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Frequency-dependent growth in class-structured populations: continuous dynamics in the limit of weak selection

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Abstract In this paper we consider class-structured populations in discrete time in the limit of weak selection and with the inverse of the intensity of selection as unit of time. The aim is to establish a continuous model that approximates the discrete model. More precisely, we study frequency-dependent growth in an infinite haploid population structured into a finite number of classes such that individuals in each class contribute to a given subset of classes from one time step to the next. These contributions take the form of generalized fecundity parameters with perturbations of order $1/N$ that depends on the class frequencies of each type and the type frequencies. Moreover, they satisfy some mild conditions that ensure mixing in the long run. The dynamics in the limit as $N \to \infty$ with N time steps as unit of time is considered first in the case of a single type, and second in the case of multiple types. The main result is that the type frequencies as $N \to \infty$ obey the replicator equation with instantaneous growth rates for the different types that depend only on instantaneous equilibrium class frequencies and reproductive values. An application to evolutionary game theory complemented by simulation results is presented.

Keywords Class-structured populations · Age-structured populations · Demographic models · Population growth · Frequency-dependent selection · Timescale separation · Reproductive value · Replicator equation · Perron–Frobenius theory · Evolutionary game theory

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1 Introduction

Consider constant age-specific survival probabilities and fecundities for a discrete-time age-structured haploid population in demographic equilibrium. These demographic parameters determine the stable age distribution and the reproductive values associated with the different age classes. They are such that the geometric growth rate of the total reproductive value at any discrete time is equal to 1.

Add constant perturbations of some given order $s > 0$ to the demographic parameters. What will be the first-order effect of these perturbations with respect to s on the geometric growth rate of the population? It can be shown that this effect is given by the mean perturbation with respect to a weighted stable age distribution in the absence of perturbations with the reproductive values as weights (Lessard and Soares 2016). This is a consequence of the Perron–Frobenius theory for primitive non-negative matrices applied to Leslie matrices for age-structured populations. It can be interpreted as a two-timescale phenomenon with fast changes in the age distribution and slow changes in the population size. In the limit of small perturbations as $s \to 0$ and with $\lfloor s^{-1} \rfloor$ time steps as unit of time, the derivative of this mean perturbation with respect to s evaluated at $s = 0$ gives the exponential growth rate of the total reproductive value at any continuous time. In the same limit, the relative total reproductive values of n organisms producing copies of themselves and surviving from one age class to the next according to perturbed demographic parameters obey the classical replicator equation (Taylor and Jonker 1978; Hofbauer and Sigmund 1998, and references therein) with the exponential growth rates as constant fitnesses. Therefore, it is justified to use this equation as an approximation in the case of weak selection.

With frequency-dependent perturbations on demographic parameters, a similar conclusion is expected but with an instantaneous growth rate that depends on the current population state. In order to prove this intuitive result and find the exact expression of the growth rate, the Perron–Frobenius theory has to be extended. The reason is that the primitive non-negative matrix in the linear transformation for the amounts of individuals of the different types in the different age classes from one time step to the next depends on the distribution of those individuals at the current time step. Therefore, it changes over time. With time measured in numbers of time steps given by the inverse of the perturbation order as this order tends to 0, this leads to analyze infinite products of variable matrices. Moreover, the analysis can be extended to class-structured populations with individuals in each class contributing to a given subset of classes as long as the assumptions for the Perron–Frobenius theory hold.

Population genetics models for age-structured populations have been studied for a long time, and approximations based on stable age distributions and supported by some analytical results have already been used to predict the effects of density-dependent as well as density-independent weak selection even in diploid populations (see, e.g., Charlesworth 1994, and references therein). Still recently, Li et al. (2015) assumed a stable age distribution in a population with demographic structure to study evolutionary game dynamics in the case of life-stage dependent strategies used in pairwise interactions. See also Henson (1998) for a connection of Leslie models with McKendrick partial differential equation models.

More general class-structured populations have been considered too. The change in a weighted average frequency of a mutant allele to first order with respect to the intensity of selection, for instance, has been examined in this framework (Taylor 1990). This corresponds to an ad hoc extension of Price's (1970) covariance formula that uses the equilibrium class frequencies and the reproductive values of the alleles in those classes in the absence of selection to compute the covariance between the mutant allele frequencies and the first-order effects of selection. The expected value of such a change has also been used to get the first-order effect of selection on the probability of fixation of the mutant allele in a finite haploid population of constant size (Rousset 2004). See also Barfield et al. (2011) for a more general extension of Price's (1970) equation and applications to biological populations.

A rigorous mathematical analysis on the existence, stability and bifurcation of equilibrium points in class-structured populations of infinite size with more emphasis on age-structured populations can be found in Cushing (1998). Local stability analyses were also used, e.g., in Kebir et al. (2010) to study a mathematical model describing the dynamics of a hermaphroditic species where sex allocation is density-dependent so that the fractions of immature individuals acquiring male and female sexual roles as adults depend on current environmental conditions. In a follow up paper (Kebir et al. 2015), the stability of sexual strategies of a hermaphrodite (simultaneous or sequential, protandrous or protogynous) in a stable size-structured population distributed over a finite set of sizes is analyzed taking into account the effects of costs due to sexual competition and sex change. Notice, however, that matrix models for size-structured populations have been criticized because their outputs, and in particular the population growth rate, are sensitive to the dimension of the matrix or, equivalently, to the class width (Picard and Liang 2014).

We are interested in this paper in continuous-time approximations of discrete-time models for structured populations in the absence of stochastic effects due to a finite population size or a random environment. Notice that continuous approximations of probability models for finite populations have already been proposed, e.g., by Chalub and Souza (2009) for the Moran model and by Chalub and Souza (2014) for the Wright–Fisher model. Assuming weak frequency-dependent selection between two types of individuals in the limits of a large population size and of a small time step, three different partial differential equations are found for the limiting probability density of one of the two types depending on the relationship between the population size and the time step: the diffusion equation, the replicator-diffusion equation and the partial differential version of the replicator equation. This has been obtained under the assumption that a limiting probability density function exists and is smooth enough. Another class of macroscopic limits have been obtained by Champagnat et al. (2006, 2008) when modeling a population as a stochastic point process whose generator captures the probabilistic dynamics over continuous time of birth, mutation, and death, as influenced by the trait values of each individual, and interactions between individuals. Depending on the scalings of the model parameters, large population approximations can be deterministic, in the form of ordinary, integro-, or partial differential equations, or probabilistic, in the form of stochastic partial differential equations or superprocesses. In the limit of rare mutations, a possible approximation is a jump process, justifying the so-called trait substitution sequences and their approximation known as the canonical equation of adaptive dynamics.

In this paper we consider class-structured populations in discrete time in the limit of weak selection and with the inverse of the intensity of selection as unit of time. The objective is to establish a continuous model that approximates the discrete model. More precisely, we study frequency-dependent growth in an infinite haploid population structured into a finite number of classes such that individuals in each class contribute to a given subset of classes from one time step to the next. These contributions take the form of generalized fecundity parameters with perturbations of order $1/N$ that depends on the class frequencies of each type and the type frequencies. Moreover, they satisfy some mild conditions that ensure mixing in the long run. The dynamics in the limit as $N \to \infty$ with N time steps as unit of time is considered first in the case of a single type (Sect. 2), and second in the case of multiple types (Sect. 3). The main result is that the type frequencies as $N \to \infty$ obey the replicator equation with instantaneous growth rates for the different types that depend only on instantaneous equilibrium class frequencies and reproductive values. An application to evolutionary game theory complemented by simulation results is considered next (Sect. 4). This is followed by a discussion on the assumptions of the model and the implications of the results (Sect. 6). The proofs of all the results are provided for completeness, including technical proofs of preliminary lemmas that are relegated to an appendix.

2 Single-type model

Consider an infinite population with time measured in number of time intervals of length $\Delta t = N^{-1}$ for some large positive integer N. Suppose $d \geq 1$ possible classes for the individuals in the population and let $c_k(\tau)$ be the amount of individuals in class $k = 1, \ldots, d$ at time step $\tau \geq 0$. Therefore, the frequencies of the individuals in the different classes at time step τ are given by

$$x_k(\tau) = \frac{c_k(\tau)}{\sum_{l=1}^{d} c_l(\tau)}, \tag{1}$$

for $k = 1, \ldots, d$. The array of these frequencies is represented by $\mathbf{x}(\tau) = (x_1(\tau), \ldots, x_d(\tau))$, which belongs to the simplex of all d-dimensional frequency vectors defined as

$$\Delta = \{\mathbf{x} = (x_1, \ldots, x_d) \in \mathbb{R}^d : x_1, \ldots, x_d \geq 0, x_1 + \cdots + x_d = 1\}. \tag{2}$$

Assume that an individual in class k at time step $\tau \geq 0$ leaves an expected number $a_{l,k}(\tau)$ of individuals (possibly including the individual itself) in class l at time step $\tau + 1$, for $k, l = 1, \ldots, d$. This expected number, which can be viewed as a generalized fecundity parameter, depends only on the frequency vector $\mathbf{x}(\tau)$ as a result of interactions between individuals.

Weak frequency-dependent selection is modeled by assuming

$$a_{l,k}(\tau) = a_{l,k} + \frac{1}{N} b_{l,k}(\mathbf{x}(\tau)), \tag{3}$$

for $k, l = 1, \ldots, d$. Here, $A = \left(a_{l,k}\right)$ is a matrix with all constant non-negative entries, while $B(\mathbf{x}) = \left(b_{l,k}(\mathbf{x})\right)$ is a matrix with all continuous non-negative entries with the same null entries for all $\mathbf{x} \in \Delta$. Note that the entries of $B(\mathbf{x})$ are uniformly bounded on the compact set Δ. On the other hand, the quantity $s = N^{-1}$ where N is a positive integer represents the intensity of selection.

It is assumed throughout that A is primitive, which means that A^L is a positive matrix for some integer $L \geq 1$. The Perron–Frobenius theory (see, e.g., Appendix in Karlin and Taylor 1975, or Lancaster and Tismenetsky 1985) ensures that the leading eigenvalue of A, represented by λ, is positive and simple with associated positive left and right eigenvectors $\mathbf{v} = (v_1, \ldots, v_d)^T$ and $\mathbf{u} = (u_1, \ldots, u_d)^T$. These are unique under the conditions

$$\mathbf{v}^T \mathbf{u} = \sum_{k=1}^{d} v_k u_k = 1 \quad \text{and} \quad \mathbf{1}^T \mathbf{u} = \sum_{k=1}^{d} u_k = 1, \tag{4}$$

where $\mathbf{1}$ denotes a d-dimensional vector of all ones. Moreover, it is assumed that $\lambda = 1$, so that

$$A\mathbf{u} = \mathbf{u}, \quad \mathbf{v}^T A = \mathbf{v}^T \quad \text{and} \lim_{\tau \to \infty} A^\tau = \mathbf{u}\mathbf{v}^T. \tag{5}$$

From time step τ to time step $\tau + 1$, the amounts of individuals in the different classes satisfy the recurrence equation

$$\mathbf{c}(\tau + 1) = (c_1(\tau + 1), \ldots, c_d(\tau + 1))^T = A(\tau)\mathbf{c}(\tau), \tag{6}$$

where $\mathbf{c}(\tau) = (c_1(\tau), \ldots, c_d(\tau))^T$ and

$$A(\tau) = A + \frac{B(\mathbf{x}(\tau))}{N}. \tag{7}$$

Therefore, from time 0 to time $t > 0$ in number of N time steps, which represents a new time scale, these quantities are given by

$$\mathbf{c}(\lfloor Nt \rfloor) = \left(\prod_{\tau=0}^{\lfloor Nt \rfloor - 1} A(\tau) \right) \mathbf{c}(0), \tag{8}$$

where $\lfloor Nt \rfloor$ denotes the floor value of Nt which corresponds to the integer part of Nt. Moreover, the above product like all the products throughout this paper is understood in the backward order, which means that

$$\left(\prod_{\tau=0}^{\lfloor Nt\rfloor-1} A(\tau)\right) = A(\lfloor Nt\rfloor - 1)\cdots A(1)\cdot A(0). \tag{9}$$

Notice that the non-negative matrix $A(\tau)$ depends not only on τ but also on N. It is primitive since A^L has all positive entries for some integer $L \geq 1$ by assumption, and

$$A(\tau)^L \geq A^L, \tag{10}$$

the inequality being understood entrywise. This implies that $A(\tau)^L$ has all positive entries for all $\tau \geq 0$. Moreover, since the entries of $B(\mathbf{x}(\tau))$ are uniformly bounded for all $\tau \geq 0$, we have

$$A(\tau) \to A, \tag{11}$$

entrywise and uniformly for all $\tau \geq 0$ as $N \to \infty$.

Let us define

$$\mathbf{C}(t) = \lim_{N\to\infty} \mathbf{c}(\lfloor Nt\rfloor), \tag{12}$$

if this limit exists.

Note that, in the absence of selection, which occurs when $B(\mathbf{x})$ is a null matrix for every frequency vector $\mathbf{x}$, we have

$$\mathbf{C}(t) = \lim_{N\to\infty} A^{\lfloor Nt\rfloor}\mathbf{c}(0) = \mathbf{u}\mathbf{v}^T\mathbf{c}(0). \tag{13}$$

This result is a direct consequence of the Perron–Frobenius theory.

On the other hand, if $B(\mathbf{x}) = B$ for every d-dimensional frequency vector $\mathbf{x}$, which means frequency-independent selection, and if B commutes with A, which is further assumed to be invertible, then

$$\mathbf{C}(t) = \lim_{N\to\infty}\left(A + \frac{B}{N}\right)^{\lfloor Nt\rfloor}\mathbf{c}(0) \tag{14}$$

$$= \lim_{N\to\infty} A^{\lfloor Nt\rfloor}\left(I + \frac{A^{-1}B}{N}\right)^{\lfloor Nt\rfloor}\mathbf{c}(0) \tag{15}$$

$$= \mathbf{u}\mathbf{v}^T \exp\left\{tA^{-1}B\right\}\mathbf{c}(0) \tag{16}$$

owing to the Perron–Frobenius theory and the definition of the exponential function. Since $AB = BA$ and $\mathbf{v}^T A = \mathbf{v}^T$, then $BA^{-1} = A^{-1}B$ and $\mathbf{v}^T = \mathbf{v}^T A^{-1}$. This leads to

$$\mathbf{u}\mathbf{v}^T \exp\left\{tA^{-1}B\right\} = \mathbf{u}\mathbf{v}^T\sum_{n=0}^{+\infty}\frac{t^n\left(A^{-1}B\right)^n}{n!} = \mathbf{u}\sum_{n=0}^{+\infty}\frac{t^n\mathbf{v}^T B^n}{n!}. \tag{17}$$

Moreover, we have $\mathbf{v}^T B = \mathbf{v}^T AB = \mathbf{v}^T BA$. In this case, the Perron–Frobenius theory ensures that $\mathbf{v}^T B = m\mathbf{v}^T$ with $m = m\mathbf{v}^T\mathbf{u} = \mathbf{v}^T B\mathbf{u}$. Therefore,

$$\mathbf{u}\mathbf{v}^T \exp\left\{tA^{-1}B\right\} = \mathbf{u}\mathbf{v}^T \sum_{n=0}^{+\infty} \frac{t^n \left(\mathbf{v}^T B\mathbf{u}\right)^n}{n!} = \mathbf{u}\mathbf{v}^T \exp\left\{t\mathbf{v}^T B\mathbf{u}\right\}. \tag{18}$$

The objective of this section is to extend the convergence result to the case of frequency-dependent selection by showing the limit exists and is given by

$$\mathbf{C}(t) = \mathbf{u}\mathbf{v}^T \exp\left\{t\mathbf{v}^T B(\mathbf{u})\mathbf{u}\right\} \mathbf{c}(0), \tag{19}$$

when $B(\mathbf{x})$ is allowed to depend on $\mathbf{x}$ and not to commute with A, invertible or not. This result implies that

$$\frac{d\mathbf{C}(t)}{dt} = m\mathbf{C}(t), \tag{20}$$

where

$$m = \mathbf{v}^T B(\mathbf{u})\mathbf{u} \tag{21}$$

and

$$\mathbf{C}(0) = \mathbf{u}\mathbf{v}^T \mathbf{c}(0). \tag{22}$$

Therefore, m is the exponential growth rate of the population in the continuous-time limit.

Theorem 1 *Suppose that $A = (a_{l,k})$ is a primitive non-negative $d \times d$ matrix with leading eigenvalue 1 and associated positive left and right eigenvectors $\mathbf{v}$ and $\mathbf{u}$ such that $\mathbf{v}^T\mathbf{u} = \mathbf{1}^T\mathbf{u} = 1$. Let*

$$\mathbf{x}(\tau) = \frac{\mathbf{c}(\tau)}{\mathbf{1}^T\mathbf{c}(\tau)}, \tag{23}$$

where $\mathbf{c}(\tau)$ is a d-dimensional non-negative vector satisfying the recurrence equation

$$\mathbf{c}(\tau + 1) = \left(A + \frac{B(\mathbf{x}(\tau))}{N}\right) \mathbf{c}(\tau), \tag{24}$$

for all $\tau \geq 0$ with $B(\mathbf{x})$ being a non-negative $d \times d$ matrix with the same non-null entries that are continuous with respect to all d-dimensional frequency vectors $\mathbf{x}$. Then,

$$\lim_{N\to\infty} \prod_{\tau=0}^{\lfloor Nt\rfloor-1} \left(A + \frac{B(\mathbf{x}(\tau))}{N}\right) = \mathbf{u}\mathbf{v}^T \exp\left\{t\mathbf{v}^T B(\mathbf{u})\mathbf{u}\right\}, \tag{25}$$

for every real number $t > 0$.

The proof of this theorem will rely on a stability result (Lemma 1) and a consequence of the Perron–Frobenius theory (Lemma 2).

Lemma 1 *Let A be a primitive non-negative $d \times d$ matrix with leading eigenvalue* 1 *and associated positive left and right eigenvectors* $\mathbf{v}$ *and* $\mathbf{u}$ *such that* $\mathbf{v}^T\mathbf{u} = \mathbf{1}^T\mathbf{u} = 1$. *Let $A(\tau)$ for $\tau \geq 0$ be a sequence of primitive non-negative $d \times d$ matrices given by*

$$A(\tau) = A + \frac{B(\mathbf{x}(\tau))}{N}, \tag{26}$$

where $\mathbf{x}(\tau)$ for $\tau \geq 0$ is a sequence in the simplex of all d-dimensional frequency vectors Δ, defined recursively by

$$\mathbf{x}(\tau+1) = \frac{A(\tau)\mathbf{x}(\tau)}{\mathbf{1}^T A(\tau)\mathbf{x}(\tau)}, \tag{27}$$

while the entries of $B(\mathbf{x}(\tau))$ are non-negative and uniformly bounded for all $\tau \geq 0$. Then, there exists a norm $\|\cdot\|$ on $\mathbb{R}^d$ that depends only on A and is such that, for every real number $\delta > 0$,

$$\|\mathbf{x}(\tau) - \mathbf{u}\| \leq \delta, \tag{28}$$

as soon as $N \geq N_1$ and $\tau \geq \tau_1$ for some positive integers $N_1 = N_1(\delta)$ and $\tau_1 = \tau_1(\delta)$.

Remark 1 The exact form of $A(\tau)$ does not come into play in the proof of Lemma 1, only the property that $A(\tau) \to A$ entrywise and uniformly with respect to all $\tau \geq 0$ as $N \to \infty$.

Lemma 2 *Let A be a primitive non-negative $d \times d$ matrix with leading eigenvalue* 1 *and associated positive left and right eigenvectors* $\mathbf{v}$ *and* $\mathbf{u}$ *such that* $\mathbf{v}^T\mathbf{u} = \mathbf{1}^T\mathbf{u} = 1$. *Then, as $N \to \infty$,*

$$\left(A + \frac{B}{N}\right)^{\lfloor Nt \rfloor - \tau} \to \mathbf{u}\mathbf{v}^T \exp\left\{t\mathbf{v}^T B\mathbf{u}\right\}, \tag{29}$$

for any fixed real number $t > 0$, any fixed integer τ and any fixed non-negative $d \times d$ matrix B.

Remark 2 Since the matrix $A + B/N$ is not necessarily invertible, it is assumed that N is large enough so that $\lfloor Nt \rfloor - \tau \geq 1$. For the same reason, only positive powers of matrices are considered throughout the paper.

Proofs of the above two lemmas are relegated to Appendix A. We are now in a position to prove Theorem 1.

Proof Let $\|\cdot\|$ be the norm on $\mathbb{R}^d$ in the statement of Lemma 1 for

$$A(\tau) = A + \frac{B(\mathbf{x}(\tau))}{N}, \tag{30}$$

with $A(\tau)$ primitive for all $\tau \geq 0$. By continuity, given any positive real number $\epsilon \leq 1$, there exists a real number $\delta > 0$ such that

$$(1-\epsilon)B(\mathbf{u}) \leq B(\mathbf{x}(\tau)) \leq (1+\epsilon)B(\mathbf{u}), \tag{31}$$

as soon as

$$\|\mathbf{x}(\tau) - \mathbf{u}\| \leq \delta, \tag{32}$$

which holds as soon as $N \geq N_1$ and $\tau \geq \tau_1$ with $N_1 = N_1(\delta)$ and $\tau_1 = \tau_1(\delta)$ defined in Lemma 1. The inequalities in (31) are understood entrywise. These inequalities for $\tau = \tau_1, \ldots, \lfloor Nt \rfloor - 1$, for N large enough so that $N \geq N_1$ and $\lfloor Nt \rfloor \geq \tau_1 + 1$ for any fixed real number $t > 0$, lead to the inequalities

$$\begin{aligned}\left(A + \frac{(1-\epsilon)B(\mathbf{u})}{N}\right)^{\lfloor Nt \rfloor - \tau_1} &\leq \prod_{\tau=\tau_1}^{\lfloor Nt \rfloor - 1}\left(A + \frac{B(\mathbf{x}(\tau))}{N}\right) \\ &\leq \left(A + \frac{(1+\epsilon)B(\mathbf{u})}{N}\right)^{\lfloor Nt \rfloor - \tau_1}.\end{aligned} \tag{33}$$

As $N \to \infty$, Lemma 2 ensures that

$$\left(A + \frac{(1-\epsilon)B(\mathbf{u})}{N}\right)^{\lfloor Nt \rfloor - \tau_1} \to \mathbf{u}\mathbf{v}^T \exp\left\{t\mathbf{v}^T B(\mathbf{u})\mathbf{u}\right\} \exp\left\{-\epsilon t\mathbf{v}^T B(\mathbf{u})\mathbf{u}\right\} \tag{34}$$

and

$$\left(A + \frac{(1+\epsilon)B(\mathbf{u})}{N}\right)^{\lfloor Nt \rfloor - \tau_1} \to \mathbf{u}\mathbf{v}^T \exp\left\{t\mathbf{v}^T B(\mathbf{u})\mathbf{u}\right\} \exp\left\{\epsilon t\mathbf{v}^T B(\mathbf{u})\mathbf{u}\right\}. \tag{35}$$

On the other hand,

$$\prod_{\tau=0}^{\tau_1 - 1}\left(A + \frac{B(\mathbf{x}(\tau))}{N}\right) \to A^{\tau_1}. \tag{36}$$

Since $\epsilon > 0$ can be chosen arbitrarily small, we conclude that

$$\prod_{\tau=0}^{\lfloor Nt \rfloor - 1}\left(A + \frac{B(\mathbf{x}(\tau))}{N}\right) \to A^{\tau_1}\mathbf{u}\mathbf{v}^T \exp\left\{t\mathbf{v}^T B(\mathbf{u})\mathbf{u}\right\} = \mathbf{u}\mathbf{v}^T \exp\left\{t\mathbf{v}^T B(\mathbf{u})\mathbf{u}\right\}. \tag{37}$$

This completes the proof of Theorem 1. □

3 Multi-type model

In this section, assume $n \geq 1$ types of individuals distributed in $d \geq 1$ classes. Let $c_{i,k}(\tau)$ be the amount of individuals of type i in class $k = 1, \ldots, d$ at time step $\tau \geq 0$ for $i = 1, \ldots, n$. Suppose that such an individual leaves an expected number $a_{i,l,k}(\tau)$ of individuals (possibly including the individual itself) of type i in class $l = 1, \ldots, d$ at time step $\tau + 1$. Interactions between individuals are allowed so that this expected number, which corresponds to a generalized fecundity parameter, depends on the frequencies of the different types in the different classes at time step τ given by

$$z_{i,k}(\tau) = p_i(\tau)x_{i,k}(\tau), \tag{38}$$

for $i = 1, \ldots, n$ and $k = 1, \ldots, d$, where

$$x_{i,k}(\tau) = \frac{c_{i,k}(\tau)}{c_i(\tau)}, \tag{39}$$

with

$$c_i(\tau) = \sum_{l=1}^{d} c_{i,l}(\tau), \tag{40}$$

is the frequency of individuals in class k among the individuals of type i, while

$$p_i(\tau) = \sum_{k=1}^{d} z_{i,k}(\tau) = \frac{c_i(\tau)}{\sum_{j=1}^{n} c_j(\tau)} \tag{41}$$

is the frequency of type i among all individuals. The array of $n \times d$ frequencies at time step $\tau \geq 0$ that sum up to 1 is represented by $\mathbf{z}(\tau) = \left(z_{i,k}(\tau)\right)$.

Weak selection is modeled by assuming

$$a_{i,l,k}(\tau) = a_{l,k} + \frac{1}{N} b_{i,l,k}(\mathbf{z}(\tau)), \tag{42}$$

for $k, l = 1, \ldots, d$ and $i = 1, \ldots, n$. Here,

$$A = \left(a_{l,k}\right) \tag{43}$$

is a primitive $d \times d$ matrix with all constant non-negative entries that do not depend on i, while

$$B_i(\mathbf{z}) = \left(b_{i,l,k}(\mathbf{z})\right) \tag{44}$$

is a non-negative $d \times d$ matrix with the same non-null entries that are continuous functions with respect to frequency arrays $\mathbf{z}$ of dimension $n \times d$ that may depend on i. The special case of frequency-independent Leslie matrices for age-structured populations was studied in Lessard and Soares (2016).

The amounts of individuals of type i in the different classes satisfy

$$\mathbf{c}_i(\tau+1) = (c_{i,1}(\tau+1), \ldots, c_{i,d}(\tau+1))^T = A_i(\tau)\mathbf{c}_i(\tau) \tag{45}$$

from time step τ to time step $\tau+1$, where $\mathbf{c}_i(\tau) = (c_{i,1}(\tau), \ldots, c_{i,d}(\tau))^T$ and

$$A_i(\tau) = A + \frac{B_i(\mathbf{z}(\tau))}{N}, \tag{46}$$

and therefore,

$$\mathbf{c}_i(\lfloor Nt \rfloor) = \left(\prod_{\tau=0}^{\lfloor Nt \rfloor -1} A_i(\tau) \right) \mathbf{c}_i(0) \tag{47}$$

from time 0 to time $t > 0$ in number of N time steps, where $\lfloor Nt \rfloor$ denotes the floor value of Nt.

The main objective of this section is to prove the following result.

Theorem 2 *Let the amounts of individuals of type i in d classes from time step $\tau \geq 0$ to time step $\tau+1$ satisfy the recurrence equation*

$$\mathbf{c}_i(\tau+1) = A_i(\tau)\mathbf{c}_i(\tau), \tag{48}$$

where

$$A_i(\tau) = A + \frac{B_i(\mathbf{z}(\tau))}{N}, \tag{49}$$

for $i = 1, \ldots, n$. Here, A be a primitive non-negative $d \times d$ matrix with leading eigenvalue 1 and associated positive left and right eigenvectors $\mathbf{v}$ and $\mathbf{u}$ such that $\mathbf{v}^T\mathbf{u} = \mathbf{1}^T\mathbf{u} = 1$. On the other hand, $B_i(\mathbf{z}(\tau))$ is a non-negative $d \times d$ matrix with the same non-null entries that are functions of class C^1 (that is, continuous with continuous partial derivatives) with respect to frequency arrays

$$\mathbf{z}(\tau) = \left(p_i(\tau)x_{i,k}(\tau)\right), \tag{50}$$

where

$$p_i(\tau) = \frac{\mathbf{1}^T\mathbf{c}_i(\tau)}{\sum_{j=1}^n \mathbf{1}^T\mathbf{c}_j(\tau)} \tag{51}$$

is the frequency of individuals of type i at time step τ, and

$$x_{i,k}(\tau) = \frac{c_{i,k}(\tau)}{\mathbf{1}^T\mathbf{c}_i(\tau)} \tag{52}$$

is the frequency of individuals in class k among the individuals of type i, respectively, for $i = 1, \ldots, n$ *and* $k = 1, \ldots, d$. *Assume that*

$$\mathbf{C}_i(t) = \lim_{N\to\infty} \mathbf{c}_i(\lfloor Nt \rfloor) = \lim_{N\to\infty} \mathbf{c}_i(\lfloor Nt \rfloor + 1) \tag{53}$$

exists in $\mathbb{R}^d_+$, *the set of d-dimensional real vectors with non-negative components, for every real scaled time* $t > 0$, *for* $i = 1, \ldots, n$. *Then,*

$$P_i(t) = \lim_{N\to\infty} p_i(\lfloor Nt \rfloor), \tag{54}$$

for $i = 1, \ldots, n$, *which exists in* $[0, 1]$ *for every real scaled time* $t > 0$, *satisfies the replicator equation*

$$\frac{dP_i(t)}{dt} = P_i(t)\left(m_i(t) - \overline{m}(t)\right), \tag{55}$$

where

$$m_i(t) = \mathbf{v}^T B_i(\mathbf{P}(t)\mathbf{u}^T)\mathbf{u}, \tag{56}$$

with

$$\overline{m}(t) = \sum_{j=1}^{n} m_j(t) P_j(t) \tag{57}$$

and $\mathbf{P}(t) = (P_1(t), \ldots, P_n(t))^T$.

This theorem shows that the instantaneous growth rate of type i at time $t > 0$ in the continuous-time limit is given by $m_i(t)$ for $i = 1, \ldots, n$. The proof will rely on Lemmas 1 and 2, and the following lemma whose proof is also given in Appendix A for completeness.

Lemma 3 *Under the assumptions and notations of Theorem 2, we have*

$$\mathbf{C}_i(t) = \mathbf{v}^T \mathbf{C}_i(t)\mathbf{u} \tag{58}$$

and

$$\mathbf{v}^T \mathbf{c}_i(\tau) = \mathbf{v}^T \mathbf{C}_i(t) + O(h), \tag{59}$$

uniformly for N large enough and $\lfloor Nt \rfloor \le \tau \le \lfloor N(t+h) \rfloor$ *with* $t > 0$ *and* $h > 0$ *small enough.*

We are now ready to prove Theorem 2.

Proof Owing to Lemma 3, we have

$$P_i(t) = \lim_{N\to\infty} \frac{\mathbf{1}^T \mathbf{c}_i(\lfloor Nt \rfloor)}{\sum_{j=1}^n \mathbf{1}^T \mathbf{c}_j(\lfloor Nt \rfloor)} = \frac{\mathbf{1}^T \mathbf{C}_i(t)}{\sum_{j=1}^n \mathbf{1}^T \mathbf{C}_j(t)} = \frac{\mathbf{v}^T \mathbf{C}_i(t)}{\sum_{j=1}^n \mathbf{v}^T \mathbf{C}_j(t)}, \tag{60}$$

for $i = 1, \ldots, n$. Notice that if

$$\frac{d\mathbf{v}^T \mathbf{C}_i(t)}{dt} = m_i(t)\mathbf{v}^T \mathbf{C}_i(t), \tag{61}$$

then we have

$$\begin{aligned} \frac{dP_i(t)}{dt} &= \frac{m_i(t)\mathbf{v}^T \mathbf{C}_i(t) \sum_{j=1}^n \mathbf{v}^T \mathbf{C}_j(t) - \mathbf{v}^T \mathbf{C}_i(t) \sum_{j=1}^n m_j(t)\mathbf{v}^T \mathbf{C}_j(t)}{\sum_{j=1}^n (\mathbf{v}^T \mathbf{C}_i(t))^2} \\ &= P_i(t)\left(m_i(t) - \overline{m}(t)\right), \end{aligned} \tag{62}$$

for $i = 1, \ldots, n$. Therefore, it suffices to show that

$$\mathbf{v}^T \mathbf{C}_i(t+h) - \mathbf{v}^T \mathbf{C}_i(t) = hm_i(t)\mathbf{v}^T \mathbf{C}_i(t) + o(h), \tag{63}$$

for $i = 1, \ldots, n$.

Notice that there exists a continuous one-to-one correspondence between all possible frequency arrays $\mathbf{z}(\tau) = \left(z_{i,k}(\tau)\right) = \left(p_i(\tau)x_{i,k}(\tau)\right)$ and the weighted-frequency arrays $\mathbf{w}(\tau) = \left(w_{i,k}(\tau)\right) = \left(q_i(\tau)y_{i,k}(\tau)\right)$ defined by

$$q_i(\tau) = \frac{\mathbf{v}^T \mathbf{c}_i(\tau)}{\sum_{j=1}^n \mathbf{v}^T \mathbf{c}_j(\tau)} \tag{64}$$

and

$$y_{i,k}(\tau) = \frac{v_k c_{i,k}(\tau)}{\mathbf{v}^T \mathbf{c}_i(\tau)}, \tag{65}$$

so that

$$w_{i,k}(\tau) = \frac{v_k c_{i,k}(\tau)}{\sum_{j=1}^n \sum_{l=1}^d v_l c_{j,l}(\tau)} = \frac{v_k z_{i,k}(\tau)}{\sum_{j=1}^n \sum_{l=1}^d v_l z_{j,l}(\tau)}, \tag{66}$$

for $i = 1, \ldots, n$ and $k = 1, \ldots, d$. Using this change of arrays, let

$$H_i(\mathbf{w}(\tau)) = B_i(\mathbf{z}(\tau)), \tag{67}$$

for $\lfloor Nt \rfloor \le \tau \le \lfloor N(t+h) \rfloor$ with $t > 0$ and $h > 0$ small enough. The mean value theorem for the continuous entries of this matrix, the extreme value theorem for their continuous partial derivatives and the Cauchy–Schwarz inequality entail that

$$H_i(\mathbf{w}(\tau)) - H_i(\mathbf{w}(\lfloor Nt \rfloor)) \le K|\mathbf{w}(\tau) - \mathbf{w}(\lfloor Nt \rfloor)| B_i(\mathbf{P}(t)\mathbf{u}^T), \tag{68}$$

where $K > 0$ is some positive constant that depends on the positive entries of $B_i(\mathbf{P}(t)\mathbf{u}^T)$ and the maxima of the partial derivatives in absolute value on the simplex of $(n \times d)$-dimensional frequency arrays. Owing to Lemmas 1 and 2, we have

$$z_{i,k}(\tau) = u_k + O(h), \quad q_i(\tau) = P_i(t) + O(h), \tag{69}$$

and then,

$$\mathbf{w}(\tau) = \left(q_i(\tau) y_{i,k}(\tau)\right) = ((P_i(t) + O(h))(v_k u_k + O(h))) = (P_i(t) v_k u_k + O(h)), \tag{70}$$

for $\lfloor Nt \rfloor \le \tau \le \lfloor N(t+h) \rfloor$ if N is large enough. This implies that there exists a constant $L > 0$ such that

$$|\mathbf{w}(\tau) - \mathbf{w}(\lfloor Nt \rfloor)| \le \frac{Lh}{2K}. \tag{71}$$

Finally, if N is large enough so that

$$H_i(\mathbf{w}(\lfloor Nt \rfloor)) = B_i(\mathbf{z}(\lfloor Nt \rfloor)) \le B_i(\mathbf{P}(t)\mathbf{u}^T) + \frac{Lh}{2} B_i(\mathbf{P}(t)\mathbf{u}^T), \tag{72}$$

then

$$A \le A_i(\tau) = A + \frac{B_i(\mathbf{z}(\tau))}{N} \le A + \frac{(1 + Lh) B_i(\mathbf{P}(t)\mathbf{u}^T)}{N}, \tag{73}$$

which holds for $\lfloor Nt \rfloor \le \tau \le \lfloor N(t+h) \rfloor$. Using the fact that

$$\mathbf{c}_i(\lfloor N(t+h) \rfloor) = \left(\prod_{\tau=\lfloor Nt \rfloor}^{\lfloor N(t+h) \rfloor - 1} A_i(\tau) \right) \mathbf{c}_i(\lfloor Nt \rfloor), \tag{74}$$

the above inequalities lead to

$$\begin{aligned} \mathbf{v}^T \mathbf{c}_i(\lfloor Nt \rfloor) &\le \mathbf{v}^T \mathbf{c}_i(\lfloor N(t+h) \rfloor) \\ &\le \mathbf{v}^T \left(A + \frac{(1 + Lh) B_i(\mathbf{P}(t)\mathbf{u}^T)}{N} \right)^{\lfloor N(t+h) \rfloor - \lfloor Nt \rfloor} \mathbf{c}_i(\lfloor Nt \rfloor). \end{aligned} \tag{75}$$

In the limit as $N \to \infty$, Lemma 2 yields

$$\left(A + \frac{(1+Lh)B_i(\mathbf{P}(t)\mathbf{u}^T)}{N}\right)^{\lfloor N(t+h)\rfloor - \lfloor Nt \rfloor} \to \mathbf{u}\mathbf{v}^T \exp\left\{h(1+Lh)m_i(t)\right\}, \quad (76)$$

where

$$m_i(t) = \mathbf{v}^T B_i(\mathbf{P}(t)\mathbf{u}^T)\mathbf{u}. \quad (77)$$

Therefore,

$$\mathbf{v}^T \mathbf{C}_i(t) \leq \mathbf{v}^T \mathbf{C}_i(t+h) \leq \mathbf{v}^T \mathbf{C}_i(t) \exp\left\{h(1+Lh)m_i(t)\right\}, \quad (78)$$

with

$$\exp\left\{h(1+Lh)m_i(t)\right\} = 1 + hm_i(t) + o(h). \quad (79)$$

The proof is complete. □

4 Application to evolutionary game theory

In this section, we consider a game with n possible strategies in a class-structured population. The type of an individual corresponds to the strategy that this individual uses in pairwise interactions. These interactions are assumed to occur at random so that the expected payoffs are linear functions of the strategy frequencies. These expected payoffs, multiplied by a small factor $1/N$, as well as type- and class-specific payoff allocation frequencies, perturb the fecundity parameters given by the entries of a primitive non-negative matrix $A = (a_{l,k})$ whose leading eigenvalue is 1. This is a linear case of the frequency-dependent growth model described in Sect. 3.

The payoff matrix is class-dependent and given by

$$M_{k,l} = (m_{i,j,k,l}), \quad (80)$$

where $m_{i,j,k,l}$ is the payoff that an individual of type i in class k receives when in interaction with an individual of type j in class l for $i, j = 1, \ldots, n$ and $k, l = 1, \ldots, d$.

If the strategy frequencies in the different classes are given by the array $\mathbf{z} = (z_{j,l})$ as in (38), then the expected payoff of an individual of type i in class k is

$$\beta_{i,k}(\mathbf{z}) = \sum_{l=1}^{d} \sum_{j=1}^{n} m_{i,j,k,l} z_{j,l}, \quad (81)$$

for $i = 1, \ldots, n$ and $k = 1, \ldots, d$. Following allocation theory (see, e.g., Baudisch and Vaupel 2012), it is assumed that this expected payoff is allocated to the production of an excess of individuals of type i in class l with probability $q_{i,l,k}$ so that the total expected number is given by

$$b_{i,l,k}(\mathbf{z}) = q_{i,l,k}\beta_{i,k}(\mathbf{z}), \tag{82}$$

for $l = 1, \ldots, d$. Moreover,

$$0 \leq q_{i,l,k} \leq 1 \quad \text{with} \quad \sum_{l=1}^{d} q_{i,l,k} \leq 1 \tag{83}$$

and $q_{i,l,k} = 0$ for the same couples (l, k) with $1 \leq l, k \leq d$ for $i = 1, \ldots, n$. The parameters $q_{i,l,k}$ determine how available resources are allocated, e.g., to survival and reproduction at all ages over the life span in an age-structured population. Note that $1 - \sum_{l=1}^{d} q_{i,l,k}$ represents the fraction of wasted resources by an individual of type i in class k for $i = 1, \ldots, n$ and $k = 1, \ldots, d$.

According to Theorem 2, the strategy frequencies at time $t > 0$ in number of time steps as $N \to \infty$ satisfy the replicator equation (55) with

$$m_i(t) = \mathbf{v}^T B_i(\mathbf{P}(t)\mathbf{u}^T)\mathbf{u} \tag{84}$$

as instantaneous rate of increase of strategy i for $i = 1, \ldots, n$, where

$$B_i(\mathbf{P}(t)\mathbf{u}^T) = \left(q_{i,l,k}\beta_{i,k}(\mathbf{P}(t)\mathbf{u}^T)\right) \tag{85}$$

with $\mathbf{P}(t) = (P_1(t), \ldots, P_n(t))^T$ being the current strategy frequency vector, while

$$A\mathbf{u} = \mathbf{u} = (u_1, \ldots, u_d)^T \quad \text{and} \quad \mathbf{v}^T A = \mathbf{v}^T = (v_1, \ldots, v_d) \tag{86}$$

are positive vectors satisfying

$$\mathbf{v}^T\mathbf{u} = \sum_{l=1}^{d} v_l u_l = 1 \quad \text{and} \quad \mathbf{1}^T\mathbf{u} = \sum_{l=1}^{d} u_l = 1. \tag{87}$$

Since $\mathbf{P}(t)\mathbf{u}^T = (P_j(t)u_l)$, we have

$$\beta_{i,k}(\mathbf{P}(t)\mathbf{u}^T) = \sum_{j=1}^{n} m_{i,j,k} P_j(t), \tag{88}$$

where

$$m_{i,j,k} = \sum_{l=1}^{d} m_{i,j,k,l} u_l \tag{89}$$

is the expected payoff of an individual of type i in class k in interaction with an individual chosen at random in a population with class probability distribution given by $\mathbf{u}$. This leads to

$$m_i(t) = \sum_{j=1}^{n} \overline{m}_{i,j} P_j(t), \tag{90}$$

where

$$\overline{m}_{i,j} = \sum_{l=1}^{d} \sum_{k=1}^{d} v_l q_{i,l,k} m_{i,j,k} u_k. \tag{91}$$

This represents the expected payoff in reproductive value of an individual of type i in a population exhibiting stable class frequencies and reproductive values in the absence of selection. Moreover, the replicator equation (55) is the same in this case as in the case of a linear game in a well-mixed population with game matrix $\overline{M} = (\overline{m}_{ij})$. Therefore, this matrix is called an effective game matrix.

4.1 Evolutionary game in an age-structured population

Consider an age-structured haploid population with d age classes. From one time step to the next, an individual in age class k can produce new individuals entering age class 1, and survive to the next age class $k+1$, for $k = 1, \ldots, d$ with age class $d+1$ corresponding to death. This is done according to some allocation of the payoff to n possible individual strategies in the context of a linear game as a result of random pairwise interactions and class-dependent payoff matrices in the form $M_{k,l} = (m_{i,j,k,l})$ as in (80). More precisely, the payoff of an individual of type i for $i = 1, \ldots, n$ in age class $k = 1, \ldots, d$ is allocated to reproduction with probability $q_{i,1,k}$ and to survival with probability $q_{i,k+1,k}$. There is no contribution to the other age classes, so that $q_{i,l,k} = 0$ if $l \neq 1$ and $l \neq k+1$.

According to (91), the entries of the effective game matrix $\overline{M} = (\overline{m}_{ij})$ in the continuous-time limit are given by

$$\overline{m}_{i,j} = \sum_{k=1}^{d} m_{i,j,k} u_k \left(v_1 q_{i,1,k} + v_{k+1} q_{i,k+1,k} \right) \tag{92}$$

with $m_{i,j,k}$ defined in (89) and $v_{d+1} = 0$. In the case of two age-independent individual strategies, that is $n = 2$, the replicator equation (62) with $P(t) = P_1(t)$ and $1 - P(t) = P_2(t)$ becomes

$$\frac{dP(t)}{dt} = P(t)(1 - P(t)) \left(m_1(t) - m_2(t) \right), \tag{93}$$

where

$$m_i(t) = P(t)\overline{m}_{i,1} + (1 - P(t))\overline{m}_{i,2}. \tag{94}$$

With two age classes and two pure strategies, 1 and 2, but in the case where an individual can use different strategies in the two age classes as considered in Li et al. (2015), there are four possible individual strategies, namely, 1 for (1, 1), 2 for (1, 2), 3 for (2, 1) and 4 for (2, 2). Assuming a constant payoff matrix for the pure strategies given by

$$M = \begin{pmatrix} a & b \\ c & d \end{pmatrix}, \tag{95}$$

and defining the permutation matrix

$$E = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}, \tag{96}$$

the class-dependent payoff matrices in (80) for the age-dependent individual strategies are given by

$$M_{1,1} = \begin{pmatrix} a & a & b & b \\ a & a & b & b \\ c & c & d & d \\ c & c & d & d \end{pmatrix} \tag{97}$$

and

$$M_{1,2} = M_{1,1}E, \quad M_{2,1} = EM_{1,1}, \quad M_{2,2} = EM_{1,1}E. \tag{98}$$

According to (92), this leads to an effective game matrix $\overline{M} = (\overline{m}_{ij})$ in the continuous-time limit whose entries are given by

$$\overline{m}_{ij} = (m_{i,j,1,1}u_1 + m_{i,j,1,2}u_2)u_1q_{i,1} + (m_{i,j,2,1}u_1 + m_{i,j,2,2}u_2)u_2q_{i,2} \tag{99}$$

with

$$q_{i,1} = v_1q_{i,1,1} + v_2q_{i,2,1}, \quad q_{i,2} = v_1q_{i,1,2}, \tag{100}$$

for $i, j = 1, 2, 3, 4$. If

$$q_{i,1} = q_1, \quad q_{i,2} = q_2, \tag{101}$$

for $i = 1, 2, 3, 4$, then the effective game matrix is

$$\overline{M} = u_1^2 q_1 M_{1,1} + u_1 u_2 (q_1 M_{2,1} + q_2 M_{1,2}) + u_2^2 q_2 M_{2,2}. \tag{102}$$

A variant of this model assumes that an individual can use different strategies according to the age class of the interacting individual which leads to an effective game matrix

$$\overline{M} = u_1^2 q_1 M_{1,1} + u_1 u_2 (q_1 M_{2,1} + q_2 M_{1,2}) + u_2^2 q_2 M_{2,2} \tag{103}$$

under the condition (101).

4.2 Simulation results with two strategies in two age classes

In the case of two age-independent strategies in two age classes, the population dynamics from time step τ to time step $\tau + 1$ given by (45) reduces to the recurrence equations

$$\mathbf{c}_1(\tau + 1) = \left(A + \frac{1}{N} B_1(\mathbf{z}(\tau)) \right) \mathbf{c}_1(\tau), \tag{104}$$

$$\mathbf{c}_2(\tau + 1) = \left(A + \frac{1}{N} B_2(\mathbf{z}(\tau)) \right) \mathbf{c}_2(\tau), \tag{105}$$

while the frequency of strategy 1 at time step $\tau \geq 0$ is given by

$$p(\tau) = \frac{\mathbf{1}^T \mathbf{c}_1(\tau)}{\mathbf{1}^T \mathbf{c}_1(\tau) + \mathbf{1}^T \mathbf{c}_2(\tau)}. \tag{106}$$

Here, we use

$$A = \begin{pmatrix} 0.65 & 0.50 \\ 0.70 & 0 \end{pmatrix} \text{ with } A\mathbf{u} = \mathbf{u} = \begin{pmatrix} 0.59 \\ 0.41 \end{pmatrix} \text{ and } \mathbf{v}^T A = \mathbf{v}^T = \begin{pmatrix} 1.26 & 0.63 \end{pmatrix}, \tag{107}$$

while we set $N = 100$. Moreover, the entries of $B_1(\mathbf{z}(\tau))$ and $B_2(\mathbf{z}(\tau))$ are in the form (82), where

$$q_{1,1,2} = q_{2,1,2} = 1, \quad q_{1,2,2} = q_{2,2,2} = 0, \tag{108}$$

and

$$q_{1,1,1} = q_1, \quad q_{1,2,1} = 1 - q_1, \quad q_{2,1,1} = q_2, \quad q_{2,2,1} = 1 - q_2, \tag{109}$$

with $q_1 = 0.50$ and $q_2 = 0.30$.

Without loss of generality, the payoffs are chosen so that the effective payoffs in the limit as $N \to \infty$ given by (91) satisfy the inequality $\overline{m}_{11} > \overline{m}_{22}$. Otherwise, it

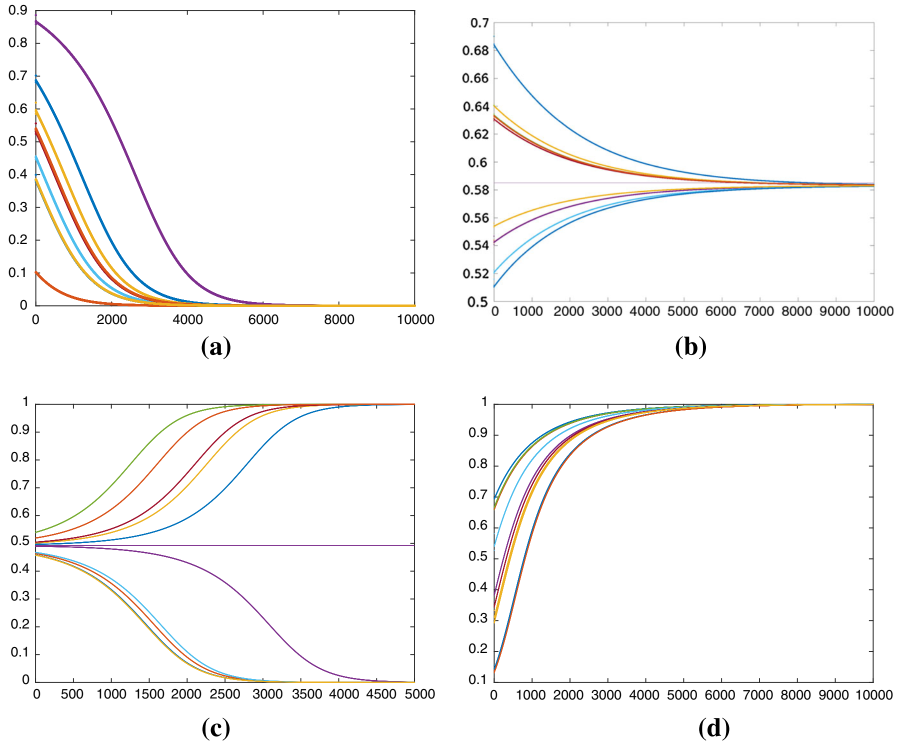

Fig. 1 Frequency of strategy 1 $p(\tau)$ at time step $\tau \geq 0$ in two age classes for a selection of 10 initial conditions. **a** Prisoner's dilemma with $\overline{m}_{21} > \overline{m}_{11}$ and $\overline{m}_{22} > \overline{m}_{12}$. **b** Snowdrift game with $\overline{m}_{21} > \overline{m}_{11}$ and $\overline{m}_{12} > \overline{m}_{22}$. **c** Stag hunt game with $\overline{m}_{11} > \overline{m}_{21}$ and $\overline{m}_{22} > \overline{m}_{12}$. **d** No conflict with $\overline{m}_{11} > \overline{m}_{21}$ and $\overline{m}_{12} > \overline{m}_{22}$

suffices to permute the strategies 1 and 2 or to smally perturb their payoffs. Four cases are considered: (a) $\overline{m}_{21} > \overline{m}_{11}$ and $\overline{m}_{22} > \overline{m}_{12}$, which corresponds to the Prisoner's Dilemma, (b) $\overline{m}_{21} > \overline{m}_{11}$ and $\overline{m}_{12} > \overline{m}_{22}$, which is known as the Snowdrift game, (c) $\overline{m}_{11} > \overline{m}_{21}$ and $\overline{m}_{22} > \overline{m}_{12}$, which is referred to as the Stag Hunt game, and (d) $\overline{m}_{11} > \overline{m}_{21}$ and $\overline{m}_{12} > \overline{m}_{22}$, which is the case with no conflict that is symmetric to case (a). A review of these four possible situations can be found for example in Archetti and Scheuring (2012).

The numerical values of the different payoffs are given in Supplementary Material and the simulation results for the dynamics of the frequency of strategy 1 for a selection of 10 initial conditions in each case are shown in Fig. 1. These are consistent with the dynamics described by the replicator equation with the effective game matrix $\overline{M} = (\overline{m}_{ij})$. This supports convergence to this equation in the continuous-time limit.

5 Discussion

According to (19) proved in Theorem 1, our continuous-time limit ascertains an exponential growth rate $\mathbf{v}^T B(\mathbf{u})\mathbf{u}$ for the size of a single type in a class-structured population under frequency-dependent selection with the inverse of the intensity of selection as unit of time. Here, the components of $\mathbf{u}$ and $\mathbf{v}$ are the equilibrium class frequencies and reproductive values in the absence of selection, while the entries of $B(\mathbf{u})$ are the coefficients of the first-order effects of selection. As the continuous time t goes to ∞, the population size goes to 0 if $\mathbf{v}^T B(\mathbf{u})\mathbf{u} < 0$, while it goes to infinity if $\mathbf{v}^T B(\mathbf{u})\mathbf{u} > 0$. This gives the condition for the extinction equilibrium to be locally asymptotically stable or unstable, respectively, in agreement with Cushing (1998).

With multiple types, the growth rate of each type depends on the population state so that the instantaneous rate of increase of type i at continuous time $t > 0$ is $\mathbf{v}^T B_i(\mathbf{P}(t)\mathbf{u}^T)\mathbf{u}$, where the components of $\mathbf{P}(t)$ are the type frequencies at this time. These are the rates that come into play in the replicator equation for the type frequencies according to (55) in the statement of Theorem 2. Such rates can be traced back to a covariance formula for the change in the frequency of an allele, from one time step to the next and to first order with respect to the intensity of selection, proposed by Taylor (1990). The continuous-time limit requires to consider a number of time steps that goes to infinity, however, and this is what makes the analysis so difficult even under the assumption that the limits of the type frequencies exist. Notice that this assumption holds in the case of a single type as shown in Theorem 1, and is supported by simulations in the case of multiple types as illustrated in Sect. 4.2.

Finally, the instantaneous growth rates that have been confirmed in the continuous-time limit, which relies on two-timescale arguments, can be used to get effective game matrices in the case of evolutionary games in class-structured populations as shown in Sect. 4 and applied to an age-structured population in Sect. 4.1. Notice that two-timescale arguments have already been applied to deduce effective payoffs in other structured populations such as group-structured or hierarchically structured populations (Lessard 2009, 2011; Kroumi and Lessard 2015a, b). The main difference—and difficulty—in the case of class-structured populations is that the class sizes depend on the composition of the population.

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6 Appendix A: Proofs of Lemmas

6.1 Proof of Lemma 1

The proof of this lemma will rely on three well-known facts in matrix analysis and real analysis.

Fact 1 *Let* $\|\cdot\|$ *be a norm on* $\mathbb{R}^d$*, so that*

1. $\|\mathbf{x}\| \geq 0$ *for every* $\mathbf{x} \in \mathbb{R}^d$ *with equality if and only if* $\mathbf{x} = 0$*;*
2. $\|a\mathbf{x}\| = |a| \cdot \|\mathbf{x}\|$ *for every* $\mathbf{x} \in \mathbb{R}^d$ *and every* $a \in \mathbb{R}$ *with modulus* $|a|$*;*
3. $\|\mathbf{x} + \mathbf{y}\| \leq \|\mathbf{x}\| + \|\mathbf{y}\|$ *for every* $\mathbf{x} \in \mathbb{R}^d$ *and every* $\mathbf{y} \in \mathbb{R}^d$.

Moreover, let

$$\|M\| = \sup\left\{\frac{\|M\mathbf{x}\|}{\|\mathbf{x}\|} : \mathbf{x} \in \mathbb{R}^d, \mathbf{x} \neq \mathbf{0}\right\}, \tag{110}$$

where $\mathbf{0}$ *denotes a* d*-dimensional vector of all zeros, be the induced norm of a real* $d \times d$ *matrix* M*. Then, there exist real numbers* $c, C > 0$ *such that for every* $\mathbf{x} = (x_1, \ldots, x_d) \in \mathbb{R}^d$*,*

$$c|\mathbf{x}| \leq \|\mathbf{x}\| \leq C|\mathbf{x}|, \tag{111}$$

where

$$|\mathbf{x}| = \sqrt{x_1^2 + \cdots + x_d^2} \tag{112}$$

defines the Euclidian norm. Moreover, there exist real numbers $r, R > 0$ *such that*

$$r|M| \leq \|M\| \leq R|M|. \tag{113}$$

Therefore, every norm $\|\cdot\|$ *on* $\mathbb{R}^d$ *is equivalent to the Euclidian norm and continuous with respect to this norm. Actually, all norms on* $\mathbb{R}^d$ *are equivalent to one another.*

Fact 2 *Let* M *be a real* $d \times d$ *matrix with all eigenvalues, real or complex, less than* 1 *in modulus. Then, there exist a norm* $\|\cdot\|$ *on* $\mathbb{R}^d$ *and* $0 < \alpha < 1$ *such that for every* $\mathbf{x} \in \mathbb{R}^d$*,*

$$\|M\mathbf{x}\| \leq \alpha\|\mathbf{x}\|. \tag{114}$$

Fact 3 *Let* $\mathbf{f}(\mathbf{x}) = (f_1(\mathbf{x}), \ldots, f_d(\mathbf{x}))$ *be a continuously differentiable transformation of the frequency simplex* $\Delta \subseteq \mathbb{R}^d$ *into itself. Suppose that* $\mathbf{f}(\mathbf{x}^\circ) = \mathbf{x}^\circ \in \Delta$ *is a fixed point of this transformation such that the gradient matrix evaluated at* $\mathbf{y} \in \Delta$*, namely*

$$\mathbf{f}'(\mathbf{y}) = \left(\frac{\partial f_l}{\partial x_k}(\mathbf{y})\right), \tag{115}$$

satisfies

$$\|\mathbf{f}'(\mathbf{x}^\circ + t(\mathbf{x} - \mathbf{x}^\circ))\| \leq \gamma, \tag{116}$$

for some $\mathbf{x} \in \Delta$ *and all* $0 \leq t \leq 1$*, for some real number* $\gamma > 0$ *and some norm* $\|\cdot\|$ *on* $\mathbb{R}^d$*. Then,*

$$\|\mathbf{f}(\mathbf{x}) - \mathbf{x}^\circ\| \leq \gamma\|\mathbf{x} - \mathbf{x}^\circ\|. \tag{117}$$

Proofs of Facts 1 and 2 can be found, e.g., in Horn and Johnson (2012), and proof of Fact 3 in Rudin (1976, p. 218). For completeness, proofs of these facts that follow closely unpublished notes by Samuel Karlin (SIAM REVIEW, Chapter 1, Section 2, Stanford University, 1981) are provided in Supplementary Material. We are now in a position to prove Lemma 1.

Since the non-negative $d \times d$ matrix $A(\tau)$ is primitive, then the Perron–Frobenius theory (see, e.g., Appendix in Karlin and Taylor 1975, or Lancaster and Tismenetsky 1985) ascertains that there exist $\lambda(\tau) > 0$ and positive d-dimensional vectors $\mathbf{v}(\tau)$ and $\mathbf{u}(\tau)$ such that

$$\begin{aligned} \mathbf{v}(\tau)^T A(\tau) = \lambda(\tau)\mathbf{v}(\tau)^T, \quad A(\tau)\mathbf{u}(\tau) = \lambda(\tau)\mathbf{u}(\tau), \\ \mathbf{v}(\tau)^T\mathbf{u}(\tau) = 1 \quad \text{and} \quad \mathbf{1}^T\mathbf{u}(\tau) = 1. \end{aligned} \tag{118}$$

Notice that $A(\tau)$, $\lambda(\tau)$, $\mathbf{v}(\tau)$ and $\mathbf{u}(\tau)$ all depend on N. Moreover, as $N \to \infty$,

$$A(\tau) \to A \tag{119}$$

uniformly with respect to $\tau \geq 0$ using any induced matrix norm (see Fact 1). Then by continuity, as $N \to \infty$,

$$\lambda(\tau) \to 1, \quad \mathbf{v}(\tau)^T \to \mathbf{v}^T \quad \text{and} \quad \mathbf{u}(\tau) \to \mathbf{u} \tag{120}$$

uniformly with respect to $\tau \geq 0$ using the same norm.

Note that

$$\mathbf{x}(\tau+1) = \mathbf{f}_\tau(\mathbf{x}(\tau)), \tag{121}$$

for $\tau \geq 0$, where

$$\mathbf{f}_\tau(\mathbf{x}) = \frac{A(\tau)\mathbf{x}}{\mathbf{1}^T A(\tau)\mathbf{x}}, \tag{122}$$

for all $\mathbf{x} \in \Delta$. This transformation is such that

$$\mathbf{f}_\tau(\mathbf{u}(\tau)) = \frac{A(\tau)\mathbf{u}(\tau)}{\mathbf{1}^T A(\tau)\mathbf{u}(\tau)} = \frac{\lambda(\tau)\mathbf{u}(\tau)}{\lambda(\tau)\mathbf{1}^T\mathbf{u}(\tau)} = \mathbf{u}(\tau). \tag{123}$$

For $\mathbf{x} = \mathbf{u}(\tau) + \boldsymbol{\xi} \in \Delta$, we have

$$\begin{aligned} \mathbf{f}_\tau(\mathbf{u}(\tau) + \boldsymbol{\xi}) &= \frac{A(\tau)\mathbf{u}(\tau) + A(\tau)\boldsymbol{\xi}}{\mathbf{1}^T A(\tau)\mathbf{u}(\tau) + \mathbf{1}^T A(\tau)\boldsymbol{\xi}} \\ &= \frac{\lambda(\tau)\mathbf{u}(\tau) + A(\tau)\boldsymbol{\xi}}{\lambda(\tau) + \mathbf{1}^T A(\tau)\boldsymbol{\xi}} \\ &= \mathbf{u}(\tau) + \left(\frac{A(\tau) - \mathbf{u}(\tau)\mathbf{1}^T A(\tau)}{\lambda(\tau)}\right)\boldsymbol{\xi} + o(|\boldsymbol{\xi}|). \end{aligned} \tag{124}$$

Therefore, the gradient matrix of $\mathbf{f}_\tau$ evaluated at $\mathbf{u}(\tau)$ is given by

$$\mathbf{f}'_\tau(\mathbf{u}(\tau)) = \frac{A(\tau) - \mathbf{u}(\tau)\mathbf{1}^T A(\tau)}{\lambda(\tau)}. \tag{125}$$

Moreover,

$$\mathbf{f}'_\tau(\mathbf{u}(\tau)) \to A - \mathbf{u}\mathbf{1}^T A = \mathbf{f}'(\mathbf{u}), \tag{126}$$

uniformly with respect to $\tau \geq 0$ as $N \to \infty$, where $\mathbf{f}'(\mathbf{u})$ is the gradient matrix of the transformation

$$\mathbf{f}(\mathbf{x}) = \frac{A\mathbf{x}}{\mathbf{1}^T A\mathbf{x}}, \tag{127}$$

evaluated at $\mathbf{u}$.

Note that

$$\mathbf{f}'_\tau(\mathbf{x}) = \frac{A(\tau)}{\mathbf{1}^T A(\tau)\mathbf{x}} - \frac{A(\tau)\mathbf{x}\mathbf{1}^T A(\tau)}{(\mathbf{1}^T A(\tau)\mathbf{x})^2} \tag{128}$$

and

$$\mathbf{f}'_\tau(\mathbf{x}) \to \frac{A}{\mathbf{1}^T A\mathbf{x}} - \frac{A\mathbf{x}\mathbf{1}^T A}{(\mathbf{1}^T A\mathbf{x})^2} = \mathbf{f}'(\mathbf{x}) \tag{129}$$

uniformly with respect to $\tau \geq 0$ and $\mathbf{x} \in \Delta$ as $N \to \infty$. Note also that the matrix $\mathbf{f}'(\mathbf{u})$ admits 0 as an eigenvalue with associated left and right eigenvectors $\mathbf{1}$ and $\mathbf{u}$, respectively. As a matter of fact,

$$\mathbf{1}^T \left(A - \mathbf{u}\mathbf{1}^T A\right) = \mathbf{1}^T A - \mathbf{1}^T\mathbf{u}\mathbf{1}^T A = \mathbf{1}^T A - \mathbf{1}^T A = \mathbf{0} \tag{130}$$

and

$$\left(A - \mathbf{u}\mathbf{1}^T A\right)\mathbf{u} = A\mathbf{u} - \mathbf{u}\mathbf{1}^T A\mathbf{u} = \mathbf{u} - \mathbf{u} = \mathbf{0}, \tag{131}$$

where $\mathbf{0}$ denotes a d-dimensional vector of all zeros. The other eigenvalues of $\mathbf{f}'(\mathbf{u})$ are associated with left eigenvectors $\mathbf{z} \in \mathbb{C}^d$ which are also left eigenvectors of A, since they must satisfy $\mathbf{z}^T\mathbf{u} = 0$. Therefore, they are associated with eigenvalues of A different from 1, which are necessarily less than 1 in modulus owing to the Perron–Frobenius theory. Then Fact 2 ascertains that there exist a norm $\|\cdot\|$ on $\mathbb{R}^d$ and $0 < \alpha < 1$ such that

$$\|\mathbf{f}'(\mathbf{u})\mathbf{x}\| \leq \alpha\|\mathbf{x}\|, \tag{132}$$

for every $\mathbf{x} \in \mathbb{R}^d$, which means that $\|\mathbf{f}'(\mathbf{u})\| \leq \alpha$. By continuity of $\mathbf{f}'(\mathbf{x})$ with respect to $\mathbf{x} \in \Delta$ and uniform convergence of $\mathbf{f}'_\tau(\mathbf{x})$ as $N \to \infty$, with respect to all $\tau \geq 0$

and all $\mathbf{x}$ in any compact subset of Δ, there exist a real number $\delta_0 > 0$ and an integer $N_0 = N_0(\delta_0) \geq 1$ that depend only on A such that

$$\|\mathbf{f}'(\mathbf{x}) - \mathbf{f}'(\mathbf{u})\| \leq \frac{1-\alpha}{4} \tag{133}$$

and

$$\|\mathbf{f}'_\tau(\mathbf{x}) - \mathbf{f}'(\mathbf{x})\| \leq \frac{1-\alpha}{4}, \tag{134}$$

as soon as $N \geq N_0$ and $\mathbf{x} \in \Delta$ with $\|\mathbf{x} - \mathbf{u}\| \leq \delta_0$. Under the same conditions, we have

$$\begin{aligned}\|\mathbf{f}'_\tau(\mathbf{x})\| &= \|\mathbf{f}'_\tau(\mathbf{x}) - \mathbf{f}'(\mathbf{x}) + \mathbf{f}'(\mathbf{x}) - \mathbf{f}'(\mathbf{u}) + \mathbf{f}'(\mathbf{u})\| \\ &\leq \|\mathbf{f}'_\tau(\mathbf{x}) - \mathbf{f}'(\mathbf{x})\| + \|\mathbf{f}'(\mathbf{x}) - \mathbf{f}'(\mathbf{u})\| + \|\mathbf{f}'(\mathbf{u})\| \\ &\leq \frac{1-\alpha}{4} + \frac{1-\alpha}{4} + \alpha = \gamma < 1. \end{aligned} \tag{135}$$

On the other hand, for every positive real number $\delta \leq \delta_0$, there exist integers $N_1 = N_1(\delta) \geq N_0$ and $\tau_1 = \tau_1(\delta) \geq 1$ such that

$$\|\mathbf{u}(\tau) - \mathbf{u}\| \leq \frac{\delta(1-\gamma)}{2}, \tag{136}$$

$$\left\|\mathbf{x}(\tau_1) - \frac{A^{\tau_1}\mathbf{x}(0)}{\mathbf{1}^T A^{\tau_1}\mathbf{x}(0)}\right\| \leq \frac{\delta(1-\gamma)}{4} \tag{137}$$

and

$$\left\|\frac{A^{\tau_1}\mathbf{x}(0)}{\mathbf{1}^T A^{\tau_1}\mathbf{x}(0)} - \mathbf{u}\right\| \leq \frac{\delta(1-\gamma)}{4}, \tag{138}$$

as soon as $N \geq N_1$ and $\tau \geq \tau_1$. The last inequality comes from the fact that

$$\frac{A^{\tau}\mathbf{x}(0)}{\mathbf{1}^T A^{\tau}\mathbf{x}(0)} \to \frac{\mathbf{u}\mathbf{v}^T\mathbf{x}(0)}{\mathbf{1}^T\mathbf{u}\mathbf{v}^T\mathbf{x}(0)} = \mathbf{u}, \tag{139}$$

as $\tau \to \infty$, owing to the Perron–Frobenius theory. The second inequality holds by continuity, since

$$\mathbf{x}(\tau_1) = \frac{\left(\prod_{\tau=0}^{\tau_1-1} A(\tau)\right)\mathbf{x}(0)}{\mathbf{1}^T\left(\prod_{\tau=0}^{\tau_1-1} A(\tau)\right)\mathbf{x}(0)} \to \frac{A^{\tau_1}\mathbf{x}(0)}{\mathbf{1}^T A^{\tau_1}\mathbf{x}(0)}, \tag{140}$$

as $N \to \infty$ for any fixed integer $\tau_1 \geq 1$. Finally, the fact that

$$\mathbf{u}(\tau) \to \mathbf{u}, \tag{141}$$

uniformly with respect to $\tau \geq 0$ as $N \to \infty$, entails the first inequality.

Note that (136) implies that

$$\begin{aligned}\|\mathbf{u}(\tau) + t(\mathbf{x} - \mathbf{u}(\tau)) - \mathbf{u}\| &= \|t(\mathbf{x} - \mathbf{u}) + (1-t)(\mathbf{u}(\tau) - \mathbf{u})\| \\ &\leq t\|\mathbf{x} - \mathbf{u}\| + (1-t)\|\mathbf{u}(\tau) - \mathbf{u}\| \\ &\leq t\delta + (1-t)\frac{\delta(1-\gamma)}{2} \\ &\leq \delta, \end{aligned} \tag{142}$$

for $0 \leq t \leq 1$, as soon as

$$\|\mathbf{x} - \mathbf{u}\| \leq \delta. \tag{143}$$

Under the same condition and the inequality $\delta \leq \delta_0$, (135) ensures that

$$\|\mathbf{f}'_\tau(\mathbf{u}(\tau) + t(\mathbf{x} - \mathbf{u}(\tau)))\| \leq \gamma, \tag{144}$$

and then Lemma 3 that

$$\|\mathbf{f}_\tau(\mathbf{x}) - \mathbf{u}(\tau)\| \leq \gamma\|\mathbf{x} - \mathbf{u}(\tau)\|. \tag{145}$$

On the other hand, (137) and (138) imply that

$$\begin{aligned}\|\mathbf{x}(\tau_1) - \mathbf{u}\| &\leq \left\|\mathbf{x}(\tau_1) - \frac{A^{\tau_1}\mathbf{x}(0)}{\mathbf{1}^T A^{\tau_1}\mathbf{x}(0)}\right\| + \left\|\frac{A^{\tau_1}\mathbf{x}(0)}{\mathbf{1}^T A^{\tau_1}\mathbf{x}(0)} - \mathbf{u}\right\| \\ &\leq \frac{\delta(1-\gamma)}{4} + \frac{\delta(1-\gamma)}{4} \\ &= \frac{\delta(1-\gamma)}{2} \\ &\leq \delta, \end{aligned} \tag{146}$$

and with (136) that

$$\begin{aligned}\|\mathbf{x}(\tau_1) - \mathbf{u}(\tau_1)\| &\leq \|\mathbf{x}(\tau_1) - \mathbf{u}\| + \|\mathbf{u} - \mathbf{u}(\tau_1)\| \\ &\leq \frac{\delta(1-\gamma)}{2} + \frac{\delta(1-\gamma)}{2} \\ &= \delta(1-\gamma), \end{aligned} \tag{147}$$

as soon as $N \geq N_1$.

We will show that

$$\|\mathbf{x}(\tau_1 + k) - \mathbf{u}\| \leq \delta, \tag{148}$$

for all integers $k \geq 0$ as soon as $N \geq N_1$. This will be proved by induction along with

$$\|\mathbf{x}(\tau_1 + k) - \mathbf{u}(\tau_1 + k)\| \leq \delta(1-\gamma) \sum_{i=0}^{k} \gamma^i, \tag{149}$$

for all integers $k \geq 0$ as soon as $N \geq N_1$. Equations (148) and (149) hold for $k = 0$ owing to Eqs. (146) and (147). Let us assume that they hold for some integer $k \geq 0$. Then, using (136) and (145) for $\tau = \tau_1 + k$, $\mathbf{x} = \mathbf{x}(\tau_1 + k)$ and $\mathbf{f}_\tau(\mathbf{x}) = \mathbf{x}(\tau_1 + k + 1)$ leads to

$$\begin{aligned} \|\mathbf{x}(\tau_1 + k + 1) - \mathbf{u}(\tau_1 + k + 1)\| &\leq \|\mathbf{x}(\tau_1 + k + 1) - \mathbf{u}(\tau_1 + k)\| + \|\mathbf{u}(\tau_1 + k) - \mathbf{u}\| \\ &\quad + \|\mathbf{u} - \mathbf{u}(\tau_1 + k + 1)\| \\ &\leq \gamma \|\mathbf{x}(\tau_1 + k) - \mathbf{u}(\tau_1 + k)\| + \frac{\delta(1-\gamma)}{2} \\ &\quad + \frac{\delta(1-\gamma)}{2} \\ &\leq \delta(1-\gamma) \sum_{i=0}^{k} \gamma^{i+1} + \delta(1-\gamma) \\ &= \delta(1-\gamma) \sum_{i=0}^{k+1} \gamma^i \end{aligned} \tag{150}$$

and

$$\begin{aligned} \|\mathbf{x}(\tau_1 + k + 1) - \mathbf{u}\| &\leq \|\mathbf{x}(\tau_1 + k + 1) - \mathbf{u}(\tau_1 + k)\| + \|\mathbf{u}(\tau_1 + k) - \mathbf{u}\| \\ &\leq \gamma \|\mathbf{x}(\tau_1 + k) - \mathbf{u}(\tau_1 + k)\| + \frac{\delta(1-\gamma)}{2} \\ &\leq \delta\gamma(1-\gamma) \sum_{i=0}^{k} \gamma^i + \delta(1-\gamma) \\ &\leq \delta\gamma + \delta(1-\gamma) \\ &= \delta, \end{aligned} \tag{151}$$

as soon as $N \geq N_1$. This establishes (148) and (149) for $k + 1$.

Therefore, we have proved that, for every positive real number $\delta \leq \delta_0$, there exist positive integers $N_1 = N_1(\delta)$ and $\tau_1 = \tau_1(\delta)$ such that

$$\|\mathbf{x}(\tau) - \mathbf{u}\| \leq \delta \tag{152}$$

as soon as $N \geq N_1$ and $\tau \geq \tau_1$. For $\delta > \delta_0$, it suffices to pose $N_1(\delta) = N_1(\delta_0)$ and $\tau_1(\delta) = \tau_1(\delta_0)$ to conclude.

6.2 Proof of Lemma 2

The Jordan normal form of the $d \times d$ primitive matrix

$$A(s) = A + sB, \tag{153}$$

for s close enough to 0, leads to a decomposition in the form

$$A(s) = \begin{pmatrix} \mathbf{u}(s) & P(s) \end{pmatrix} \begin{pmatrix} \lambda(s) & \mathbf{0}^T \\ \mathbf{0} & J(s) \end{pmatrix} \begin{pmatrix} \mathbf{v}(s)^T \\ R(s) \end{pmatrix}. \tag{154}$$

Here,

$$\lambda(s) = 1 + ms + o\left(s\right), \tag{155}$$

is the leading positive eigenvalue of $A(s)$, which is a differentiable function with respect to s in a neighborhood of 0. Let $\mathbf{v}(s)$ and $\mathbf{u}(s)$ be the associated positive left and right eigenvectors, respectively, that satisfy

$$\mathbf{1}^T\mathbf{u}(s) = 1, \quad \mathbf{v}(s)^T\mathbf{u}(s) = 1. \tag{156}$$

We use $\mathbf{1}$ and $\mathbf{0}$ to denote vectors of all ones and all zeros, respectively. Moreover, $J(s)$ is a Jordan matrix of size $(d-1) \times (d-1)$ associated with eigenvalues of $A(s)$ whose moduli are all less than $\lambda(s)$ and, by continuity, less than some positive number strictly smaller than $\lambda(0) = 1$ for s small enough. Note that the matrices $P(s)$ and $R(s)$ of sizes $d \times (d-1)$ and $(d-1) \times d$, respectively, satisfy

$$\mathbf{v}(s)^T P(s) = \mathbf{0}^T, \quad R(s)\mathbf{u}(s) = \mathbf{0}, \quad R(s)P(s) = I, \tag{157}$$

where I denotes the $(d-1) \times (d-1)$ identity matrix.

The above decomposition leads to

$$A(s)^{\lfloor s^{-1}t\rfloor-\tau} = \begin{pmatrix} \mathbf{u}(s) & P(s) \end{pmatrix} \begin{pmatrix} \lambda(s)^{\lfloor s^{-1}t\rfloor-\tau} & \mathbf{0}^T \\ \mathbf{0} & J(s)^{\lfloor s^{-1}t\rfloor-\tau} \end{pmatrix} \begin{pmatrix} \mathbf{v}(s)^T \\ R(s) \end{pmatrix}, \tag{158}$$

for any real number $t > 0$ and any integer $\tau \leq \lfloor s^{-1}t\rfloor$, where

$$\lambda(s)^{\lfloor s^{-1}t\rfloor-\tau} = \left((1 + ms + o\left(s\right))^{s^{-1}}\right)^{s(\lfloor s^{-1}t\rfloor-\tau)} \to \exp\{mt\} \tag{159}$$

and

$$J(s)^{\lfloor s^{-1}t\rfloor-\tau} \to 0_{(d-1)\times(d-1)}, \tag{160}$$

as $s \to 0$, with $0_{(d-1)\times(d-1)}$ denoting the null matrix of size $(d-1)\times(d-1)$. Therefore,

$$A(s)^{\lfloor s^{-1}t\rfloor-\tau} \to \mathbf{u}(0)\mathbf{v}(0)^T \exp\{mt\}, \tag{161}$$

as $s \to 0$. This is the case with $s = N^{-1}$ as $N \to \infty$. Moreover, by continuity, $\mathbf{v}(0) = \mathbf{v}$ and $\mathbf{u}(0) = \mathbf{u}$ are the positive left and right eigenvectors, respectively, associated with the eigenvalue 1 of $A(0) = A$ that satisfy $\mathbf{1}^T\mathbf{u} = 1$ and $\mathbf{v}^T\mathbf{u} = 1$.

It remains to calculate m which is the derivative of the leading eigenvalue $\lambda(s)$ of $A(s)$ evaluated at $s = 0$. Note that

$$\lambda(s) = \lambda(s)\mathbf{v}(s)^T\mathbf{u}(s) = \mathbf{v}(s)^T A(s)\mathbf{u}(s) = \mathbf{v}(s)^T(A + sB)\mathbf{u}(s). \tag{162}$$

Therefore,

$$\begin{aligned} m = \lambda'(0) &= \mathbf{v}(0)^T B\mathbf{u}(0) + \mathbf{v}'(0)^T A\mathbf{u}(0) + \mathbf{v}(0)^T A\mathbf{u}'(0) \\ &= \mathbf{v}^T B\mathbf{u} + \mathbf{v}'(0)^T\mathbf{u}(0) + \mathbf{v}(0)^T\mathbf{u}'(0) \\ &= \mathbf{v}^T B\mathbf{u}, \end{aligned} \tag{163}$$

owing to (156). This is in agreement with a well-known result on the leading eigenvalue of an irreducible aperiodic (primitive) non-negative matrix (see, e.g., Lancaster and Tismenetsky 1985, Section 11.6, or Cushing 1998, p. 20), and completes the proof of Lemma 2.

6.3 Proof of Lemma 3

From (48) and (53), we have

$$\mathbf{C}_i(t) = \lim_{N\to\infty} \mathbf{c}_i(\lfloor Nt\rfloor + 1) = \left(\lim_{N\to\infty} A_i(\lfloor Nt\rfloor)\right)\left(\lim_{N\to\infty} \mathbf{c}_i(\lfloor Nt\rfloor)\right) = A\mathbf{C}_i(t) \tag{164}$$

with $\mathbf{C}_i(t) \in \mathbb{R}^d_+$. Then the Perron–Frobenius theory for primitive non-negative matrices ensures that

$$\mathbf{C}_i(t) = \mathbf{v}^T\mathbf{C}_i(t)\mathbf{u}. \tag{165}$$

Owing to (51), (53) and (54), it remains to show that

$$\mathbf{v}^T\mathbf{c}_i(\tau) = \mathbf{v}^T\mathbf{C}_i(t) + O(h), \tag{166}$$

uniformly for N larger than some threshold value N_0 and $\lfloor Nt\rfloor \le \tau \le \lfloor N(t+h)\rfloor$. By the extreme value theorem for continuous functions, there exists a non-negative non-null $d \times d$ matrix B such that

$$B_i(\mathbf{z}(\tau)) \leq B, \tag{167}$$

entrywise for all $\tau \geq 0$. For $\lfloor Nt \rfloor \leq \tau \leq \lfloor N(t+h) \rfloor$, we have

$$\begin{aligned} A^{\tau - \lfloor Nt \rfloor} \mathbf{c}_i(\lfloor Nt \rfloor) &\leq \left(\prod_{k=\lfloor Nt \rfloor}^{\tau - 1} \left(A + \frac{B_i(\mathbf{z}(k))}{N} \right) \right) \mathbf{c}_i(\lfloor Nt \rfloor) \\ &\leq \left(A + \frac{B}{N} \right)^{\tau - \lfloor Nt \rfloor} \mathbf{c}_i(\lfloor Nt \rfloor), \end{aligned} \tag{168}$$

where the inequalities hold entrywise, and multiplying on the left by $\mathbf{v}^T A^{\lfloor Nh \rfloor + 2 - \tau + \lfloor Nt \rfloor}$ yields

$$\mathbf{v}^T A^{\lfloor Nh \rfloor + 2} \mathbf{c}_i(\lfloor Nt \rfloor) \leq \mathbf{v}^T A^{\lfloor Nh \rfloor + 2 - \tau + \lfloor Nt \rfloor} \mathbf{c}_i(\tau) \leq \mathbf{v}^T \left(A + \frac{B}{N} \right)^{\lfloor Nh \rfloor + 2} \mathbf{c}_i(\lfloor Nt \rfloor). \tag{169}$$

Therefore,

$$\mathbf{v}^T \mathbf{c}_i(\lfloor Nt \rfloor) \leq \mathbf{v}^T \mathbf{c}_i(\tau) \leq \mathbf{v}^T \left(A + \frac{B}{N} \right)^{\lfloor Nh \rfloor + 2} \mathbf{c}_i(\lfloor Nt \rfloor). \tag{170}$$

Moreover, as $N \to \infty$, Lemma 2 ensures that

$$\begin{aligned} \mathbf{v}^T \left(A + \frac{B}{N} \right)^{\lfloor Nh \rfloor + 2} &\to \mathbf{v}^T \mathbf{u} \mathbf{v}^T \exp\left\{ h \mathbf{v}^T B \mathbf{u} \right\} \\ &= \mathbf{v}^T \exp\left\{ h \mathbf{v}^T B \mathbf{u} \right\} \leq \mathbf{v}^T \left(1 + h \mathbf{v}^T B \mathbf{u} \right) \end{aligned} \tag{171}$$

for $h > 0$ small enough and $\mathbf{v}^T B \mathbf{u} > 0$, while

$$\mathbf{v}^T \mathbf{c}_i(\lfloor Nt \rfloor) \to \mathbf{v}^T \mathbf{C}_i(t). \tag{172}$$

Therefore, for N larger than some threshold value N_0 that depends on $t > 0$ and $h > 0$ small enough, we have

$$\mathbf{v}^T \mathbf{C}_i(t)(1 - 2h\mathbf{v}^T B\mathbf{u}) \leq \mathbf{v}^T \mathbf{c}_i(\tau) \leq \mathbf{v}^T \mathbf{C}_i(t)(1 + 2h\mathbf{v}^T B\mathbf{u}), \tag{173}$$

for $\lfloor Nt \rfloor \leq \tau \leq \lfloor N(t+h) \rfloor$. This completes the proof of Lemma 3.

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