

NOTE

Generation Time in Stage-Structured Populations under Fluctuating Environments

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ABSTRACT: A common measure of generation time is the average distance between two recruitment events along a genetic lineage. In populations with stage structure that live in a constant environment, this generation time can be computed from the elasticities of stable population growth to fecundities, and it is equivalent to another common measure of generation time: the average parental age of reproductive-value-weighted offspring. Here, we show three things. First, when the environment fluctuates, the average distance between two recruitment events along a genetic lineage is computed from the elasticities of the stochastic growth rate to fecundities. Second, under environmental stochasticity, this measure of generation time remains equivalent to the average parental age of reproductive-value-weighted offspring. Third, the generation time of a population in a fluctuating environment may deviate from the generation time the population would have in the average environment.

Keywords: age, environmental stochasticity, elasticities, genetic lineage, reproductive value.

Introduction

Roughly, a generation is the time separating the birth of parents from the birth of their offspring. Generations set a natural timescale for many ecological and evolutionary processes. For example, mutations occur in the parental germline. But their presence is first detected in the offspring. The rate of genetic substitutions in a population is then conveniently expressed in units of generations (Kimura 1968). Looking at the ability to adapt to ecological changes, a given rate of environmental change per unit time requires species with generations of different lengths to evolve at different rates per generation to secure survival (Chevin et al. 2010). In conservation studies of endangered species, life span may differ wildly, ranging from days to years. Expressing population decline and extinction risks over

generations helps cross-species comparison (Mace et al. 2008).

Computing the time distance between generations is not entirely obvious when populations have stage structure. In these populations, individuals belong to distinct stages depending on the value of some trait (e.g., age, size, or developmental phase). Individuals may produce offspring at different points in life. For example, reproduction may be possible only at a minimal size. However, attaining this size requires sufficient resources, which the members of a newborn cohort may not be able to accrue simultaneously. Because of later heterogeneous scarcity of such resources, some individuals could fail to maintain the minimal size and, thus, discontinue reproduction. When reproduction eventually occurs, offspring may be born in different stages (e.g., large individuals may contribute large offspring). Stage at birth impacts the timing of one's future production of offspring, as larger offspring should reach the minimal reproductive size quicker.

The intricacies inherent to population structure have led to devise distinct measures of generation time (Cochran and Ellner 1992; Caswell 2009; Steiner et al. 2014; Bienvenu and Legendre 2015), which only in some cases are equivalent (Ellner 2018; Jonasson et al. 2022). A shared feature of these measures, however, is their assumption that the population lives in a constant environment. But populations typically experience fluctuating environmental conditions.

A measure of generation time under stochastic demography has been derived for the special case of age structure (Lehmann 2014)—that is, stages are ages. Another measure has been proposed to account for environmental stochasticity (Hernandez-Suarez et al. 2012). But this measure relies on an approach (i.e., the megamatrix model) that is not directly informative about the long-term growth of a single population (Tuljapurkar et al. 2003). To the best of our knowledge, no measure proposed so far appears both to

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apply to any stage structure and to build on the usual machinery for demography in variable environments, as in Tuljapurkar (1990). The purpose of the present work is to obtain a measure of generation time with both these characteristics.

To this aim, we first review some demographic notions and introduce two common concepts of generation time. Building on the approach of Bienvenu and Legendre (2015) for a constant environment and using insights from the work of Lehmann (2014), Ellner (2018), and Lion (2018), we extend both concepts to the case of environmental stochasticity and show their equivalence. In the end, we illustrate the usefulness of our proposed measure of generation time. Analyzing published demographic data, we show that the generation time of a population in a fluctuating environment may be only poorly approximated by the generation time the population would have in the average environment. This exposes the limited validity of estimating the former via the latter.

Demographic Model

We adopt the framework of matrix population models (for an introduction, see Caswell 2001). The matrix $\mathbf{A}(t) = [a_{ij}(t)]$ projects the vector $\mathbf{x}(t)$ of individual stage-specific abundances so that $a_{ij}(t)$ is the number of individuals in stage i at $t + 1$ per individual in stage j at t and

$$\mathbf{x}(t + 1) = \mathbf{A}(t)\mathbf{x}(t). \tag{1}$$

Distinguishing survival events from recruitment events, the projection matrix decomposes into a sum $\mathbf{A}(t) = \mathbf{S}(t) + \mathbf{F}(t)$ between the survival matrix $\mathbf{S}(t) = [s_{ij}(t)]$ and the fecundity matrix $\mathbf{F}(t) = [f_{ij}(t)]$, where $s_{ij}(t)$ is the probability that an individual in stage j at t survives to be found in stage i at $t + 1$, while f_{ij} is the number of new recruits in stage i at $t + 1$ that were born to an individual in stage j at t . The projection matrix depends on t because at each time point the environment is in one of a finite number of states. To each state, there corresponds a projection matrix that reflects population demographics in that state. A stochastic process governs the time sequence of environmental states and, consequently, of projection matrices. While this accounts for environmental stochasticity, we ignore demographic stochasticity (i.e., sampling variation in survival and fecundity) by assuming that the population is large enough so that the realized matrix at t deterministically projects the population to $t + 1$. We also assume that the environmental and demographic processes are stationary and ergodic and that a stochastic growth rate $\ln \lambda_s$ characterizes every realization of the demographic process so that, almost surely,

$$\ln \lambda_s = \lim_{t \rightarrow \infty} [(t^{-1}(\ln X(t) - \ln X(0))), \tag{2}$$

where $X(t)$ is the population size at t and $\ln \lambda_s$ is a constant independent of the stage distribution at $t = 0$. A detailed treatment of ergodicity in demography and of the existence conditions of $\ln \lambda_s$ is given in Cohen (1977a, 1977b) and Tuljapurkar (1990).

When the environment is constant, there is a single projection matrix $\mathbf{A} = \mathbf{S} + \mathbf{F}$. At demographic stability, the population size changes by a constant factor λ per time step. This factor is equal to the dominant eigenvalue of \mathbf{A} .

Generation Time in a Constant Environment

In genetics, the generation time is usually defined as the average time from zygote to zygote along a genetic lineage (Scully 2016). A genetic lineage is the path that a randomly sampled gene follows in backward time through all of the individuals that have hosted the gene (fig. 1). At some point in the past along the genetic lineage, the individual currently hosting the gene becomes a zygote. Hence, the gene next moves (as a copy) into the parent of this individual. This parent also becomes a zygote at some point in backward time, and the gene then moves to the grandparent of the initial individual. This cycle repeats itself indefinitely. Break down the genetic lineage into segments joining successive zygote formation events. The generation time is the average length of these segments.

Bienvenu and Legendre (2015) quantified this genetic notion of generation time for stage-structured populations that live in a constant environment and are demographically stable. Demographic models, however, rarely include a zygote stage. Thus, these authors focused on the average time G between two successive recruitment events along a genetic lineage. Bienvenu and Legendre (2015) proposed the formula

$$G = \frac{\lambda}{\mathbf{v}^T \mathbf{F} \mathbf{w}} \tag{3}$$

for this generation time, where \mathbf{w} is the stage distribution at demographic stability and \mathbf{v} is the vector of stage-specific reproductive values. These vectors are assumed scaled so that the components of \mathbf{w} add up to 1 and $\mathbf{v}^T \mathbf{w} = 1$, where \mathbf{T} indicates vector transposition. Note that the time length that G captures is not equivalent to the demographic notion of interbirth interval (Keyfitz and Caswell 2005, chap. 16). The quantity G is backward looking and lineage centered. It captures the time elapsed since the birth of an offspring to the birth of its mother

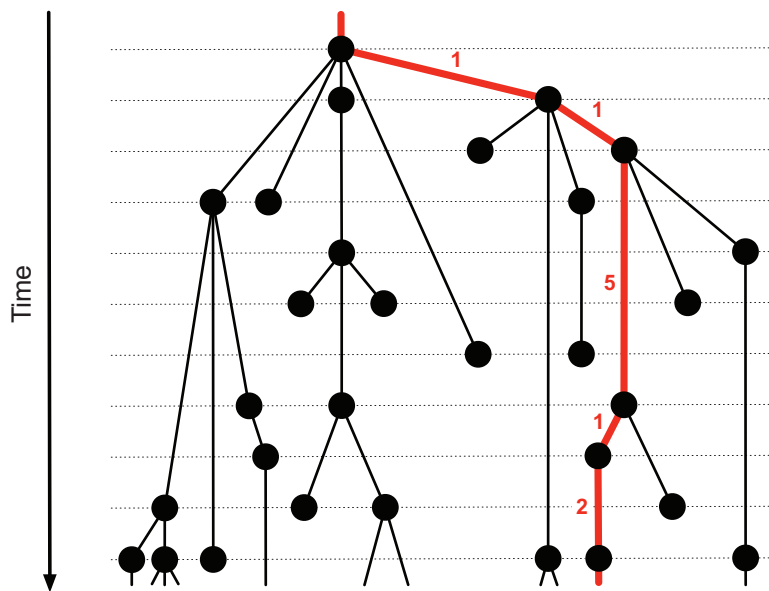


Figure 1: Genetic lineage and generation time. In this scheme, horizontal dashed lines indicate discrete time points. Each circle on a line is an individual at the time of first appearance (age 1) in the population regardless of stage. Lines between circles indicate parent-offspring relationships. Individuals can have offspring at different ages in their life. Individual age increases with time. The number of offspring produced at each time point and the probability of surviving to the next age depend on individual stage and on environmental state (neither are shown here). Sampling a random gene in the future and tracking its path (red) in backward time as it climbs up from offspring to parent along the genealogy defines a genetic lineage. The relevant quantity here is the time distance (red numbers) between two successive recruitment events. The generation time is defined here as the average of this distance along the entire genetic lineage.

and from the birth of this mother to the birth of the grandmother of the initial offspring and so on. The interbirth interval is forward looking and individual centered. It measures how far apart, on average, are all offspring births to the same mother. However, lineage-based considerations are common in demography as well, as they are behind renewal equations like the Euler-Lotka model (Keyfitz and Caswell 2005, chap. 7; Bienvenu and Legendre 2015; Inaba 2017, chap. 1).

Biodemography has produced distinct measures of generation time for stage-structured populations that experience a constant environment (Cochran and Ellner 1992; Caswell 2001; Steiner et al. 2014; Ellner 2018). One of these measures is the weighted average age \bar{A} at t of the parents of new recruits at $t + 1$ (Cochran and Ellner 1992; Ellner 2018). Assuming demographic stability, the age-stage distribution of individuals, and therefore of parents, is constant, and so are the production of new recruits and their stage distribution. The average can then be taken at any time point. The weights for this average are the reproductive value of new recruits. Since new recruits can be found in different stages, this weighting accounts for their different future contributions to the population. As Ellner (2018) notes, the reproductive-value weighting is entirely natural in this context. Some newborns die before their first census. Thus, they are in-

visible to the demographic model. (For the very same reason, G takes a generation to be the time between recruitment events, and not between zygotes, along a genetic lineage.) By extension, Ellner argues, one should explicitly discount those offspring that are first observed in stages (e.g., too small) that make any contribution of these offspring to the population unlikely. This is exactly what the reproductive-value weighting accomplishes. The formula for \bar{A} is complex (Cochran and Ellner 1992, eq. [26]), so we do not give it here. However, this formula is not really needed because the genetic measure G and the biodemographic measure \bar{A} of generation time can be shown equivalent:

$$A = G. \quad (4)$$

See Bienvenu and Legendre (2015) and Ellner (2018). In the next section, we separately extend each of these two measures of generation time to the case of environmental stochasticity, and we show that an equivalence still holds.

We end this section by recalling that \bar{A} should not be confused with the cohort generation time μ_1 , which gives the mean age at which a cohort of new recruits give birth, or with the time T that it takes for a population to change in size by a factor equal to the net reproduction rate (R_0) of the average individual (Cochran and Ellner 1992; Caswell 2001, chap. 5.3.5). Both μ_1 and T have been used to measure

the length of a generation in a constant environment. Some version of μ_1 (possibly with reproductive-value weighting) is common in demographic and evolutionary analyses that use the next-generation matrix (e.g., Durinx et al. 2008; Metz and de Kovel 2013; Steiner et al. 2014; Inaba 2017, chap. 9; Ellner 2018) or approximate stable population growth from R_0 (e.g., Tuljapurkar et al. 2009; Steiner et al. 2014). An overview of the relationships among \bar{A} , T , and μ_1 is given in Ellner (2018) and Jonasson et al. (2022).

Generation Time and Environmental Stochasticity

Elasticities

Tuljapurkar (1990) pioneered a form of sensitivity analysis of the stochastic growth rate that is now common in empirical studies of populations living in a fluctuating environment (e.g., Jonzén et al. 2010; Gaoue et al. 2011; Smallegange and Coulson 2011; van der Meer et al. 2014; Gamelon et al. 2016; Paniw et al. 2020). For our purposes, we recall here one quantity from this analysis: the elasticity e_{ij}^s , which quantifies the sensitivity of $\ln \lambda_s$ to the same proportional change in the (i, j) entry of all projection matrices. The relevant formula is

$$e_{ij}^s = \lim_{L \rightarrow \infty} \frac{1}{L} \sum_{t=0}^{L-1} \frac{v_i(t+1)a_{ij}(t)w_j(t)}{\lambda(t)} \quad (5)$$

(see Caswell 2001, eq. [14.98]), where $v_i(t)$ is the reproductive value of individuals in stage i at time t and $w_j(t)$ is the population fraction in stage j at time t . These quantities are assumed scaled so that for all t the components of the time-specific stage distribution $\mathbf{w}(t)$ add up to 1 and

$$\mathbf{v}^T(t)\mathbf{w}(t) = 1. \quad (6)$$

The quantity $\lambda(t)$ in equation (5) is the factor by which the population size changes between t and $t + 1$:

$$\lambda(t) = \frac{X(t+1)}{X(t)}. \quad (7)$$

Since $a_{ij}(t)$ is a random variable, the elasticity e_{ij}^s can be seen as the sensitivity of $\ln \lambda_s$ to a proportional change of the same magnitude in both the mean and the standard deviation of this variable, thereby leaving its coefficient of variation unaltered (Tuljapurkar et al. 2003).

The elasticity e_{ij} of stable population growth λ is the sensitivity of $\ln \lambda$ to a proportional change in the (i, j) entry of \mathbf{A} . A formula for this quantity is

$$e_{ij} = \frac{v_i a_{ij} w_j}{\lambda} \quad (8)$$

(see, e.g., de Kroon et al. 1986).

Genetic Approach

Using equation (8), Bienvenu and Legendre (2015) proposed the following alternative formula for G in equation (3):

$$G = \frac{1}{e_F}, \quad (9)$$

where $e_F = \sum_{ij} v_i f_{ij} w_j / \lambda = \lambda^{-1} \mathbf{v}^T \mathbf{F} \mathbf{w}$ is the sum of the elasticities of λ to fecundities. This result and the close correspondence between equation (5) and equation (8) are clues that the genetic concept that is behind G could extend to fluctuating environments via the stochastic elasticities. In particular, one can envisage that the sum e_F^s of the elasticities of λ_s to fecundities, which by equation (5) is

$$e_F^s = \lim_{L \rightarrow \infty} \frac{1}{L} \sum_{t=0}^{L-1} \frac{\mathbf{v}^T(t+1)\mathbf{F}(t)\mathbf{w}(t)}{\lambda(t)}, \quad (10)$$

may play a role in this extension. Here, we show that this indeed is the case.

Following Bienvenu and Legendre (2015), we look at a genetic lineage traveling in backward time through the individuals of a stage-structured population. Of our interest are the visits of the genetic lineage to new recruits at their first census. We assign age 1 to these recruits, and we count age in the same time units as demographic projection. Thus, an individual of age j at t is of age $j + 1$ at $t + 1$, and new recruits at their first census exactly form age class 1. The generation time of our interest then is the mean first return time of the genetic lineage to age class 1 (Lehmann 2014).

We recall the work of Lion (2018), who noted that when demographic parameters change with time,

$$b_{ij}(t) = \frac{a_{ij}(t)w_j(t)}{\lambda(t)w_i(t+1)} \quad (11)$$

is the probability that a randomly sampled gene in stage i at $t + 1$ is in stage j at t . This is because there are $w_j(t)X(t)$ individuals in stage j at t , where $X(t)$ is the total population size at t . They each contribute $a_{ij}(t)$ individuals to stage i at $t + 1$. These contributed individuals are a fraction $a_{ij}(t)w_j(t)X(t)/X(t+1)$ of the total population size $X(t+1)$ at $t + 1$. Taking the ratio of this fraction to the total fraction $w_i(t+1)$ in stage i at $t + 1$ gives the probability that a random gene in stage i at $t + 1$ is in stage j at t . Expressing this ratio by using equation (7) yields equation (11). Lion (2018) also noted that the matrix $\mathbf{B}(t) = [b_{ij}(t)]$ is row stochastic and updates in backward time the vector with component i equal to $v_i(t+1)w_i(t+1)$ (see the appendix). Thus, $v_i(t+1)w_i(t+1)$ can be interpreted as the probability that a gene randomly sampled in the future population belongs to a genetic lineage that was in stage i at $t + 1$ when looking backward in the past. The matrix $\mathbf{B}(t)$ generalizes a Markov chain model of genetic lineages over stages that is

classic to the population genetics of stable populations in a constant environment (Bodmer and Cavalli-Sforza 1968; Hill 1972; Taylor 1990, 1996; Rousset 2004; Lehmann 2014).

We leverage this result of Lion (2018) by defining

$$w_{ij}(t) = \text{population fraction in stage } i \text{ and of age } j \text{ at } t \quad (12)$$

as the component i of the vector $\mathbf{w}_j(t)$, which contains the stage distribution aged j . Thus, $\mathbf{v}^\top(t+1)\mathbf{w}_1(t+1)$ is the probability that a gene randomly sampled in the future population belongs to a genetic lineage that was in age class 1 at $t+1$, independently of the stage it was in at $t+1$. Suppose we can take the limit

$$\pi_1 = \lim_{L \rightarrow \infty} \frac{1}{L} \sum_{t=0}^{L-1} \mathbf{v}^\top(t+1)\mathbf{w}_1(t+1). \quad (13)$$

If it exists, this limit is the long-run fraction of time that the gene spends in age class 1. To establish the existence of this limit, we recall that the fraction aged 1 of the stage distribution at $t+1$ is the number of new recruits produced by the population at t relative to the total population size at $t+1$. Using the fecundity matrix $\mathbf{F}(t)$ and equation (7),

$$\mathbf{w}_1(t+1) = \frac{\mathbf{F}(t)\mathbf{X}(t)\mathbf{w}(t)}{\mathbf{X}(t+1)} = \frac{\mathbf{F}(t)\mathbf{w}(t)}{\lambda(t)}. \quad (14)$$

Plugging equation (14) into equation (13) and looking at the formula for the stochastic elasticities in equation (5) shows that

$$\pi_1 = e_F^s. \quad (15)$$

Therefore, the limit in equation (13) exists and is equal to the sum of the elasticities of λ_s to fecundities. By Markov chain theory (Kemeny and Snell 1983, p. 218), the inverse of this limit is the mean first return time to age class 1 by the genetic lineage. Hence, we suggest that the quantity

$$G_s = \frac{1}{e_F^s} \quad (16)$$

measures the generation time under a fluctuating environment, as the measure G proposed by Bienvenu and Legendre (2015) does under a constant environment.

Biodemographic Approach

Cochran and Ellner (1992) measured the generation time in the demographically stable state as the average parental age \bar{A} of offspring weighted by their reproductive value. Here, we propose an analog \bar{A}_s of \bar{A} under environmental stochasticity. From equations (12) and (14), the reproductive value of new recruits at $t+1$ that are contributed by individuals of age j at t independently of parental stage is

$$c_j(t) = \frac{\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}_j(t)}{\lambda(t)}. \quad (17)$$

The sum of these contributions over all parental ages,

$$c(t) = \sum_j c_j(t), \quad (18)$$

is the total reproductive value in new recruits at $t+1$. The average parental age at t of all new recruits at $t+1$ when these are weighted by their reproductive values then is

$$\bar{A}_s(t) = \frac{\sum_j j c_j(t)}{\sum_j c_j(t)}. \quad (19)$$

When the environment is constant and the population stable, this formula for $\bar{A}_s(t)$ reduces to that for \bar{A} (see the appendix). It would be tempting to regard the long-run average of $\bar{A}_s(t)$ over time—that is, the limit of $L^{-1} \sum_{t=0}^{L-1} \bar{A}_s(t)$ as $L \rightarrow \infty$ —as the analog of \bar{A} under environmental stochasticity. However, this would miss a key aspect played by the assumption of demographic stability in the case of a constant environment. The assumption implies that whenever we look at the population, the fraction of the stage distribution composed of those aged 1 is $\mathbf{w}_1 = \lambda^{-1}\mathbf{F}\mathbf{w}$. This fraction always contains a reproductive value of $\lambda^{-1}\mathbf{v}^\top\mathbf{F}\mathbf{w}$. Thus, we can compute \bar{A} indifferently at any time point. This average of parental ages will always be taken over the parents of the average reproductive-value-weighted offspring. But when the environment fluctuates, neither the stage distribution nor the reproductive values are constant. Both the fraction of the stage distribution composed of those aged 1 and its reproductive value content vary with time, and so do the overall stage distribution of individuals and their fecundities. Therefore, we should average the $\bar{A}_s(t)$ by weighting them to account for how the population fraction aged 1 at $t+1$ compares in terms of reproductive values with respect to the fraction aged 1 at all considered time points. In this way, we can get the average parental age of the average reproductive-value-weighted offspring. Looking at the demographic process from time 0 up to some time L and using equation (18), the appropriate weight for $\bar{A}_s(t)$ then is

$$C(t) = \frac{c(t)}{\sum_{k=0}^{L-1} c(k)}, \quad (20)$$

where the reproductive value contained in new recruits at $t+1$ is normalized to the reproductive value contained in new recruits over the whole time interval under consideration (see also Lehmann 2014). Hence, we suggest that the quantity

$$\bar{A}_s = \lim_{L \rightarrow \infty} \sum_{t=0}^{L-1} C(t)\bar{A}_s(t) \quad (21)$$

measures the generation time under a fluctuating environment as the measure \bar{A} proposed by Cochran and Ellner (1992) does under a constant environment.

Two issues, however, remain to be addressed. The first is the existence of the limit in equation (21). Second, given that $\bar{A} = G$, it is natural to wonder whether an equivalence holds between \bar{A}_s and G_s too. In the appendix, we show that indeed

$$A_s = G_s, \tag{22}$$

which solves both issues at once. This result and equation (4) are conceptually relevant in that they tell us that both when the environment is constant and when it fluctuates, the generation time can indifferently be measured as the average time interval between successive recruitment events along a genetic lineage and as the average parental age of the average reproductive-value-weighted offspring. Equation (22) also is computationally relevant because the formula for G_s is much less computationally demanding than that for \bar{A}_s . The latter hinges on the age-within-stage distribution, which varies with time throughout the demographic process. The formula for G_s instead does not rely on any information about the population age distribution.

Age Structure

For stable populations with age structure, the classic genetic measure of generation time is

$$G_a = \sum_j j l_j m_j \lambda^{-j} \tag{23}$$

(see Charlesworth 1994), where l_j is the probability of surviving at least to age j for an individual of age 1, m_j is the number of individuals of age 1 at $t + 1$ per individual of age j at t , and λ is stable population growth. Bienvenu and Legendre (2015) showed that G_a is a special case of G when stages are ages.

Lehmann (2014) derived a stochastic generalization of equation (23) for age-structured populations. His result is based on a model of genetic lineages that is slightly different from ours and can account for both demographic and environmental stochasticity. In particular, Lehmann (2014) considered an ergodic Markov chain on a finite number of states. Each state corresponds to a possible population configuration (i.e., abundances in each age). We can nevertheless express Lehmann’s measure of generation time, which we shall call $G_{s,a}$, within our framework. Suppose the stages 1, 2, ..., n are successive ages. The result of Lehmann (2014, eq. [20]) translates to our setting as

$$G_{s,a} = \left(\lim_{L \rightarrow \infty} \frac{1}{L} \sum_{t=0}^{L-1} v_1(t+1) w_1(t+1) \right)^{-1}. \tag{24}$$

For age structure, our formula for G_s in equation (16) takes exactly this form. Consider the fraction $w_1(t)$ of the stage distribution at t that is composed of individuals of age 1 at t . When stages are ages, the only nonzero component of $w_1(t)$ always is the first and equal to the first component $w_1(t)$ of the overall stage distribution $w(t)$, which now is the age distribution. Therefore, for age structure the right-hand side of equation (24) corresponds to the inverse of the right-hand side of equation (13). Thus, we recover the result of Lehmann (2014) as a special case.

Application

A natural question is whether a separate formula to measure generation time under fluctuating environments is worth having. Perhaps formulas devised for a constant environment could well approximate the generation time when they are applied to average demographics. Here, we address this doubt. We took demographic data of the volunteer (weedy) oilseed rape (*Brassica napus*) from Claessen (2005) and Claessen et al. (2005). In this data set, three stages are distinguished: flowering plants, seeds in a shallow seed bank, and seeds in a deep seed bank. At each time point, the environment is in one of two possible states: “good” (with probability 0.1) and “bad” (with probability 0.9). A good year results from failure to remove a small patch of this weed. In poor years, the plant reproduces much less; seeds tend to survive but are very unlikely to lead to flowering plants. The parameter $0 \leq \theta \leq 1$ tunes between-year variability. The projection matrix for good years is $\mathbf{U} + \theta(\mathbf{A}_g - \mathbf{U})$ and the projection matrix for bad years is $\mathbf{U} + \theta(\mathbf{A}_b - \mathbf{U})$, where $\mathbf{U} = 0.1\mathbf{A}_g + 0.9\mathbf{A}_b$. To get a sense of the impact of θ , consider its effect on fecundity. When $\theta = 1$, in a good year a flowering plant contributes almost 15 new flowering plants, between one and two seeds in the shallow seed bank, and almost 1,000 seeds in the deep seed bank. In a bad year, a flowering plant rarely contributes a single new flowering plant; it contributes at most one seed in the shallow seed bank and less than 400 seeds in the deep seed bank. When $\theta = 0$, there is no difference between bad and good years, and a flowering plant always contributes between one and two flowering plants, approximately one seed in the shallow seed bank, and between 400 and 500 seeds in the deep seed bank. Contributions occur over a year.

In the projection matrices, we took the column corresponding to the stage of flowering plants as containing all fecundities. We computed the generation time for all θ values in four different ways. After estimating the elasticities of λ_s to fecundities from simulation that was 50,000 time steps long, we computed G_s using the formula in equation (16). We retrieved the fecundity elasticities of the dominant eigenvalue of the matrix for good years, of

the matrix for bad years, and of the weighted average of these matrices where the weights are the probabilities of the corresponding environmental state. (This is a common way of averaging projection matrices. An alternative averaging method proposed by Logofet [2013, 2019] may be more recommendable, but we do not explore it here.) With these elasticities and the formula in equation (9), we computed the generation time in a constantly good environment, in a constantly bad environment, and in the average environment. We called \bar{G} the generation time in the average environment. Results (fig. 2) show that for small between-year variability, G_s and \bar{G} are relatively close to one another. However, as this variability becomes substantial, the two quantities progressively diverge: while G_s increases with θ , \bar{G} is almost insensitive to this parameter. At maximum variability ($\theta = 1$), G_s is approximately three times larger than \bar{G} . Hence, the latter cannot be taken, in general, as a good proxy for the former. Systematically exploring the relationship between G_s and \bar{G} is an open problem. Data and code for the simulations in figure 2 are in Giaimo and Traulsen (2022).

Discussion

The generation time is a key quantity in ecology and evolution. However, defining and measuring it under envi-

ronmental stochasticity for stage-structured populations has been deemed difficult (Dalglish et al. 2010). Here, we have proposed one possible way of overcoming this difficulty. We have quantified the generation time in a fluctuating environment in two equivalent ways: the average distance between successive recruitment events along a genetic lineage and the average parental age of the average reproductive-value-weighted offspring. The obtained formula is easy to evaluate. It seamlessly merges with the computation of the elasticities of the stochastic growth rate, which are customary quantities for ecologists and evolutionary biologists interested in stochastic population dynamics. Computational procedures for these elasticities are widely available; see Caswell (2001) and Morris and Doak (2002).

Elasticities of population growth, both stochastic and stable, to matrix entries add up to 1 (de Kroon et al. 1986; Caswell 2001). From this and the fact that the sum of fecundity elasticities equals the inverse of the generation time, Biennu and Legendre (2015, p. 840) observed that for stage-structured populations in a constant environment, the sum of survival elasticities is equal to 1 minus the inverse of the generation time. This was an observation previously limited to populations with age structure (Houllier and Lebreton 1986; Lebreton 1996). Giaimo and Traulsen (2019) made a further, related observation based on the

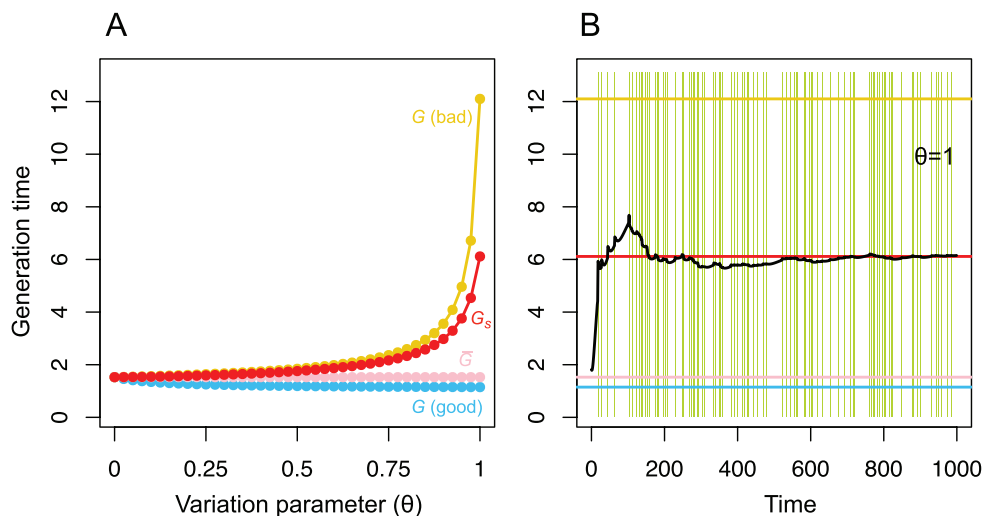


Figure 2: Generation time for the volunteer oilseed rape (*Brassica napus*). In good years, the plant reproduces more than in bad years. Parameter θ modulates how much fecundity and survival vary between good years and bad years (see the main text). *A*, The generation time G for different θ values is reported when the environment is permanently good or bad and when it fluctuates. Under fluctuations, we computed both the generation time, \bar{G} , via stable population theory by applying the formula in equation (3) to the constant projection matrix for the average year and the generation time, G_s , via theory for environmental stochastic demography by applying the formula in equation (16). *B*, The stochastic generation time (black line) is reported as progressively computed along a realization of the demographic process when $\theta = 1$ using equation (21). In the initial population, maximum age is set equal to 3 years, and the age distribution is random. Horizontal lines mark the generation time when the environment is permanently in one state or it fluctuates. Vertical green bars mark good years. The analysis is based on data from Claessen (2005) and Claessen et al. (2005). Data and code behind this figure are provided in Giaimo and Traulsen (2022).

identification of stable growth λ with fitness: if there is a trade-off between survival and fecundity, the rate at which survival can increment at the expense of a proportional decrease in fecundity around a fitness optimum is equal to 1 minus the optimal generation time. Our result that the generation time is the inverse of the stochastic elasticities to fecundities extends these observations to fluctuating environments, provided $\ln \lambda_s$ gives fitness (Tuljapurkar 1982; Metz et al. 1992; Tuljapurkar et al. 2009).

There is a need in biodemography for distinct concepts of the time interval separating generations (Caswell 2001, chap. 5.3.5; Ellner 2018). Measures of generation time under fluctuating environments that are alternative to ours are likely to emerge out of the same need. In particular, a stochastic analog of the cohort generation time can be envisaged. In its version for constant demography, this measure has been employed in approximations to the stochastic growth rate (Tuljapurkar et al. 2009) and has been generalized to populations with age-stage structure using reproductive-value weighting (Steiner et al. 2014). A megamatrix approach to this quantity under environmental stochasticity is given in Hernandez-Suarez et al. (2012). No version of the cohort generation time appears to exist where the weights are the reproductive values as defined for variable environments in Tuljapurkar (1990). However, developments in capturing cohort dynamics (Tuljapurkar and Horvitz 2006) and reproduction numbers (Inaba 2012) when the environment varies indicate that such generalization might be feasible.

Lack of a spectrum of measures of generation time for fluctuating environments has sometimes forced researchers interested in stochastic population dynamics to apply to the average demographics some formula of generation time that was devised for the case of a constant environment (Dalglish et al. 2010). Here, we have given an example where a similar strategy can fail in approximating the true generation time in the population. This highlights once more the importance of accounting for environmental stochasticity in demographic modeling (Steiner 2020). Tuljapurkar et al. (2009) similarly found that for life histories with identical net reproduction rates, fitness in the average environment may not be a good proxy to true fitness in a fluctuating environment. Differences in generation times in the average environment explain part of this discrepancy. It would be interesting to look at how these life histories compare in terms of their generation times computed for the fluctuating environment. The formula we have derived, however, may be not directly relevant in this case, as Tuljapurkar et al. (2009) looked at the cohort generation time.

The generation time may play a role in the diversity of mutation rates (Martin and Palumbi 1993; Ohta 1993; Li et al. 1996; Thomas et al. 2010; Sayres et al. 2011; Weller

and Wu 2015; Amster and Sella 2016; Gao et al. 2016). For example, molecular evolution might be faster in vertebrates with shorter generation times as a result of a higher yearly number of DNA replication events (Bromham 2009), which are occasions for mutations to occur. Critical to this research is a sound way of measuring the generation time (Thomas et al. 2010). Presumably, this can get complicated by the generalized absence of detailed demographic data (Amster and Sella 2016; Conde et al. 2019). Our work reveals a further layer of complexity: solid estimates of the generation time require explicitly accounting for the demographic effects of environmental variability.

More generally, we hope that our work can contribute to understand the role of environmental stochasticity in shaping a crucial life history trait like the intergenerational distance.

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Statement of Authorship

S.G. conceived and developed the project and wrote the code and the first draft of the manuscript. S.G. and A.T. reviewed the analysis. S.G. wrote the final version of the manuscript with feedback from A.T.

Data and Code Availability

All data and code for this work have been deposited in the Dryad Digital Repository and Zenodo (<https://doi.org/10.5061/dryad.x95x69pmt>; Giaimo and Traulsen 2022).

APPENDIX

Derivations

Genetic Lineage Update

Here, we recall the result by Lion (2018) that the matrix where $a_{ij}(t)w_j(t)/(\lambda(t)w_i(t+1))$ is the (i, j) entry updates in backward time the row vector, of which the component i is $v_i(t+1)w_i(t+1)$. Suppose we observe the demographic process generated by the recursion $\mathbf{x}(t+1) = \mathbf{A}(t)\mathbf{x}(t)$ from some initial time 0 up to some time L . The recursion for the stage distribution for this process is

$$\mathbf{w}(t+1) = \frac{\mathbf{A}(t)\mathbf{w}(t)}{\lambda(t)}, \quad (\text{A1})$$

where $\mathbf{w}(0)$ is an arbitrary nonnegative vector whose only constraint is that its components add up to 1. According

to the scaling in equation (6), the recursion for the reproductive value is

$$\mathbf{v}^\top(t) = \frac{\mathbf{v}^\top(t+1)\mathbf{A}(t)}{\lambda(t)}, \tag{A2}$$

where $\mathbf{v}(L)$ is an arbitrary nonnegative vector whose only constraint is that $\mathbf{v}^\top(L)\mathbf{w}(L) = 1$. Form the row vector with the i th component $v_i(t+1)w_i(t+1)$ and the matrix with the (i, j) entry equal to $a_{ij}(t)w_j(t)/(\lambda(t)w_i(t+1))$. Using equations (A1) and (A2), the result of multiplying this vector on the left of this matrix simplifies to

$$\begin{aligned} & \sum_i v_i(t+1)w_i(t+1) \frac{a_{ij}(t)w_j(t)}{\lambda(t)w_i(t+1)} \\ &= \sum_i \frac{v_i(t+1)a_{ij}(t)w_j(t)}{\lambda(t)} = v_j(t)w_j(t). \end{aligned} \tag{A3}$$

That is, the matrix updates the vector in backward time. Eliminating time indexing from equation (A3), one gets the classic result for the case of stable demography that the matrix with the (i, j) entry equal to $a_{ij}w_j/(\lambda w_i)$ has a left eigenvector (corresponding to the eigenvalue 1) with component i equal to $v_i w_i$ (Bodmer and Cavalli-Sforza 1968; Hill 1972; Taylor 1990, 1996; Rousset 2004; Lehmann 2014; Bienvenu and Legendre 2015).

*Average Parental Age of
Reproductive-Value-Weighted Offspring*

Here, following a reasoning analogous to that of Ellner (2018, eq. [12]), we show that in the absence of environmental variability, $\bar{A}_s(t)$ in equation (19) is equal to \bar{A} when the population is demographically stable. Removing time indexing from equation (19) and using equation (17),

$$\frac{\sum_{j=1}^{\infty} j c_j}{\sum_{j=1}^{\infty} c_j} = \frac{\lambda^{-1} \mathbf{v}^\top \mathbf{F} \sum_{j=1}^{\infty} j \mathbf{w}_j}{\lambda^{-1} \mathbf{v}^\top \mathbf{F} \mathbf{w}}. \tag{A4}$$

To simplify this expression, we recall three facts.

First, \mathbf{w}_j is the present stage distribution aged j . It consists of those recruits that were first censused j time steps before in relative number \mathbf{Fw} and have survived until now. Since the birth of these recruits, the population has stably grown by a factor λ . By virtue of demographic stability, \mathbf{Fw} is a constant vector. Survival is regulated by the matrix \mathbf{S} . Hence, $\mathbf{w}_j = \lambda^{-j} \mathbf{S}^{j-1} \mathbf{Fw}$.

Second, the survival-fecundity decomposition of \mathbf{A} together with the eigenvector equations for this matrix imply that $\mathbf{v}^\top \mathbf{F} = \mathbf{v}^\top (\lambda \mathbf{I} - \mathbf{S})$ and $\mathbf{Fw} = (\lambda \mathbf{I} - \mathbf{S})\mathbf{w}$, where \mathbf{I} is the identity matrix.

Third, recall the series expansion $(\mathbf{I} - \mathbf{M})^{-2} = \mathbf{I} + 2\mathbf{M} + 3\mathbf{M}^2 + \dots$ for a matrix \mathbf{M} with $\rho(\mathbf{M}) < 1$, where ρ is the spectral radius. To apply this expansion to $\lambda^{-1} \mathbf{S}$, we assume, as is customary in demography (Caswell 2001),

that λ is the Perron root of \mathbf{A} and therefore $\lambda = \rho(\mathbf{A})$. By the Perron-Frobenius theorem (Varga 2000, chap. 2.7), the spectral radius of \mathbf{A} is an increasing function of its entries. Since the eigenvector equation $\lambda \mathbf{w} = \mathbf{A}\mathbf{w}$ implies that 1 is the Perron root of $\lambda^{-1} \mathbf{A}$, we have that $1 > \rho(\lambda^{-1} \mathbf{S})$ because $\mathbf{A} - \mathbf{S} = \mathbf{F} \geq 0$ is not the zero matrix.

Let us then focus on the numerator of equation (A4),

$$\begin{aligned} \lambda^{-1} \mathbf{v}^\top \mathbf{F} \sum_{j=1}^{\infty} j \mathbf{w}_j &= \lambda^{-1} \mathbf{v}^\top \mathbf{F} \sum_{j=1}^{\infty} j \lambda^{-j} \mathbf{S}^{j-1} \mathbf{Fw} \\ &= \mathbf{v}^\top \mathbf{F} (\lambda \mathbf{I} - \mathbf{S})^{-2} \mathbf{Fw} \\ &= \mathbf{v}^\top \mathbf{w} \\ &= 1, \end{aligned} \tag{A5}$$

where in the last line we have used the normalization in equation (6). Therefore, from equations (3) and (A5), the right-hand side of equations (A4) is equal to $\lambda/(\mathbf{v}^\top \mathbf{Fw}) = G$. By equation (4), we have that in a constant environment and at demographic stability, the quantity $\bar{A}_s(t)$ is equal to \bar{A} .

Derivation of Equation (22)

Here, we derive equation (22) under the biologically realistic assumption that there is a maximum age ω , possibly very large, beyond which survival is not possible. In the next section, we relax this assumption by giving sufficient conditions to consider an infinity of ages in a way that parallels the proof of equation (4) contained in the previous section of this appendix. Note that equation (4) is the analog of equation (22) for a constant environment.

We start by observing that the stage distribution aged $j + 1$ at $t + 1$ is

$$\mathbf{w}_{j+1}(t+1) = \frac{\mathbf{S}(t)\mathbf{w}_j(t)}{\lambda(t)}, \tag{A6}$$

which is the surviving fraction of the stage distribution j at t scaled to account for population growth between t and $t + 1$. The full stage distribution at t is

$$\mathbf{w}(t) = \sum_{j=1}^{\omega} \mathbf{w}_j(t) \tag{A7}$$

with

$$\|\mathbf{w}(t)\| = 1, \tag{A8}$$

where $\|\cdot\|$ is the 1-norm (i.e., the sum of the absolute values of the vector components) and $\mathbf{w}_j(t)$ is the zero vector for $j > \omega$. We then follow a reasoning analogous to that of Lehmann (2014, app. C). Let us multiply the fraction $\mathbf{w}_j(t)$ of the stage distribution composed of those aged j on the right of $\mathbf{v}(t)$ in equation (A2) and use equation (A6):

$$\begin{aligned}
 \mathbf{v}^\top(t)\mathbf{w}_j(t) &= \frac{\mathbf{v}^\top(t+1)\mathbf{S}(t)\mathbf{w}_j(t)}{\lambda(t)} \\
 &\quad + \frac{\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}_j(t)}{\lambda(t)} \\
 &= \mathbf{v}^\top(t+1)\mathbf{w}_{j+1}(t+1) \\
 &\quad + \frac{\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}_j(t)}{\lambda(t)}.
 \end{aligned} \tag{A9}$$

Multiplying both sides of equation (A9) by $j+1$, subtracting the first term of the right-hand side, adding equations for all ages, and then flipping sides, we find that

$$\begin{aligned}
 &\sum_{j=1}^{\omega} \frac{(j+1)\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}_j(t)}{\lambda(t)} \\
 &= \sum_{j=1}^{\omega} (j+1)\mathbf{v}^\top(t)\mathbf{w}_j(t) - \sum_{j=1}^{\omega} (j+1)\mathbf{v}^\top(t+1)\mathbf{w}_{j+1}(t+1),
 \end{aligned} \tag{A10}$$

On the right-hand side of equation (A10), we reindex the second sum and use equations (6) and (A7) to simplify the first one:

$$\begin{aligned}
 &\sum_{j=1}^{\omega} \frac{(j+1)\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}_j(t)}{\lambda(t)} \\
 &= 1 + \sum_{j=1}^{\omega} j\mathbf{v}^\top(t)\mathbf{w}_j(t) - \sum_{j=2}^{\omega} j\mathbf{v}^\top(t+1)\mathbf{w}_j(t+1).
 \end{aligned} \tag{A11}$$

Next, we multiply out and use equation (A7) for the sum on the left-hand side, and we rewrite the second sum on the right-hand side of equation (A11):

$$\begin{aligned}
 &\sum_{j=1}^{\omega} \frac{j\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}_j(t)}{\lambda(t)} + \frac{\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}(t)}{\lambda(t)} \\
 &= 1 + \sum_{j=1}^{\omega} j\mathbf{v}^\top(t)\mathbf{w}_j(t) + \mathbf{v}^\top(t+1)\mathbf{w}_1(t+1) \\
 &\quad - \sum_{j=1}^{\omega} j\mathbf{v}^\top(t+1)\mathbf{w}_j(t+1).
 \end{aligned} \tag{A12}$$

By equation (14), the second term on the left-hand side and the third term on the right-hand side of equation (A12) cancel out. Thus, equation (A12) simplifies to

$$\begin{aligned}
 \sum_{j=1}^{\omega} \frac{j\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}_j(t)}{\lambda(t)} &= 1 + \sum_{j=1}^{\omega} j\mathbf{v}^\top(t)\mathbf{w}_j(t) \\
 &\quad - \sum_{j=1}^{\omega} j\mathbf{v}^\top(t+1)\mathbf{w}_j(t+1).
 \end{aligned} \tag{A13}$$

Taking the sum from $t=0$ to $t=L-1$ over equation (A13), we obtain a telescoping sum on the right-hand side. Dividing then by L ,

$$\begin{aligned}
 &\frac{1}{L} \sum_{t=0}^{L-1} \sum_{j=1}^{\omega} \frac{j\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}_j(t)}{\lambda(t)} \\
 &= 1 + \frac{1}{L} \left(\sum_{j=1}^{\omega} j\mathbf{v}^\top(0)\mathbf{w}_j(0) - \sum_{j=1}^{\omega} j\mathbf{v}^\top(L)\mathbf{w}_j(L) \right).
 \end{aligned} \tag{A14}$$

Taking the limit of equation (A14) as $L \rightarrow \infty$, the term on the right-hand side vanishes because the quantity between parentheses is bounded. We are then left with

$$\lim_{L \rightarrow \infty} \left(\frac{1}{L} \sum_{t=0}^{L-1} \sum_{j=1}^{\omega} \frac{j\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}_j(t)}{\lambda(t)} \right) = 1. \tag{A15}$$

Using equations (17), (19), (20), and (A7), we express \bar{A}_s in equation (21) as

$$\bar{A}_s = \lim_{L \rightarrow \infty} \left(\frac{\sum_{t=0}^{L-1} \sum_{j=1}^{\omega} \frac{j\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}_j(t)}{\lambda(t)}}{\sum_{t=0}^{L-1} \frac{\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}(t)}{\lambda(t)}} \right). \tag{A16}$$

From equations (13)–(16) and (A15),

$$\bar{A}_s = \left(\lim_{L \rightarrow \infty} \frac{1}{L} \sum_{t=0}^{L-1} \frac{\mathbf{v}^\top(t+1)\mathbf{F}(t)\mathbf{w}(t)}{\lambda(t)} \right)^{-1} = G_s, \tag{A17}$$

which proves equation (22).

No Maximum Age

Assuming no maximum age, we set $\omega = \infty$ in all equations of the previous section of this appendix. Here, we propose one possible set of sufficient conditions that ensure that the calculations therein remain valid. In particular, we show how these conditions ensure both that in the step from equation (A9) to equation (A10), the series on the right-hand side of equation (A10) that arise when we set $\omega = \infty$ are convergent, and that in the step from equation (A14) to equation (A15), we have convergence to zero of the second term on the right-hand side of equation (A14) as $L \rightarrow \infty$ when we set $\omega = \infty$ in the terms between parentheses.

First of all, we make some preliminary considerations and assumptions. We use $\|\cdot\|$ to denote the 1-norm both for vectors (i.e., the sum of the absolute values of the vector components) and for matrices (i.e., the maximum

column sum of the absolute values of the matrix entries). We assume that the maximal individual survival p per time step that the survival matrices $\mathbf{S}(t)$ allow for is such that

$$p < \lambda_s. \tag{A18}$$

Suppose that there are q environmental states. Then, $\mathbf{S}(t) \in \{\mathbf{S}_1, \mathbf{S}_2, \dots, \mathbf{S}_q\}$. Survival to $t + 1$ (independently of stage at $t + 1$) for an individual in stage h at t equals the sum of column h of $\mathbf{S}(t)$. Hence,

$$p = \max_i \|\mathbf{S}_i\|. \tag{A19}$$

For our purposes, we also define

$$m = \max_i \|\mathbf{F}_i\|, \tag{A20}$$

where the maximum is taken over the set $\{\mathbf{F}_1, \mathbf{F}_2, \dots, \mathbf{F}_q\}$ in which $\mathbf{F}(t)$ takes values. We also recall from equations (2) and (7) that, almost surely, we have

$$\ln \lambda_s = \lim_{L \rightarrow \infty} \frac{1}{L} \sum_{t=0}^{L-1} \ln \lambda(t) \tag{A21}$$

because the sequence $\ln \lambda(0), \ln \lambda(1), \dots$ is ergodic (Tuljapurkar 1990). Let then $Z(t) = (\mathbf{w}(t+1), \mathbf{A}(t))$. In the long run, the sequence $Z(0), Z(1), \dots$ of population stage distribution and projection matrix approaches a stationary sequence and the stage distribution $\mathbf{w}(t)$ is component-wise positive independently of initial conditions (Tuljapurkar 1990). Here, we assume stationarity of the sequence $Z(0), Z(1), \dots$ and positivity of $\mathbf{w}(t)$ throughout. We also suppose that the demographic process described by equation (1) has been stationary indefinitely backward in time before we started observing the population at $t = 0$. The only difference is then that only for $t \geq 0$ are we in position to observe the realization of $\mathbf{A}(t)$ into one of its q values. Thus, the time variable t runs from $-\infty$ to ∞ . This assumption is coherent with the approach in the main text where a genetic lineage is observed indefinitely in backward time as the population is subject to the same stochastic environmental process in the stationary phase. Note that from equation (7),

$$\begin{aligned} \lambda(t) &= \frac{X(t+1)}{X(t)} = \frac{\|\mathbf{A}(t)\mathbf{x}(t)\|}{\|\mathbf{x}(t)\|} = \frac{X(t)\|\mathbf{A}(t)\mathbf{w}(t)\|}{X(t)\|\mathbf{w}(t)\|} \\ &= \frac{\|\mathbf{A}(t)\mathbf{w}(t)\|}{\|\mathbf{w}(t)\|} = \|\mathbf{A}(t)\mathbf{w}(t)\|. \end{aligned} \tag{A22}$$

Hence, the time-specific growth rate can be seen as a function $\lambda(t) = f(Z(t), Z(t-1))$ of the joint stationary sequence of population stage distributions and projection matrices. Moreover, a sequence obtained from a (measurable) function of a stationary sequence is stationary as well

(Krengel 2011, chap. 1, proposition 4.1, corollary 4.2). Therefore, the sequences $\{\ln \lambda(t)\}_{t=-\infty}^{\infty}$ and $\{\lambda(t)\}_{t=-\infty}^{\infty}$ are stationary. In fact, a shift in $(Z(t), Z(t-1))$ from t to $t+k$ with k an integer leads to an equal shift in $\lambda(t)$. By virtue of stationarity, we can set the origin of the time average in equation (A21) to $t = k$ with k any integer and not only to $t = 0$.

After these preliminary considerations, we address the first problem, which is to show convergence of the series

$$\eta(t) = \sum_{j=1}^{\infty} j \mathbf{v}^{\top}(t) \mathbf{w}_j(t), \tag{A23}$$

which appears twice on the right-hand side of equation (A10), as equation (A11) shows, once we set $\omega = \infty$. Observe that $\eta(t)$ can be written as a dot product

$$\eta(t) = \mathbf{v}^{\top}(t) \sum_{j=1}^{\infty} j \mathbf{w}_j(t). \tag{A24}$$

For each vector $\mathbf{w}(t)$, we can define a norm $\|\mathbf{y}\|_{\mathbf{w}(t)} = \sum_{i=1}^n w_i(t) |y_i|$ for vectors \mathbf{y} in \mathbb{R}^n , where n is the number of stages in the life cycle (i.e., the number of dimensions of the matrix model). That $\|\cdot\|_{\mathbf{w}(t)}$ is a norm follows from the following facts: the vectors $\mathbf{w}(t)$ are component-wise positive for all t , and the defined norm clearly is absolutely homogeneous and obeys the triangle inequality. Since equation (6) holds for all t by assumption and the vectors $\mathbf{v}(t)$ are nonnegative, each of them is bounded in some norm (i.e., $\|\cdot\|_{\mathbf{w}(t)}$). Given the equivalence of norms in finite dimensions, the vectors $\mathbf{v}(t)$ are uniformly bounded in t . Therefore, there exists a finite number

$$\beta = \sup_{i,t} \{v_i(t)\}, \tag{A25}$$

where “sup” indicates the supremum, here taken over all time points and components of $\mathbf{v}(t)$. Thus, we can form a vector $\boldsymbol{\beta} = \beta[1, 1, \dots, 1]^{\top}$ with n components so that

$$\eta(t) \leq \boldsymbol{\beta}^{\top} \sum_{j=1}^{\infty} j \mathbf{w}_j(t) = \beta \left\| \sum_{j=1}^{\infty} j \mathbf{w}_j(t) \right\|, \tag{A26}$$

where the expression is meaningful provided the involved series are convergent. Thus, to study the convergence of $\eta(t)$, we can focus on the average age $\bar{j}(t)$ in the population at t , which is

$$\bar{j}(t) = \sum_{j=1}^{\infty} j \|\mathbf{w}_j(t)\|, \tag{A27}$$

where $\|\mathbf{w}_j(t)\|$ is the population fraction of age j at t . Note that if $\bar{j}(t)$ is convergent, say to M , then using equation (A26) the homogeneity of norms and going from absolute convergence to convergence of the series, we obtain

$$\begin{aligned}
 \beta M &= \beta \sum_{j=1}^{\infty} j \|\mathbf{w}_j(t)\| \\
 &= \beta \sum_{j=1}^{\infty} \|j\mathbf{w}_j(t)\| \\
 &\geq \beta \left\| \sum_{j=1}^{\infty} j\mathbf{w}_j(t) \right\| \geq \eta(t),
 \end{aligned} \tag{A28}$$

so that $\eta(t)$ is bounded and, therefore, convergent. To prove convergence of $\bar{j}(t)$ we use equations (14) and (A6) to write

$$\begin{aligned}
 \mathbf{w}_j(t) &= \\
 &\frac{\mathbf{S}(t-1) \dots \mathbf{S}(t-j+2) \mathbf{S}(t-j+1) \mathbf{F}(t-j) \mathbf{w}(t-j)}{\lambda(t-1) \dots \lambda(t-j+2) \lambda(t-j+1) \lambda(t-j)}.
 \end{aligned} \tag{A29}$$

Using this expression and equations (A8) and (A19), we can bound the terms of the series in equation (A27) as follows:

$$\begin{aligned}
 j \|\mathbf{w}_j(t)\| &= j \left\| \frac{\mathbf{S}(t-1) \dots \mathbf{S}(t-j+1) \mathbf{F}(t-j) \mathbf{w}(t-j)}{\lambda(t-1) \dots \lambda(t-j+1) \lambda(t-j)} \right\| \\
 &\leq \frac{j \|\mathbf{S}(t-1)\| \dots \|\mathbf{S}(t-j+1)\| \|\mathbf{F}(t-j)\| \|\mathbf{w}(t-j)\|}{\lambda(t-1) \dots \lambda(t-j+1) \lambda(t-j)} \\
 &= \frac{j \|\mathbf{S}(t-1)\| \dots \|\mathbf{S}(t-j+1)\| \|\mathbf{F}(t-j)\|}{\lambda(t-1) \dots \lambda(t-j+1) \lambda(t-j)} \\
 &\leq \frac{j p^j p^{-1} m}{\lambda(t-1) \dots \lambda(t-j+1) \lambda(t-j)}.
 \end{aligned} \tag{A30}$$

From this bound, we define

$$r(t) = \sum_{j=1}^{\infty} \frac{j p^j p^{-1} m}{\lambda(t-1) \dots \lambda(t-j+1) \lambda(t-j)}, \tag{A31}$$

so that

$$r(t) \geq \bar{j}(t), \tag{A32}$$

where the expression is meaningful provided $r(t)$ converges. Consider then the following geometric series, which by virtue of equation (A18) is convergent:

$$\sum_{j=1}^{\infty} \frac{j p^j p^{-1} m}{\lambda_s^j} = p^{-1} m \sum_{j=1}^{\infty} j \left(\frac{p}{\lambda_s} \right)^j = \frac{m \lambda_s}{(\lambda_s - p)^2}. \tag{A33}$$

Since we can obtain from equation (A21) that, almost surely,

$$\lim_{L \rightarrow \infty} \frac{\prod_{y=0}^{L-1} \lambda(t)}{\lambda_s^L} = 1, \tag{A34}$$

and we can use any starting point for the product in the numerator, we have that equations (A31)–(A34) and the

limit comparison test imply that $r(t)$ is, almost surely, convergent pointwise in t , and therefore by equations (A28) and (A32) so is $\eta(t)$. As a consequence, both series on the right-hand side of equation (A10) are convergent.

Next, we consider the problem of convergence to zero of the second term on the right-hand side of equation (A14) as $L \rightarrow \infty$ when we set $\omega = \infty$ in the terms between parentheses in this equation. The proven pointwise convergence of $\eta(t)$ guarantees that each term of the sequence $\{\eta(t)\}_{t=-\infty}^{\infty}$ is finite. Moreover, $r(t)$ is a function $r(t) = g(\lambda(t-1), \lambda(t-2), \dots)$ of the stationary sequence $\{\lambda(t)\}_{t=-\infty}^{\infty}$. In particular, a shift in the argument $(\lambda(t-1), \lambda(t-2), \dots)$ of g from t to $t+k$ with k an integer leads to an equal shift in $r(t)$. Hence, the sequence $\{r(t)\}_{t=-\infty}^{\infty}$ is stationary, and so is the sequence $\{\beta r(t)\}_{t=-\infty}^{\infty}$. We can then use equations (A26), (A28), and (A32) to bound the second term on the right-hand side of equation (A14) as follows:

$$\begin{aligned}
 &\frac{1}{L} \left(\sum_{j=1}^{\omega} j \mathbf{v}^{\top}(0) \mathbf{w}_j(0) - \sum_{j=1}^{\omega} j \mathbf{v}^{\top}(L) \mathbf{w}_j(L) \right) \\
 &\leq \frac{\beta[r(0) + r(L)]}{L},
 \end{aligned} \tag{A35}$$

where $r(0)$ converges to a finite value almost surely. Stationary sequences are $O_p(1)$ (Davidson 2013, p. 186), that is, bounded in probability. Therefore, $\{t^{-1} \beta r(t)\}_{t=0}^{\infty}$ is $o_p(1)$ and

$$\frac{1}{L} \left(\sum_{j=1}^{\omega} j \mathbf{v}^{\top}(0) \mathbf{w}_j(0) - \sum_{j=1}^{\omega} j \mathbf{v}^{\top}(L) \mathbf{w}_j(L) \right) \rightarrow 0 \tag{A36}$$

in probability as $L \rightarrow \infty$. This proves that the identity in equation (A17) extends to the case of infinite ages (i.e., when $\omega = \infty$), provided that equation (A18) holds.

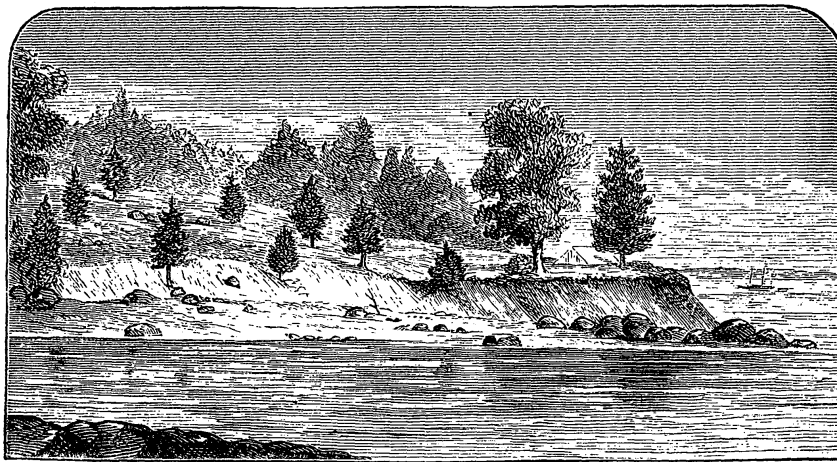
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