$ using the reproductive values as weights is given by

$$\begin{aligned} \bar{\lambda}(\tau) &= \frac{\sum_{k=0}^{\omega-1} \sum_{i=1}^n c_i(k, \tau)v(k, \tau)\lambda_i(k, \tau)}{\sum_{k=0}^{\omega-1} \sum_{i=1}^n c_i(k, \tau)v(k, \tau)} \\ &= \frac{\sum_{k=0}^{\omega-1} \sum_{i=1}^n c_i(k, \tau)(v(0, \tau)f_i(k) + v(k+1, \tau)s_i(k))}{\sum_{k=0}^{\omega-1} \sum_{i=1}^n c_i(k, \tau)v(k, \tau)} \\ &= \frac{\sum_{k=0}^{\omega-1} \sum_{i=1}^n c_i(k, \tau)(v(0, \tau)\bar{f}(k, \tau) + \bar{s}(k, \tau)v(k+1, \tau))}{\sum_{k=0}^{\omega-1} \sum_{i=1}^n c_i(k, \tau)v(k, \tau)} \\ &= \frac{\sum_{k=0}^{\omega-1} \sum_{i=1}^n c_i(k, \tau)\lambda(\tau)v(k, \tau)}{\sum_{k=0}^{\omega-1} \sum_{i=1}^n c_i(k, \tau)v(k, \tau)} = \lambda(\tau). \end{aligned} \tag{48}$$

In conclusion, the mean fitness in Grafen's sense in a discrete-time age-structured haploid population at any time step is equal to the geometric rate of increase or decrease in the total reproductive value of the population with average age-specific survival probabilities and fecundities at this time step.

In a continuous-time version, the fitness of an individual of haplotype $i = 1, \dots, n$ of age $x \geq 0$ at time $t \geq 0$, denoted by $m_i(x, t)$, is defined by

$$m_i(x, t)v(x, t) = \frac{dv(x, t)}{dx} + b_i(x)v(0, t) - \mu_i(x)v(x, t), \tag{49}$$

where

$$m(t)v(x, t) = \frac{dv(x, t)}{dx} + \bar{b}(x, t)v(0, t) - \bar{\mu}(x, t)v(x, t), \tag{50}$$

with

$$\bar{b}(x, t) = \frac{\sum_{i=1}^n b_i(x)c_i(x, t)}{\sum_{i=1}^n c_i(x, t)} \tag{51}$$

and

$$\bar{\mu}(x, t) = \frac{\sum_{i=1}^n \mu_i(x, t)c_i(x, t)}{\sum_{i=1}^n c_i(x, t)} \tag{52}$$

being the average birth and death rates of the individuals of age $x \geq 0$ at time $t \geq 0$ (Grafen, 2015a).

As in discrete time, we have

$$\bar{m}(t) = \frac{\int_0^\infty \sum_{i=1}^n c_i(x, t)v(x, t)m_i(x, t) dx}{\int_0^\infty \sum_{i=1}^n c_i(x, t)v(x, t) dx} = m(t), \tag{53}$$

which says that the mean fitness in Grafen's sense in a continuous-time age-structured haploid population at any time is equal to the Malthusian parameter of the population with average age-specific survival probabilities and fecundities at this time. Owing to the property of the Malthusian parameter given in Eq. (9), this is also the mean fitness for each age x as shown in Grafen (2015a, Eq. (16)). This ensures neutrality as defined in Grafen (2015b).

The mean fitness in Grafen's sense does not necessarily increase with time. This will be illustrated by a discrete-time example with two haplotypes in two age classes. The corresponding Leslie matrices are given by

$$A_1 = \begin{pmatrix} 9 & 4 \\ 0.4 & 0 \end{pmatrix}, \quad A_2 = \begin{pmatrix} 8 & 7 \\ 0.6 & 0 \end{pmatrix}, \tag{54}$$

with $\lambda_1 = 9.17$ and $\lambda_2 = 8.56$, respectively, being leading eigenvalues. The initial population state is chosen to be

$$\mathbf{c}_1(0) = \begin{pmatrix} c_1(0, 0) \\ c_1(1, 0) \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \quad \mathbf{c}_2(0) = \begin{pmatrix} c_2(0, 0) \\ c_2(1, 0) \end{pmatrix} = \begin{pmatrix} 0 \\ 1 \end{pmatrix}. \tag{55}$$

The Leslie matrix for the whole population at time step $\tau \geq 0$ is given by

$$\bar{A}(\tau) = \begin{pmatrix} \frac{9c_1(0, \tau) + 8c_2(0, \tau)}{c_1(0, \tau) + c_2(0, \tau)} & \frac{4c_1(1, \tau) + 7c_2(1, \tau)}{c_1(1, \tau) + c_2(1, \tau)} \\ \frac{0.4c_1(0, \tau) + 0.6c_2(0, \tau)}{c_1(0, \tau) + c_2(0, \tau)} & 0 \end{pmatrix}. \tag{56}$$

The leading eigenvalue $\lambda(\tau)$ of this matrix, which corresponds to the mean fitness in Grafen's sense, is represented in Fig. 1. It sharply decreases in the beginning before increasing rapidly and then slowly to the value λ_1 .

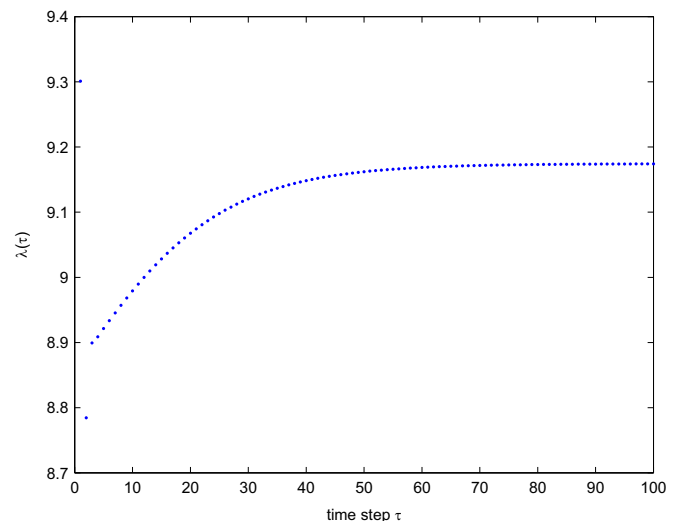


Fig. 1. Example 1.

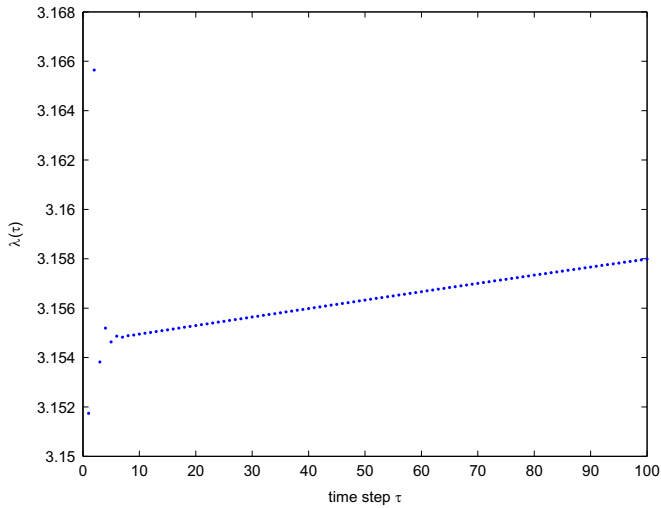


Fig. 2. Example 2.

Another example with

$$A_1 = \begin{pmatrix} 2 & 4.1 \\ 0.9 & 0 \end{pmatrix}, \quad A_2 = \begin{pmatrix} 2 & 4 \\ 0.9 & 0 \end{pmatrix}, \quad (57)$$

and

$$\mathbf{c}_1(0) = \begin{pmatrix} 0.5 \\ 0.5 \end{pmatrix}, \quad \mathbf{c}_2(0) = \begin{pmatrix} 0 \\ 1 \end{pmatrix} \quad (58)$$

leads to Fig. 2. There are oscillations between the values $\lambda_1 = 3.1656$ and $\lambda_2 = 3.1448$ followed by a slow increase to λ_1 .

The increase of the mean fitness in Grafen's sense for τ large enough observed in Figs. 1 and 2 is shown in general for two haplotypes and any number of age classes in Appendix A. This suggests quick convergence to the stable age distribution for each of the two haplotypes followed by differential increases in their sizes.

5. Fitness in the limit of weak selection

In order to model weak selection in a discrete-time age-structured asexual haploid population, let the Leslie matrix for haplotype $i = 1, \dots, n$ be given in the form

$$A_i(s) = A + sB_i, \quad (59)$$

with A as defined in (14) with leading positive eigenvalue $\lambda = 1$ and

$$B_i = \begin{pmatrix} \beta_i(0) & \beta_i(1) & \dots & \beta_i(\omega-2) & \beta_i(\omega-1) \\ \alpha_i(0) & 0 & \dots & 0 & 0 \\ 0 & \alpha_i(1) & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & \alpha_i(\omega-2) & 0 \end{pmatrix}. \quad (60)$$

This means that $s > 0$ is the intensity of selection and the entries of B_i are the coefficients of selection with respect to this intensity.

With s^{-1} time steps as unit of time, the numbers of individuals of haplotype i in the different age classes at time $t \geq 0$ are given by

$$\mathbf{c}_i(t) = (c_i(0, t), c_i(1, t), \dots, c_i(\omega-1, t))^T = A_i(s)^{\lfloor s^{-1}t \rfloor} \mathbf{c}_i(0), \quad (61)$$

where $\lfloor s^{-1}t \rfloor$ represents the integer part of $s^{-1}t$. Writing $A_i(s)$ in Jordan normal form yields

$$A_i(s) = (\mathbf{u}_i(s) \quad P_i(s)) \begin{pmatrix} \lambda_i(s) & \mathbf{0}^T \\ \mathbf{0} & J_i(s) \end{pmatrix} \begin{pmatrix} \mathbf{v}_i(s)^T \\ R_i(s) \end{pmatrix}, \quad (62)$$

where

$$\lambda_i(s) = 1 + m_i s + o(s) \quad (63)$$

is the leading positive eigenvalue of $A_i(s)$ with associated positive left and right eigenvectors $\mathbf{v}_i(s)$ and $\mathbf{u}_i(s)$, respectively, that satisfy

$$\mathbf{1}^T \mathbf{u}_i(s) = 1, \quad \mathbf{v}_i(s)^T \mathbf{u}_i(s) = 1. \quad (64)$$

Here, $\mathbf{1}$ and $\mathbf{0}$ denote vectors of all ones and all zeros, respectively. Moreover, $J_i(s)$ is a Jordan matrix associated with eigenvalues of $A_i(s)$ whose moduli are all less than $\lambda_i(s)$ and, by continuity, less than some positive number strictly smaller than $\lambda_i(0) = 1$ for s small enough. Finally, we have the equalities

$$\mathbf{v}_i(s)^T P_i(s) = \mathbf{0}^T, \quad R_i(s) \mathbf{u}_i(s) = \mathbf{0}, \quad R_i(s) P_i(s) = I, \quad (65)$$

where I designates an identity matrix. Then we get

$$A_i(s)^{\lfloor s^{-1}t \rfloor} = (\mathbf{u}_i(s) \quad P_i(s)) \begin{pmatrix} \lambda_i(s)^{\lfloor s^{-1}t \rfloor} & \mathbf{0}^T \\ \mathbf{0} & J_i(s)^{\lfloor s^{-1}t \rfloor} \end{pmatrix} \begin{pmatrix} \mathbf{v}_i(s)^T \\ R_i(s) \end{pmatrix} \rightarrow e^{m_i t} \mathbf{u} \mathbf{v}^T, \quad (66)$$

as s tends to 0 for any $t > 0$, where $\mathbf{v} = \mathbf{v}_i(0)$ and $\mathbf{u} = \mathbf{u}_i(0)$ are positive left and right eigenvectors, respectively, associated with the eigenvalue 1 of $A = A_i(0)$ that satisfy $\mathbf{1}^T \mathbf{u} = 1$ and $\mathbf{v}^T \mathbf{u} = 1$. In the same limit,

$$\mathbf{c}_i(t) \rightarrow (\mathbf{v}^T \mathbf{c}_i(0)) e^{m_i t} \mathbf{u}. \quad (67)$$

In particular, this implies a stationary age distribution given by \mathbf{u} at any time $t > 0$ in the limit of weak selection.

It remains to calculate m_i which is the derivative of the leading eigenvalue $\lambda_i(s)$ of $A_i(s)$ with respect to the intensity of selection evaluated at $s=0$. Since

$$\lambda_i(s) = \lambda_i(s) \mathbf{v}_i(s)^T \mathbf{u}_i(s) = \mathbf{v}_i(s)^T A_i(s) \mathbf{u}_i(s) = \mathbf{v}_i(s)^T (A + sB_i) \mathbf{u}_i(s), \quad (68)$$

we have

$$\begin{aligned} m_i &= \lambda'_i(0) = \mathbf{v}_i(0)^T B_i \mathbf{u}_i(0) + \mathbf{v}'_i(0)^T A \mathbf{u}_i(0) + \mathbf{v}_i(0)^T A \mathbf{u}'_i(0) \\ &= \mathbf{v}^T B_i \mathbf{u} + \mathbf{v}'_i(0)^T \mathbf{u}_i(0) + \mathbf{v}_i(0)^T \mathbf{u}'_i(0) = \mathbf{v}^T B_i \mathbf{u}, \end{aligned} \quad (69)$$

owing to (64). This is in agreement with a well-known result on irreducible aperiodic non-negative matrices (see, e.g., Lancaster and Tismenetsky, 1985).

Defining

$$V_i(t) = \mathbf{v}^T \mathbf{c}_i(t), \quad (70)$$

we have

$$\frac{dV_i(t)}{dt} = m_i V_i(t), \quad (71)$$

from which

$$\frac{d\bar{m}(t)}{dt} = \sum_{i=1}^n m_i^2 p_i(t) - \bar{m}(t)^2, \quad (72)$$

as in Section 3, where

$$\bar{m}(t) = \sum_{i=1}^n m_i p_i(t), \quad (73)$$

with

$$p_i(t) = \frac{V_i(t)}{\sum_{j=1}^n V_j(t)}. \quad (74)$$

This means that m_i is the relative rate of change of the total reproductive value of haplotype i and that the rate of change of their mean value is given by their variance. This is the growth-rate theorem in the limit of weak selection.

Finally, (69) leads to the expression

$$m_i = \sum_{k=0}^{\omega-1} u(k) (v(0) \beta_i(k) + v(k+1) \alpha_i(k)), \quad (75)$$

where $u(k)$ and $v(k)$ are the frequency and reproductive value, respectively, of the individuals of haplotype i in age class k , with $v(\omega) = 0$. This weighted average can be written into the form

$$m_i = \sum_{k=0}^{\omega-1} u(k)v(k)m_i(k), \quad (76)$$

where

$$m_i(k) = \frac{v(0)\beta_i(k) + v(k+1)\alpha_i(k)}{v(k)}. \quad (77)$$

This represents the relative rate of change of the reproductive value of the individuals of haplotype i in age class k .

A discrete-time analogue with Δt as the time step would lead to a geometric rate of increase or decrease in the total reproductive value of haplotype i given by

$$\lambda_i = 1 + m_i\Delta t + o(\Delta t) = \sum_{k=0}^{\omega-1} u(k)v(k)\lambda_i(k), \quad (78)$$

where, using (17) with $\lambda = 1$, we have

$$\begin{aligned} \lambda_i(k) &= 1 + m_i(k)\Delta t + o(\Delta t) = \frac{v(0)f(k) + v(k+1)s(k)}{v(k)} \\ &\quad + \frac{v(0)\beta_i(k) + v(k+1)\alpha_i(k)}{v(k)}\Delta t + o(\Delta t) \\ &= \frac{v(0)(f(k) + \beta_i(k)\Delta t + o(\Delta t)) + v(k+1)(s(k) + \alpha_i(k)\Delta t + o(\Delta t))}{v(k)}. \end{aligned} \quad (79)$$

This is in agreement with Grafen's definition of fitness in discrete time as described in (19) with

$$f_i(k) = f(k) + \beta_i(k)\Delta t + o(\Delta t), \quad s_i(k) = s(k) + \alpha_i(k)\Delta t + o(\Delta t). \quad (80)$$

Note that this gives an approximation for Δt small enough but much larger than the intensity of selection s .

In summary, in a discrete-time age-structured asexual haploid population in the limit of weak selection with the inverse of the intensity of selection as the unit of time, the same stationary age distribution is reached for each type and the growth-rate theorem holds with the relative rate of increase or decrease in reproductive value given by a weighted average of fitnesses in Grafen's sense as defined in Eq. (76).

6. Discussion

Grafen (2015a) argues that Fisher's (1930) FTNS in age-structured populations concerns individual rather than population fitness maximization by considering variation in the individual properties, namely birth and death rates in continuous time or fecundities and survival probabilities in discrete time, while keeping fixed the population level properties, namely the age-specific reproductive values defined with respect to mean age-specific birth and death rates. These reproductive values used in the definition of fitness ensure neutrality in mean fitness from one age class to another (Grafen, 2015b). This condition can be traced back to a notion of reproductive value introduced in Williams (1966) and agrees with Charlesworth's (1980, 1994) approximations under the assumption of demographic equilibrium. Then it is shown that the rate of change in the mean of the breeding values of fitness weighted by the reproductive values, all kept constant, is equal to the additive genetic variance in fitness.

Fisher (1930) used demographic life tables for a whole population to introduce the concepts of Malthusian parameter and reproductive value. As far as we can see, however, nothing in this book and related further works (Fisher, 1941, 1958) suggests anything else than a genotype-specific Malthusian parameter as

definition of fitness of a genotype in age-structured populations, which implies age- and genotype-specific reproductive values. We stand behind the interpretation of the FTNS given in Lessard (1997) based on this definition of fitness and the notion of genic environment as part of the environment as explained in Fisher (1941): it concerns a partial change in the mean of the Malthusian parameters weighted by the reproductive values, all kept constant, with respect to the relative changes in the genotypic frequencies as best predicted from the genes present.

Grafen's (2015a) and Lessard's (1997) analyses are both for a diploid population but the two definitions of fitness hold as well for a haploid population. In this paper, we have compared the implications of these definitions in the extreme case of an asexual haploid population. This allows us to isolate the differences between the two definitions from the differences caused by Mendelian segregation and genetic recombination.

In the framework of an age-structured asexual haploid population with constant demographic vital parameters for each type (namely, constant age-specific birth and death rates in continuous time or constant survival probabilities and fecundities in discrete time), we have recalled in Sections 2 and 3 that defining fitness as a genotype-specific Malthusian parameter and using age- and genotype-specific reproductive values as weights lead to a mean fitness whose rate of change in continuous time is exactly equal to the variance in fitness (or whose change in discrete time is exactly equal to the variance in fitness divided by the mean fitness). This is in agreement with a simplified version of Fisher's (1930) FTNS for an age-structured haploid population in continuous time in a constant environment which includes a constant genic environment (or Ewens's (1989) version of this theorem for a population in discrete time without age structure). This corresponds to a generalized growth-rate theorem.

In the same simplified framework of an asexual haploid population with constant demographic vital parameters for each type, we have shown in Section 5 that the same stationary age distribution for each type is reached in the limit of weak selection. In this limit, the life-span of an individual can be neglected compared to the inverse of differences in the vital parameters from one individual to another of the same age. Moreover, in this same limit, Grafen's (2015a) definition of individual fitness as the relative rate of change in reproductive value in continuous time (or the relative change in reproductive value in discrete time) by using common age-specific reproductive values is consistent with the growth-rate theorem.

Grafen's definition of fitness ignores differential age-specific contributions to the population in the future from one type to another. This assumes that the individuals produced are indistinguishable. Even with constant demographic vital rates and in the absence of genetic recombination and segregation, this fitness is frequency-dependent and its mean obtained by using the population age-specific reproductive values as weights can decrease. This has been shown in Section 4 by numerical iterations for two haplotypes with two age classes in discrete time. Such a decrease is rare, however, and appears to be a transient phenomenon from some initial population states. These numerical results suggest relatively quick convergence to a stationary age distribution so that Grafen's definition seems to capture the leading part of fitness in the long run. The increase of the mean fitness in Grafen's sense in the long run has been confirmed in general for two haplotypes with any number of age classes (Appendix A). This is also in agreement with our weak selection limit for any number of haplotypes which shows that Grafen's definition predicts the right population dynamics (Section 5).

Note that our numerical results are not counterexamples of the main result in Grafen (2015a) since this result concerns a partial change in mean fitness obtained by keeping the population age-

specific reproductive values constant. They show, however, that this partial change captures only a part of the partial change with the Malthusian parameter as definition of fitness. It could be argued that the population age-specific reproductive values are part of the environment. Since changes in the environment are not taken into account in Fisher's (1930) FTNS, the population age-specific reproductive values are kept constant. This is one of the conditions under which the partial rate of change in mean fitness is obtained in Grafen (2015a). However, this requires an interpretation of the environment that we have not found anywhere in Fisher's writings. This interpretation is a consequence of the definition of fitness based on population age-specific reproductive values to satisfy a principle of neutrality (Grafen, 2015b). This definition is such that the mean fitness in each age class is the same, and then equal to the population Malthusian parameter owing to the properties of this parameter.

It seems difficult to conceive from a biological point of view that the contribution of an individual in the future may have an effect on its fitness at the present time as occurs with fitness defined by a genotype-specific Malthusian parameter. Moreover, a reproductive value, which is an expected contribution to all future generations, remains an abstract concept. This may explain why Fisher (1930, 1958) did not get into the details in his formulation of the FTNS. By weighting the individuals with their reproductive values, the frequencies of types are actually frequencies of reproductive values carried by these types. The notation and the analysis, not to mention the interpretation, in the general framework of an age-structured population become rather complicated and less intuitive (see Lessard, 1997, for a full analysis).

Simplifying assumptions such as haploidy and constant vital rates made in this paper have allowed us to better compare two definitions of fitness in age-structured populations in relation with the FTNS. Moreover, we have shown that both definitions agree in the limit of weak selection (Section 5). An extension of our weak-selection limit to a multi-locus diploid age-structured population is likely possible, but it would require a much more recondite mathematical analysis than in the haploid case.

In the more general framework of a diploid population in a changing environment including a changing genic environment as a result of recombination and Mendelian segregation, Fisher's (1930, 1958) FTNS concerns a change in mean fitness that has been called by different names (change due to changes in gene frequencies, change due or ascribable to natural selection, partial change, genic evolutionary potential) and has received various interpretations (Price, 1972; Ewens, 1989; Castilloux and Lessard, 1995; Lessard, 1997; Ewens and Lessard, 2015). The total change in mean fitness has been obtained for one- and two-locus models without age structure (Kempthorne, 1957; Kimura, 1958). It has been shown that the partial change is a good approximation of the total change under weak frequency-independent viability selection even in a multilocus setting but without age structure (Nagyilaki, 1991, 1993). See also Crow (1979) for the total change in the mean of fitnesses weighted by genotype- (or allele-) and age-specific reproductive values in one-locus age-structured populations.

From a historical perspective, Edwards (2014) concludes that the FTNS expresses a gene-centered view of evolution. In comparison, Grafen (2015a) proposes an individual-centered view more in agreement with some modern trends in evolutionary biology. The ensuing result on the partial rate of change in mean fitness may be correct and its interpretation may make sense, but it is legitimate to question whether it represents Fisher's (1930) FTNS as originally stated. On the other hand, the interpretation of the theorem to support individual optimization has already been criticized for not being representative of the Fisherian tradition (Edwards, 2014).

Although it may not be the definition meant in Fisher's (1930) FTNS, Grafen's (2015a) definition of individual fitness in an age-structured population as if this population would satisfy the principle of neutrality from one age class to another is of interest: it isolates differences between individual contributions at any given time from changes in population structure and composition at that time. Moreover, it seems to give a good approximation of the Malthusian parameter in the long run, and even to predict the right dynamics in the limit of weak selection at least in haploid populations.

Recent approaches in evolutionary theory such as inclusive fitness theory (Hamilton, 1964), continuous stability theory (Eshel, 1983) and adaptive dynamics (Geritz et al., 1998) have been very successful in predicting results of evolution and, therefore, very popular in behavioral ecology. We have to remember, however, that they often rely on initial increase properties or assumptions of weak selection. The assumption of demographic equilibrium, which is akin to the principle of neutrality among different age classes, is widely spread in behavioral ecology. If this assumption is used to predict long-term and even short-term evolution, however, the underlying conditions for such an equilibrium to take place must not be forgotten.

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Appendix A

In this appendix, we show that the mean fitness in Grafen's sense in a discrete-time age-structured haploid population with two haplotypes monotonically increases in the long run to the largest geometric rate of increase of the two haplotypes.

Let A_i in the form (14) be the Leslie matrix with leading eigenvalue λ_i and associated left and right eigenvectors \mathbf{v}_i and \mathbf{u}_i , as defined in (15), for haplotype $i = 1, 2$. The Perron–Frobenius theory ascertains that the numbers of individuals of haplotype i in the different age classes at time step $\tau \geq 0$ satisfy

$$\mathbf{c}_i(\tau) = A_i^\tau \mathbf{c}_i(0) = \lambda_i^\tau \mathbf{u}_i \mathbf{v}_i^T \mathbf{c}_i(0) + o(\lambda_i^\tau), \quad (81)$$

with

$$\frac{o(\lambda_i^\tau)}{\lambda_i^\tau} \rightarrow 0, \quad (82)$$

as $\tau \rightarrow \infty$.

We assume $\lambda_1 > \lambda_2$ and we consider the difference $\bar{A}(\tau) - A_1$, where $\bar{A}(\tau)$ is the Leslie matrix for the whole population given by (48) and A_1 is the Leslie matrix for haplotype 1. The difference between the fecundities in age class $k = 0, \dots, \omega - 1$ is given by

$$\begin{aligned} \bar{f}(k, \tau) - f_1(k) &= \frac{f_1(k)c_1(k, \tau) + f_2(k)c_2(k, \tau)}{c_1(k, \tau) + c_2(k, \tau)} - f_1(k) \\ &= (f_2(k) - f_1(k)) \frac{\frac{c_2(k, \tau)}{c_1(k, \tau)}}{1 + \frac{c_2(k, \tau)}{c_1(k, \tau)}}, \end{aligned} \quad (83)$$

where

$$\frac{c_2(k, \tau)}{c_1(k, \tau)} = \frac{\lambda_2^\tau u_2(k) \mathbf{v}_2^T \mathbf{c}_2(0) + o(\lambda_2^\tau)}{\lambda_1^\tau u_1(k) \mathbf{v}_1^T \mathbf{c}_1(0) + o(\lambda_1^\tau)} = \left(\frac{\lambda_2}{\lambda_1}\right)^\tau \frac{u_2(k) \mathbf{v}_2^T \mathbf{c}_2(0)}{u_1(k) \mathbf{v}_1^T \mathbf{c}_1(0)} + o\left(\left(\frac{\lambda_2}{\lambda_1}\right)^\tau\right). \quad (84)$$

This leads to

$$\bar{f}(k, \tau) - f_1(k) = (f_2(k) - f_1(k)) \left(\frac{\lambda_2}{\lambda_1} \right)^\tau \frac{u_2(k) \mathbf{v}_2^T \mathbf{c}_2(0)}{u_1(k) \mathbf{v}_1^T \mathbf{c}_1(0)} + o \left(\left(\frac{\lambda_2}{\lambda_1} \right)^\tau \right). \quad (85)$$

Similarly, the difference between the survival probabilities in age class $k = 0, \dots, \omega - 1$ is given by

$$\bar{s}(k, \tau) - s_1(k) = (s_2(k) - s_1(k)) \left(\frac{\lambda_2}{\lambda_1} \right)^\tau \frac{u_2(k) \mathbf{v}_2^T \mathbf{c}_2(0)}{u_1(k) \mathbf{v}_1^T \mathbf{c}_1(0)} + o \left(\left(\frac{\lambda_2}{\lambda_1} \right)^\tau \right). \quad (86)$$

In matrix notation, we have

$$\bar{A}(\tau) = A_1 + \left(\frac{\lambda_2}{\lambda_1} \right)^\tau (A_2 - A_1) D + o \left(\left(\frac{\lambda_2}{\lambda_1} \right)^\tau \right),$$

with

$$D = \text{diag} \left(\frac{u_2(0) \mathbf{v}_2^T \mathbf{c}_2(0)}{u_1(0) \mathbf{v}_1^T \mathbf{c}_1(0)}, \dots, \frac{u_2(\omega-1) \mathbf{v}_2^T \mathbf{c}_2(0)}{u_1(\omega-1) \mathbf{v}_1^T \mathbf{c}_1(0)} \right).$$

As in Section 5 with $s = (\lambda_2/\lambda_1)^\tau$, $A = A_1$ and $B = (A_2 - A_1)D$, the leading eigenvalue of $\bar{A}(\tau)$ is given by

$$\lambda(\tau) = \lambda_1 + \left(\frac{\lambda_2}{\lambda_1} \right)^\tau \mathbf{v}_1^T (A_2 - A_1) D \mathbf{u}_1 + o \left(\left(\frac{\lambda_2}{\lambda_1} \right)^\tau \right). \quad (87)$$

Observe that

$$D \mathbf{u}_1 = \rho \mathbf{u}_2,$$

where

$$\rho = \frac{\mathbf{v}_2^T \mathbf{c}_2(0)}{\mathbf{v}_1^T \mathbf{c}_1(0)}$$

is a positive scalar. Therefore,

$$\mathbf{v}_1^T (A_2 - A_1) D \mathbf{u}_1 = \rho \mathbf{v}_1^T A_2 \mathbf{u}_2 - \rho \mathbf{v}_1^T A_1 \mathbf{u}_2 = \rho \mathbf{v}_1^T \mathbf{u}_2 (\lambda_2 - \lambda_1) < 0.$$

This implies that

$$\lambda_1 > \lambda(\tau + 1) > \lambda(\tau)$$

for τ large enough.

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