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Evolutionary game dynamics in a finite asymmetric two-deme population and emergence of cooperation

Véronique Ladret [a], Sabin Lessard [b,*]

[a] Centre de recherche du CHU Sainte-Justine, 3175 Côte-Ste-Catherine, Montréal, Québec, Canada H3T 1C5
[b] Département de mathématiques et de statistique, Université de Montréal, C.P. 6128 Succursale Centre-ville, Montréal, Québec, Canada H3C 3J7

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ABSTRACT

We consider evolutionary game dynamics in a finite population subdivided into two demes with both unequal deme sizes and different migration rates. Assuming viability differences in the population according to a linear game within each deme as a result of pairwise interactions, we specify conditions for weak selection favoring a mutant strategy to go to fixation, under the structured-coalescent assumptions, and their connections with evolutionary stability concepts. In the framework of the Iterated Prisoner's Dilemma with strategy 'tit-for-tat' as mutant strategy and 'always defect' as resident strategy, we deduce a condition under which the emergence of cooperation is favored by selection, when the game matrix is the same in both demes. We show how this condition extends the one-third law for a panmictic population and when an asymmetry in the spatial structure of a two-deme population facilitates the emergence of the cooperative tit-for-tat strategy in comparison with both its symmetric and panmictic population structure counterparts. We find that the condition is less stringent in the asymmetric scenario versus the symmetric scenario if both the fraction of the population in the deme where the mutant was initially introduced, and the expected proportion of migrant offspring in this deme among all migrant offspring after population regulation, are smaller than, or equal to, $\frac{1}{2}$, provided they are not too small. On the other hand, the condition is less stringent than the one-third law, which holds in the panmictic case, if the latter proportion remains not too close to 1.

1. Introduction

Evolutionary game theory (Maynard Smith, 1982) was originally expressed in terms of the replicator dynamics in an infinite population (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998). In this context, evolutionarily stable strategies (ESS) (Maynard Smith and Price, 1973; Maynard Smith, 1974) cannot be invaded by a small fraction of mutants and they are, therefore, selectively protected against replacement. However, when the number of interacting individuals is finite, any fixation state can be taken over by a single mutant due to random drift. Another definition of evolutionary stability in the case of a finite population has been proposed by Nowak et al. (2004), and it is based on the probability of fixation of a single mutant: selection is said to oppose the replacement of a resident strategy by a mutant strategy if a single mutant fixates in the population with a smaller probability than it would under neutrality. Applying this definition to 'tit-for-tat' (TFT) as mutant strategy and 'always defect' (AllD) as resident strategy in the context of the Iterated Prisoner's Dilemma (IPD), it is possible to find conditions under which the emergence of cooperation would be favored by natural selection in a finite population.

The Prisoner's Dilemma (PD) (Axelrod and Hamilton, 1981) is a common theoretical framework to understand one of the main questions in evolutionary biology: the emergence of cooperative behaviors by natural selection. In its standard version, two players can either cooperate (C) or defect (D), and the PD is described by the payoff matrix

$$\begin{array}{ccc} & C & D \\ C & R & S \\ D & T & P \end{array}. \tag{1}$$

The payoff that the players are rewarded with if they both cooperate is R, while the 'punishment' payoff that they get for mutual defection is P. Moreover, if a cooperator meets a defector, the cooperator receives the sucker's payoff S, while the defector is given the temptation to defect, T. The payoffs are assumed to satisfy the inequalities $T>R>P>S$. Therefore, in an infinite population, defectors have a higher average fitness than cooperators, regardless of what the other players do, and cooperators are ultimately wiped out from the population.

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* Corresponding author. Tel.: +1 514 343 6743; fax: +1 514 343 5700.
E-mail address: lessards@dms.umontreal.ca (S. Lessard).

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In order to overcome the inability of the simple PD to promote the emergence of cooperation, one possible solution is to consider the so-called IPD, in which the same players perform several rounds of the simple PD, and can adapt their strategy in any given round knowing the results of the previous rounds (Axelrod and Hamilton, 1981). Among such strategies is the TFT strategy, under which players always cooperate in the first round and then, in every subsequent round, imitate what their opponent did in the previous round. It occurs that if the number of rounds is large enough, with the two strategies TFT and AllD, the payoff matrix of the game takes the form

$$\begin{array}{cc} & \text{TFT}\ \ \text{AllD} \\ \begin{array}{c}\text{TFT}\\ \text{AllD}\end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \tag{2}$$

with $a>c>d>b$ (see, e.g., Hofbauer and Sigmund, 1998; Nowak et al., 2004). Under this condition, the IPD turns out to be a coordination game, since both pure strategies are strict Nash equilibria owing to the inequalities $a>c$ and $d>b$. Thus, in the framework of an infinite population, there exists a unique unstable equilibrium given by $x^* = (d-b)/(a-b-c+d)$ for the frequency of TFT: if the initial proportion of TFT is below x^*, the replicator dynamics leads to TFT vanishing from the population; while if it exceeds this threshold value, TFT takes over the whole population and, as a consequence, all the individuals end-up cooperating.

The situation is different in a finite population. In the context of a Moran population model, Nowak et al. (2004) proved that, provided selection is weak enough and the population size is large enough, a single TFT player can take over the population with a selective advantage if $x^* < \frac{1}{3}$. This rule, referred to as the one-third law, holds for any coordination game, with TFT and AllD replaced by the two strict Nash equilibria. In the case of a Wright–Fisher model (Fisher, 1930; Wright, 1931) the result also applies (Lessard, 2005; Imhof and Nowak, 2006), as well as for many other evolutionary processes (see Ohtsuki et al., 2007, and references therein).

The effects of a symmetric population structure on conditions under which a mutant strategy is selectively advantageous under weak selection have been investigated, notably in the case of Wright's island model to which the one-third law has been extended (Ladret and Lessard, 2007). In this paper, we consider the case of an asymmetric population structure, more precisely a population subdivided into two subpopulations (or demes) with both unequal deme sizes and different migration rates, and we investigate the probability of fixation of a single mutant under weak selection and the structured-coalescent assumptions (Notohara, 1990; Herbots, 1994, 1997; Wilkinson-Herbots, 1998). We assume haploid individuals and we suppose that two strategies (or types of individuals) are genetically encoded at a single locus by two alternative alleles. At the beginning of every generation, each individual produces an infinite equal number of offspring which then disperse independently among the two demes. Following migration, the offspring undergo viability differences, as a result of linear games within demes, described by deme-specific matrices, and the deme sizes are restored afterward by random sampling. An approximation for the first-order effect of selection on the probability of fixation of a single mutant is obtained, adapting a direct Markov chain method proposed by Rousset (2003) as ascertained in Lessard and Ladret (2007). When the population is panmictic (Lessard, 2005; see also Lessard, 2007) or when its structure is symmetric (Rousset and Billiard, 2000; Ladret and Lessard, 2007), the method allows to express this approximation as a function of expected coalescence times, under neutrality, for samples of individuals. In the case of unequal deme sizes and/or different migration rates, we have to resort to an extension of the direct Markov chain approach to perform the calculations. With the first-order approximation for the fixation probability in hand, we derive conditions under which a mutant strategy is selectively advantageous. When the two strategies are best replies to themselves with respect to the two game matrices, the one-third law is extended to account for the asymmetry in the population structure. In the case of identical game matrices, we show that the condition can be written as $x^* < \Lambda$, for some threshold Λ that depends on the population structure. We find that this condition is less stringent than the one-third law if migration is conservative (which means that the deme sizes are not changed by the migration process), and, in the case of non-conservative migration, provided the expected proportion of migrant offspring in the deme that initially contained the single mutant, among all the migrant offspring in both demes after population regulation, is not too close to 1. We also show that the condition is less stringent in the case of an asymmetric population structure versus a symmetric one, if both the previous proportion and the fraction of individuals living in the deme in which the mutant was initially introduced, are less or equal to $\frac{1}{2}$, provided they are not too small.

The remainder of this paper is organized as follows. In Section 2, the two-deme linear-game model is presented. Then, in Sections 3 and 4, the first-order approximation for the probability of fixation of a single mutant is derived, under weak selection and the structured-coalescent assumptions, respectively. In Section 5, the model is considered in the framework of an infinite population, which leads to a deterministic dynamics and evolutionarily stable strategies in the usual sense. In Section 6, conditions for a mutant strategy to be favored by selection to replace a resident strategy are given and connections with evolutionary stability concepts in an infinite population are discussed. The problem of the emergence of cooperation in the particular case of coordination games is investigated in Section 7, and conclusions drawn from asymmetric assumptions are compared with results obtained for a panmictic population or a symmetric population structure. A general discussion follows in Section 8.

2. Two-deme two-type linear-game model

We consider a haploid population subdivided into two demes, namely, demes 1 and 2 containing N_1 and N_2 individuals, respectively, and we assume viability differences between the individuals according to a linear-game scenario within each deme (see, e.g., Nowak et al., 2004; Wild and Taylor, 2004; Lessard, 2005).

More precisely, we assume two types of individuals, types A and B, and we suppose that, at time $t=0$, a single mutant A is introduced into deme 1. Let the population undergo discrete, non-overlapping generations represented by time steps $t = 0, 1, 2, \ldots$. At the beginning of every generation, each individual in the population produces the same very large number of offspring (in practice we treat this number as if it were infinite), which then disperse independently. Let m_{ij} be the proportion of offspring in deme i that come from deme j, for $i, j = 1, 2$, and assume these backward migration rates to be constant over time. If $x_1 = k_1/N_1$ and $x_2 = k_2/N_2$ denote the frequency of A in demes 1 and 2, respectively, at the beginning of a given generation, and $\tilde{x_1}$ and $\tilde{x_2}$, respectively, the frequency of A in demes 1 and 2, respectively, after migration, then we have

$$\tilde{x_1} = m_{11}x_1 + m_{12}x_2, \quad \tilde{x_2} = m_{21}x_1 + m_{22}x_2. \tag{3}$$

Migration is followed by selection among offspring within the same deme. We consider a linear-game scenario in which we assume that the two types of individuals, A and B, are associated with mixed strategies $\mathbf{p}_A$ and $\mathbf{p}_B$, respectively, these being frequency vectors whose components give the probabilities of using some pure strategies in a contest against an opponent. More precisely, pairwise interactions take place among the individuals within each deme and affect their viabilities (fitnesses) such that they are written

$$f_{A,1} = 1 + s\mathbf{p}_A \cdot W_1\bar{\mathbf{p}}_1, \quad f_{B,1} = 1 + s\mathbf{p}_B \cdot W_1\bar{\mathbf{p}}_1 \tag{4}$$

and

$$f_{A,2} = 1 + s\mathbf{p}_A \cdot W_2\bar{\mathbf{p}}_2, \quad f_{B,2} = 1 + s\mathbf{p}_B \cdot W_2\bar{\mathbf{p}}_2 \tag{5}$$

for types A and B and demes 1 and 2, respectively, where W_1 and W_2 refer to some game matrices, parameter $s>0$ measures the selection intensity, $\mathbf{x} \cdot \mathbf{y} = x_1y_1 + x_2y_2$ denotes the scalar product of two real vectors $\mathbf{x} = (x_1, x_2)$ and $\mathbf{y} = (y_1, y_2)$, and $\bar{\mathbf{p}}_i$ stands for the mean strategy in deme i before selection, that is,

$$\bar{\mathbf{p}}_i = \tilde{x}_i\mathbf{p}_\mathbf{A} + (1 - \tilde{x}_i)\mathbf{p}_\mathbf{B} = \tilde{x}_i(\mathbf{p}_\mathbf{A} - \mathbf{p}_\mathbf{B}) + \mathbf{p}_\mathbf{B} \tag{6}$$

for $i = 1, 2$. Following selection, the frequency of A among the individuals in deme i becomes

$$x_i' = \frac{\tilde{x}_i f_{A,i}}{\tilde{x}_i f_{A,i} + (1 - \tilde{x}_i) f_{B,i}} \tag{7}$$

for $i = 1, 2$. The next generation is obtained by sampling at random N_1 and N_2 individuals in demes 1 and 2, respectively, so that the number of A individuals in deme i follows a binomial distribution of parameters N_i and x_i', for $i = 1, 2$. After this population regulation, the frequency of A in deme i has mean x_i', for $i = 1, 2$. Throughout the paper we make the assumption that the selection intensity s is small, that is, $s = o(1)$, which models weak selection.

3. Fixation coefficient

We suppose that, at time $t = 0$, a single mutant A is introduced into deme 1. Let $X_1(t)$ and $X_2(t)$ denote the frequency of A in demes 1 and 2, respectively, at time $t \geqslant 0$, and define

$$\mathbf{X}(t) = (X_1(t), X_2(t)) \tag{8}$$

with $\mathbf{X}(0) = (1/N_1, 0)$. For simplicity, we shall denote this initial state by $\mathbf{x}_0 = \mathbf{X}(0)$.

We are interested in evaluating $u(s)$, the probability of fixation of type A in the whole population in the weak-selection scenario. The method used below is adapted from Rousset (2003). It was ascertained in Lessard and Ladret (2007). It consists in determining $u'(0)$, the derivative of u at $s = 0$, that will be referred to throughout as the fixation coefficient, in order to find the first-order development of $u(s)$ with respect to s, given by

$$u(s) = u(0) + su'(0) + o(s). \tag{9}$$

Let E (P, respectively) denote the expectation (probability, respectively), when the selection intensity is $s \geqslant 0$, and let E_0 (P_0, respectively) stand for the expectation (probability, respectively) under neutrality, that is, when $s = 0$. Denote by $\mathbf{M}$ the migration matrix whose entries are the backward migration rates, that is,

$$\mathbf{M} = \begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{21} \end{bmatrix}. \tag{10}$$

To simplify the notation and analysis, we shall write $m_1 = m_{12}$ and $m_2 = m_{21}$ for the proportion of offspring in demes 1 and 2, respectively, that come from the other deme, and assume $0 < m_1, m_2 < 1$, in which case

$$\mathbf{M} = \begin{bmatrix} 1 - m_1 & m_1 \\ m_2 & 1 - m_2 \end{bmatrix} \tag{11}$$

is an irreducible aperiodic stochastic matrix. Let (u_1, u_2), with $u_1, u_2 > 0$ and $u_1 + u_2 = 1$, be the stationary distribution of $\mathbf{M}$ so that

$$[u_1, u_2]\mathbf{M} = [u_1, u_2]. \tag{12}$$

It follows that

$$u_1 = \frac{m_2}{m_1 + m_2}, \quad u_2 = \frac{m_1}{m_1 + m_2}. \tag{13}$$

Then, consider the weighted frequency of A

$$Z(t) = u_1X_1(t) + u_2X_2(t) \tag{14}$$

for $t \geqslant 0$. For any selection intensity $s \geqslant 0$, the sequence $(Z(t))_{t \geqslant 0}$ defines a discrete-time stochastic process on the states $u_1k_1/N_1 + u_2k_2/N_2$, for $k_1 = 0, \ldots, N_1$ and $k_2 = 0, \ldots, N_2$, with initial distribution $Z(0) = u_1/N_1$, and absorbing states $z = 0$ and 1; all other states are transient. This process converges in probability to a random variable $Z(\infty)$, which takes the value 1 with probability $u(s)$, and 0 otherwise. Under neutrality ($s = 0$), the process is a bounded martingale, and then the stopping time theorem (see, e.g., Karlin and Taylor, 1975) ascertains that the probability of fixation of A, which corresponds to the absorbing state $z = 1$, is given by

$$u(0) = E_0[Z(\infty)] = Z(0) = \frac{u_1}{N_1}. \tag{15}$$

Returning to the general case $s \geqslant 0$ and following Rousset (2003), we write

$$E[Z(\infty) - Z(0)] = \sum_{t \geqslant 0} E[Z(t+1) - Z(t)], \tag{16}$$

that is,

$$u(s) - u(0) = \sum_{t \geqslant 0} E[Z(t+1) - Z(t)]. \tag{17}$$

Then, differentiating with respect to s, and assuming that the sum and the derivative can be interchanged (see Lessard and Ladret, 2007, for a formal proof under mild regularity conditions), we get

$$u'(0) = \sum_{t \geqslant 0} \frac{\mathrm{d}}{\mathrm{d}s} E[Z(t+1) - Z(t)]\bigg|_{s=0}. \tag{18}$$

Conditioning on the value $\mathbf{x} = (x_1, x_2)$ taken by $\mathbf{X}(t)$, we get

$$\begin{aligned} &E[Z(t+1) - Z(t)] \\ &\quad = \sum_{\mathbf{x}} E[Z(t+1) - Z(t) | \mathbf{X}(t) = \mathbf{x}] P(\mathbf{X}(t) = \mathbf{x}), \end{aligned} \tag{19}$$

from which

$$\begin{aligned} &\frac{\mathrm{d}}{\mathrm{d}s} E[Z(t+1) - Z(t)]\bigg|_{s=0} \\ &\quad = \sum_{\mathbf{x}} P_0(\mathbf{X}(t) = \mathbf{x}) \frac{\mathrm{d}}{\mathrm{d}s} E[Z(t+1) - Z(t) | \mathbf{X}(t) = \mathbf{x}]\bigg|_{s=0} \\ &\qquad + \sum_{\mathbf{x}} E_0[Z(t+1) - Z(t) | \mathbf{X}(t) = \mathbf{x}] \frac{\mathrm{d}}{\mathrm{d}s} P(\mathbf{X}(t) = \mathbf{x})\bigg|_{s=0}. \end{aligned} \tag{20}$$

Under neutrality, the mean of $Z(t)$ does not change over time, that is,

$$E_0[Z(t+1) - Z(t) | \mathbf{X}(t) = \mathbf{x}] = 0. \tag{21}$$

Therefore, we have

$$u'(0) = \sum_{t\geqslant 0}\sum_{\mathbf{x}} P_0(\mathbf{X}(t)=\mathbf{x}) \times \frac{\mathrm{d}}{\mathrm{d}s}E[Z(t+1)-Z(t)|\mathbf{X}(t)=\mathbf{x}]\Big|_{s=0}. \tag{22}$$

Since

$$\begin{aligned}E[Z(t+1)-Z(t)|\mathbf{X}(t)=\mathbf{x}] &= u_1\{E[X_1(t+1)|\mathbf{X}(t)=\mathbf{x}]-x_1\}\\ &\quad + u_2\{E[X_2(t+1)|\mathbf{X}(t)=\mathbf{x}]-x_2\},\end{aligned} \tag{23}$$

it follows easily from (7) and (12) that

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}s}E[Z(t+1)-Z(t)|\mathbf{X}(t)=\mathbf{x}]\Big|_{s=0} &= u_1\tilde{x_1}(1-\tilde{x_1})(\mathbf{p}_A-\mathbf{p}_B)\cdot W_1\bar{\mathbf{p}}_1\\ &\quad + u_2\tilde{x_2}(1-\tilde{x_2})(\mathbf{p}_A-\mathbf{p}_B)\cdot W_2\bar{\mathbf{p}}_2.\end{aligned} \tag{24}$$

Thus, owing to (6), we find that

$$\begin{aligned}u'(0) &= \sum_{t\geqslant 0} u_1(\mathbf{p}_A-\mathbf{p}_B)\cdot W_1\{\mathbf{p}_A\lambda(\mathbf{m}_1,\mathbf{X}(t))\\ &\quad + \mathbf{p}_B\lambda(\mathbf{m}_1,\mathbf{1}-\mathbf{X}(t))\} + \sum_{t\geqslant 0} u_2(\mathbf{p}_A-\mathbf{p}_B)\\ &\quad \cdot W_2\{\mathbf{p}_A\lambda(\mathbf{m}_2,\mathbf{X}(t)) + \mathbf{p}_B\lambda(\mathbf{m}_2,\mathbf{1}-\mathbf{X}(t))\},\end{aligned} \tag{25}$$

where $\mathbf{1}=(1,1)$, $\mathbf{m}_1=(m_{11}, m_{12})=(1-m_1,m_1)$, $\mathbf{m}_2=(m_{21}, m_{22})=(m_2,1-m_2)$, while

$$\begin{aligned}\lambda(\mathbf{c},\mathbf{X}) &= c_1^3E_0[X_1^2(1-X_1)] + c_1^2c_2E_0[X_1^2(1-X_2)]\\ &\quad + 2c_1^2c_2E_0[X_1X_2(1-X_1)]\\ &\quad + 2c_1c_2^2E_0[X_1X_2(1-X_2)] + c_2^2c_1E_0[X_2^2(1-X_1)]\\ &\quad + c_2^3E_0[X_2^2(1-X_2)]\end{aligned} \tag{26}$$

for $\mathbf{c}=(c_1,c_2)$ and $\mathbf{X}=(X_1,X_2)$. Therefore, the calculation of $u'(0)$ requires to evaluate

$$\sum_{t\geqslant 0} E_0[X_i(t)^{l_1}X_j(t)^{l_2}(1-X_i(t))^{l_3}(1-X_j(t))^{l_4}], \tag{27}$$

where $0\leqslant l_1,l_2,l_3,l_4\leqslant 2$ with $l_1+l_2+l_3+l_4=3$, for $i,j=1,2$ $(i\neq j)$.

Let us label arbitrarily the individuals in deme 1 at any given time with the integers from 1 to N_1, and define

$$\xi_k(t) = \begin{cases} 1 & \text{if individual } k \text{ in deme 1 at time } t \text{ is of type } A,\\ 0 & \text{otherwise.}\end{cases} \tag{28}$$

Then, the frequency of A in deme 1 at time t is

$$X_1(t) = \frac{1}{N_1}\sum_{k=1}^{N_1}\xi_k(t). \tag{29}$$

It follows that

$$\begin{aligned}E_0[X_1^2(t)(1-X_1(t))] &= \frac{1}{N_1^3}E_0\left[\left(\sum_{k=1}^{N_1}\xi_k(t)\right)^2\left(\sum_{l=1}^{N_1}(1-\xi_l(t))\right)\right]\\ &= \frac{1}{N_1^3}\sum_{k=1}^{N_1}\sum_{l=1}^{N_1}\sum_{m=1}^{N_1}E_0[\xi_k(t)\xi_l(t)(1-\xi_m(t))],\end{aligned} \tag{30}$$

or equivalently,

$$E_0[X_1^2(t)(1-X_1(t))] = \left(1-\frac{1}{N_1}\right)\left(1-\frac{2}{N_1}\right)\alpha(t) + \frac{1}{N_1}\left(1-\frac{1}{N_1}\right)\beta(t), \tag{31}$$

where

$$\alpha(t) = P_0(\xi_1(t)=\xi_2(t)=1,\xi_3(t)=0) \tag{32}$$

and

$$\beta(t) = P_0(\xi_1(t)=1,\xi_2(t)=0). \tag{33}$$

We shall first focus on $\alpha(t)$, which is the probability that, at time t, individuals 1 and 2 in deme 1 are both of type A, while individual 3 in the same deme is of type B. Recalling that a single mutant A was introduced at time $t=0$ and in deme 1, this will be the case if the lineages of individuals 1 and 2 coalesce from time t to time 0 and have the mutant individual of type A in deme 1 as common ancestor at time 0, while they never intersect the lineage of individual 3 from time t to time 0.

Considering the location (deme 1 or deme 2) of the ancestors of three individuals (labeled 1, 2, 3), the state space S can be partitioned into five ordered subsets according to the events that there are three ancestors, two ancestors, and then one common to either individuals 1 and 2, or 1 and 3, or 2 and 3, and only one ancestor, necessarily common to individuals 1, 2, and 3:

$$\begin{aligned}&S_{1,2,3} = (111,112,121,122,211,212,221,222),\\ &S_{12,3} = (11,12,21,22),\\ &S_{13,2} = (11,12,21,22),\\ &S_{23,1} = (11,12,21,22),\\ &S_{123} = (1,2).\end{aligned} \tag{34}$$

The element 121 in $S_{1,2,3}$, for instance, means that the ancestors of individuals 1, 2, 3 are all different and in demes 1, 2, 1, respectively, the element 12 in $S_{12,3}$ that individuals 1, 2 have a common ancestor in deme 1 different from the ancestor of individual 3, and this ancestor is in deme 2, and finally the element 1 in S_{123} that individuals 1, 2, 3 have a common ancestor, and this ancestor is in deme 1.

Let $\sigma(t)$ be the state in S for the ancestors of three individuals t generations back, for $t\geqslant 0$. The transition matrix of this Markov chain takes a block form with respect to the above ordered subsets in the corresponding order. Without loss of generality, let

$$K = \begin{bmatrix} F & Q & Q_2 & Q_1 & R_1\\ 0 & P & 0 & 0 & R\\ 0 & 0 & P & 0 & R\\ 0 & 0 & 0 & P & R\\ 0 & 0 & 0 & 0 & R_0\end{bmatrix} \tag{35}$$

be this transition matrix under neutrality. The submatrices F, Q and P are given in Appendix A.1. Note that the states in S_{123} are absorbing for this chain, while all other states are transient. The Perron–Frobënius theory for non-negative matrices (see, e.g., Karlin and Taylor, 1975) ascertains in particular that the eigenvalues of F and P are all less than 1 in modulus.

The probability for individuals 1 and 2 in deme 1 at time t to be of type A and individual 3 in the same deme at the same time to be of type B, is $1/N_1$, the frequency of A in deme 1 at time 0, times the probability for $\sigma(t)$ to be in state 11 or 12 in $S_{12,3}$, given that $\sigma(0)$ is in state 111 in $S_{1,2,3}$. This can be expressed as

$$\alpha(t) = \sum_{\tau=1}^{t}(F^{\tau-1}QP^{t-\tau}\mathbf{u})_{111}, \tag{36}$$

where $\mathbf{u}=(1/N_1,1/N_1,0,0)$ and 111 designates the vector component corresponding to that state in $S_{1,2,3}$. Summing over $t\geqslant 0$ and using the fact that $(I-F)$ and $(I-P)$ are invertible, where I denotes an identity matrix of appropriate order, we get

$$\sum_{t\geqslant 0}\alpha(t) = ((I-F)^{-1}Q(I-P)^{-1}\mathbf{u})_{111}. \tag{37}$$

Similar arguments show that

$$\sum_{t\geqslant 0}\beta(t)=((I-P)^{-1}\mathbf{u})_{11}. \tag{38}$$

Recalling (31), we find that

$$\begin{aligned}\sum_{t\geqslant 0}&E_0[(X_1(t))^2(1-X_1(t))]\\ &=\left(1-\frac{1}{N_1}\right)\left(1-\frac{2}{N_1}\right)((I-F)^{-1}Q(I-P)^{-1}\mathbf{u})_{111}\\ &\quad+\frac{1}{N_1}\left(1-\frac{1}{N_1}\right)((I-P)^{-1}\mathbf{u})_{11}.\end{aligned} \tag{39}$$

Similarly, we find that

$$\begin{aligned}\sum_{t\geqslant 0}&E_0[(X_2(t))^2(1-X_2(t))]\\ &=\left(1-\frac{1}{N_2}\right)\left(1-\frac{2}{N_2}\right)((I-F)^{-1}Q(I-P)^{-1}\mathbf{u})_{222}\\ &\quad+\frac{1}{N_2}\left(1-\frac{1}{N_2}\right)((I-P)^{-1}\mathbf{u})_{22},\end{aligned} \tag{40}$$

$$\sum_{t\geqslant 0}E_0[X_1(t)X_2(t)(1-X_2(t))]=\left(1-\frac{1}{N_2}\right)((I-F)^{-1}Q(I-P)^{-1}\mathbf{u})_{122}, \tag{41}$$

$$\sum_{t\geqslant 0}E_0[X_1(t)X_2(t)(1-X_1(t))]=\left(1-\frac{1}{N_1}\right)((I-F)^{-1}Q(I-P)^{-1}\mathbf{u})_{121}, \tag{42}$$

$$\begin{aligned}\sum_{t\geqslant 0}&E_0[(X_1(t))^2(1-X_2(t))]\\ &=\left(1-\frac{1}{N_1}\right)((I-F)^{-1}Q(I-P)^{-1}\mathbf{u})_{112}\\ &\quad+\frac{1}{N_1}((I-P)^{-1}\mathbf{u})_{12},\end{aligned} \tag{43}$$

$$\begin{aligned}\sum_{t\geqslant 0}&E_0[(X_2(t))^2(1-X_1(t))]\\ &=\left(1-\frac{1}{N_2}\right)((I-F)^{-1}Q(I-P)^{-1}\mathbf{u})_{221}\\ &\quad+\frac{1}{N_2}((I-P)^{-1}\mathbf{u})_{21}.\end{aligned} \tag{44}$$

Furthermore, a calculation similar to (31) leads to

$$\begin{aligned}E_0[X_1(t)(1-X_1(t))^2]&=\left(1-\frac{1}{N_1}\right)\left(1-\frac{2}{N_1}\right)\delta(t)\\ &\quad+\frac{1}{N_1}\left(1-\frac{1}{N_1}\right)\beta(t),\end{aligned} \tag{45}$$

where

$$\delta(t)=P_0(\xi_1(t)=\xi_2(t)=0,\xi_3(t)=1), \tag{46}$$

and $\beta(t)$ is defined as before. Here, $\delta(t)$ is the probability for individuals 1 and 2 in deme 1 at time t to be of type B, while individual 3 in the same deme at the same time is of type A. This probability can be expressed as

$$\delta(t)=\alpha(t)+\gamma(t), \tag{47}$$

where $\alpha(t)$ is the probability in the event that the lineages of individuals 1 and 2 coalesce from time t to time 0, while $\gamma(t)$ is the probability in the event of no coalescence between the lineages of individuals 1, 2 and 3, from time t to time 0. This probability is given by

$$\gamma(t)=(F^t\mathbf{v})_{111}, \tag{48}$$

where $\mathbf{v}=(1/N_1,0,1/N_1,0,1/N_1,0,1/N_1,0)$ gives the probabilities for the ancestor of individual 3 at time 0 to be of type A according to the state of $\sigma(t)$ in $S_{1,2,3}$. Thus, we find that

$$\sum_{t\geqslant 0}\delta(t)=((I-F)^{-1}\mathbf{v})_{111}+((I-F)^{-1}Q(I-P)^{-1}\mathbf{u})_{111}, \tag{49}$$

which leads to

$$\begin{aligned}\sum_{t\geqslant 0}&E_0[X_1(t)(1-X_1(t))^2]\\ &=\left(1-\frac{1}{N_1}\right)\left(1-\frac{2}{N_1}\right)((I-F)^{-1}Q(I-P)^{-1}\mathbf{u}\\ &\quad+(I-F)^{-1}\mathbf{v})_{111}+\frac{1}{N_1}\left(1-\frac{1}{N_1}\right)((I-P)^{-1}\mathbf{u})_{11}.\end{aligned} \tag{50}$$

Note that

$$\sum_{t\geqslant 0}E_0[X_1(t)(1-X_1(t))^2]>\sum_{t\geqslant 0}E_0[X_1(t)^2(1-X_1(t))], \tag{51}$$

since $\delta(t)>\alpha(t)$ for all $t\geqslant 0$, and similarly with $X_2(t)$ instead of $X_1(t)$.

In the same way, the other terms can be expressed as

$$\begin{aligned}\sum_{t\geqslant 0}&E_0[X_2(t)(1-X_2(t))^2]\\ &=\left(1-\frac{1}{N_2}\right)\left(1-\frac{2}{N_2}\right)((I-F)^{-1}Q(I-P)^{-1}\mathbf{u}\\ &\quad+(I-F)^{-1}\mathbf{v})_{222}+\frac{1}{N_2}\left(1-\frac{1}{N_2}\right)((I-P)^{-1}\mathbf{u})_{22},\end{aligned} \tag{52}$$

$$\begin{aligned}\sum_{t\geqslant 0}&E_0[X_1(t)(1-X_2(t))^2]\\ &=\left(1-\frac{1}{N_2}\right)((I-F)^{-1}Q(I-P)^{-1}\mathbf{u}+(I-F)^{-1}\mathbf{v})_{221}\\ &\quad+\frac{1}{N_2}((I-P)^{-1}\mathbf{u})_{21},\end{aligned} \tag{53}$$

$$\begin{aligned}\sum_{t\geqslant 0}&E_0[X_2(t)(1-X_1(t))^2]\\ &=\left(1-\frac{1}{N_1}\right)((I-F)^{-1}Q(I-P)^{-1}\mathbf{u}+(I-F)^{-1}\mathbf{v})_{112}\\ &\quad+\frac{1}{N_1}((I-P)^{-1}\mathbf{u})_{12},\end{aligned} \tag{54}$$

and also

$$\begin{aligned}\sum_{t\geqslant 0}&E_0[X_2(t)(1-X_1(t))(1-X_2(t))]\\ &=\left(1-\frac{1}{N_2}\right)((I-F)^{-1}Q(I-P)^{-1}\mathbf{u}+(I-F)^{-1}\mathbf{v})_{122},\end{aligned} \tag{55}$$

$$\begin{aligned}\sum_{t\geqslant 0}&E_0[X_1(t)(1-X_1(t))(1-X_2(t))]\\ &=\left(1-\frac{1}{N_1}\right)((I-F)^{-1}Q(I-P)^{-1}\mathbf{u}+(I-F)^{-1}\mathbf{v})_{121}.\end{aligned} \tag{56}$$

Finally, using the exact expressions for the entries of the transition matrices F,Q,P given in Appendix A.1, without any further assumption on the backward migration rates, the fixation coefficient can be expressed in terms of the model parameters.

4. Fixation coefficient under the structured-coalescent assumptions

In this section, we compute the fixation coefficient under the structured-coalescent scenario (Notohara, 1990; Herbots, 1994, 1997; Wilkinson-Herbots, 1998), that is, assuming a large population size, $2N=(N_1+N_2)$, with deme sizes N_1 and N_2 of order N and backward migration rates m_1 and m_2 of order $1/N$. We define the scaled migration rates $M_1=4Nm_1$, $M_2=4Nm_2$, and the relative deme sizes $e_1=N_1/(2N)$ and $e_2=N_2/(2N)$, so that M_1, M_2, e_1, e_2 are all of order 1.

With this notation, the stationary distribution of the backward migration matrix $\mathbf{M}$ is

$$u_1=\frac{M_2}{M_1+M_2},\quad u_2=\frac{M_1}{M_1+M_2}. \tag{57}$$

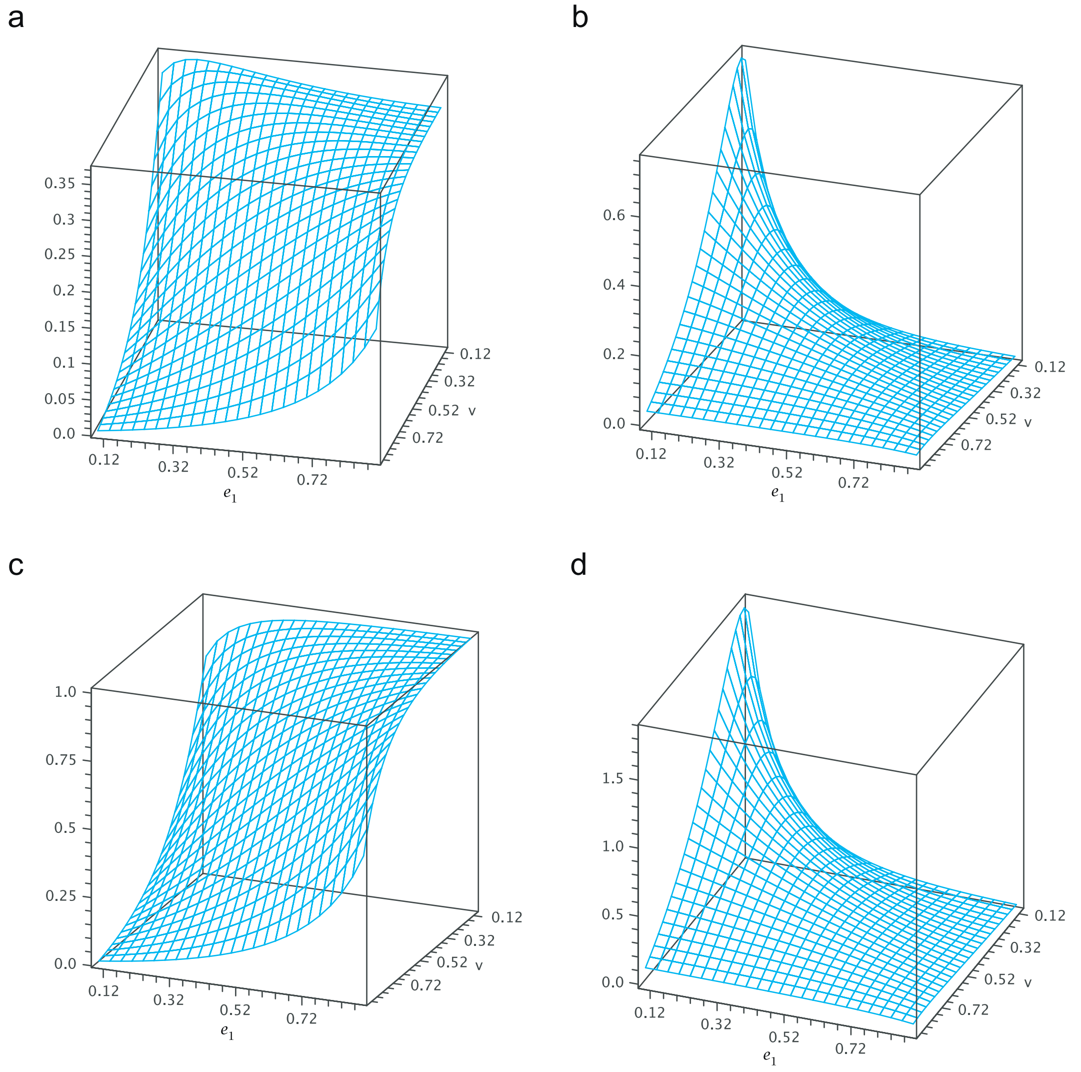

Fig. 1. Coefficients μ_1, μ_2, v_1 and v_2 as functions of e_1 and v. Parameter M is held equal to 1, while e_1 and v range from 0.1 to 0.9: (a) $\mu_1(e_1, v)$, (b) $\mu_2(e_1, v)$, (c) $v_1(e_1, v)$, and (d) $v_2(e_1, v)$.

Now, define C_0 as the constant term of $u'(0)$ as N goes to infinity so that

$$u'(0) = C_0 + O\left(\frac{1}{N}\right). \tag{58}$$

Owing to Eq. (25), the derivation of C_0 only requires the calculation of

$$\alpha_i = \lim_{N\to\infty} \sum_{t\geqslant 0} E_0[X_i(t)^2(1 - X_i(t))] \tag{59}$$

and

$$\beta_i = \lim_{N\to\infty} \sum_{t\geqslant 0} E_0[X_i(t)(1 - X_i(t)^2)] \tag{60}$$

for $i = 1, 2$, since all other sums are multiplied by migration rates of order $1/N$. Note that $\alpha_i < \beta_i$ for $i = 1, 2$. Moreover, these limits can be symbolically computed using a software like Mathematica, and lead to the expression

$$\begin{aligned} C_0 = {} & (\mathbf{p_A} - \mathbf{p_B}) \cdot (v_1 W_1 + v_2 W_2)\mathbf{p_B} \\ & + (\mathbf{p_A} - \mathbf{p_B}) \cdot (\mu_1 W_1 + \mu_2 W_2)(\mathbf{p}_A - \mathbf{p_B}), \end{aligned} \tag{61}$$

where

$$v_1 = u_1(\alpha_1 + \beta_1) = \frac{M_2(M_1M_2e_2 + 2M_1 + M_2^2e_2 + M_2)}{(M_1^2e_1 + M_1 + M_2^2e_2 + M_2)(M_1 + M_2)}, \tag{62}$$

$$v_2 = u_2(\alpha_2 + \beta_2) = \frac{e_2M_1M_2(M_1e_1 + M_2e_1 + 1)}{e_1(M_1^2e_1 + M_1 + M_2^2e_2 + M_2)(M_1 + M_2)}, \tag{63}$$

$$\mu_1 = u_1\alpha_1 = \frac{M_2\alpha_1}{M_1 + M_2} < \frac{v_1}{2}, \tag{64}$$

$$\mu_2 = u_2\alpha_2 = \frac{M_1\alpha_2}{M_1 + M_2} < \frac{v_2}{2} \tag{65}$$

with α_1 and α_2 given in Appendix A.2. Note that these coefficients do not depend on the selection parameters.

Fig. 1 plots numerical evaluations of v_1, v_2, μ_1 and μ_2 as functions of e_1, the relative size of deme 1, and the proportion

$$v = \frac{M_1e_1}{M_1e_1 + M_2e_2}, \tag{66}$$

when the parameter

$$M = \frac{M_1e_1 + M_2e_2}{2} \tag{67}$$

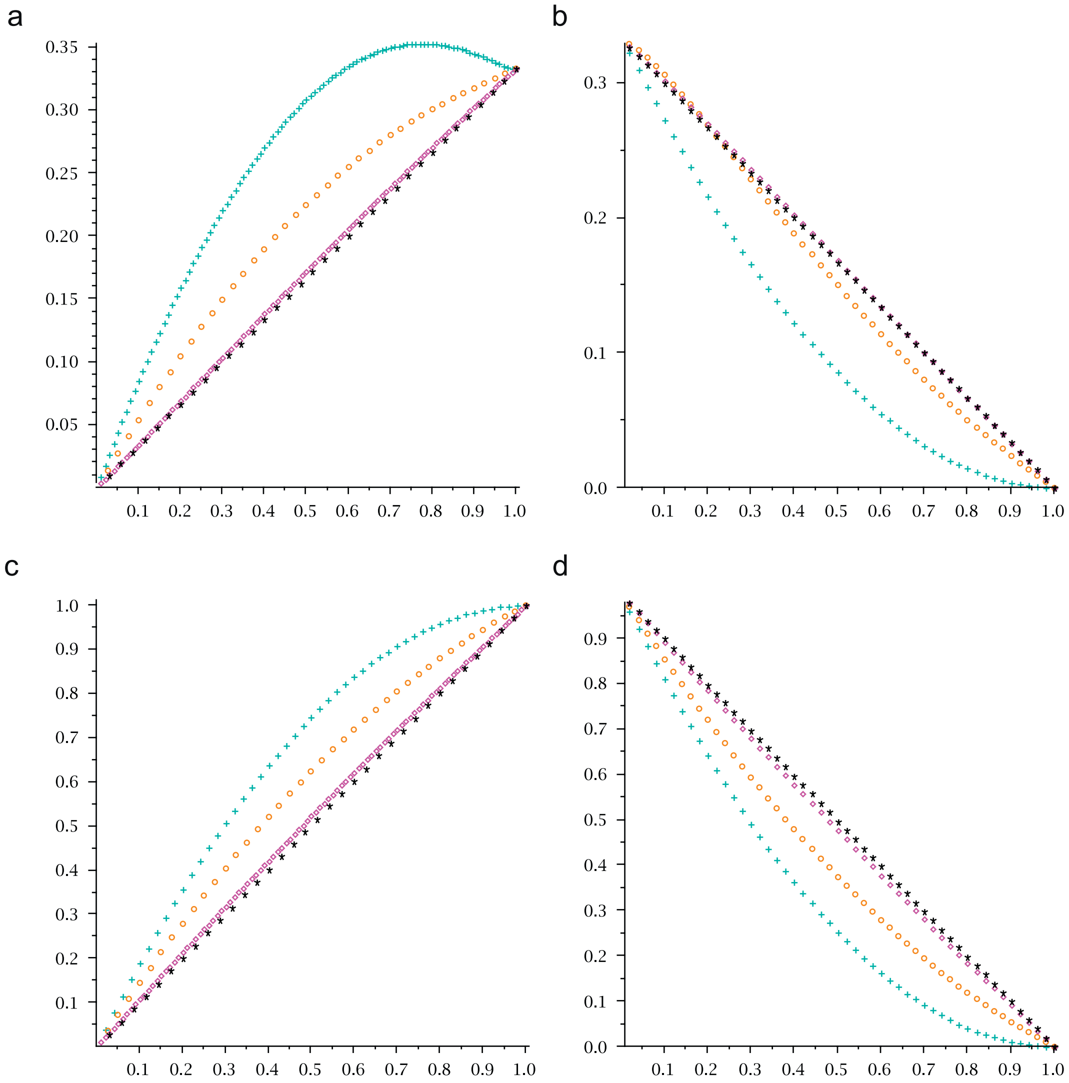

Fig. 2. Effect of unequal deme sizes in the case of conservative migration ($v=\frac{1}{2}$). Coefficients μ_1, μ_2, v_1 and v_2 as functions of e_1 for different values of M: $M=0.01$ (green crosses), $M=1$ (orange circles), $M=10$ (magenta diamonds), $M=100$ (black asterisks). Parameter e_1 ranges from 0 to 1: (a) $\mu_1(e_1)$, (b) $\mu_2(e_1)$, (c) $v_1(e_1)$, and (d) $v_2(e_1)$.

is kept equal to 1. Note that v is the expected number of migrant offspring in deme 1 after population regulation over the expected number in both demes, represented by $2M$.

It can be seen that μ_1 decreases with v and increases with e_1, provided v is not too small, and ranges from 0 to 0.38; v_1 increases with e_1 and decreases with v and varies between 0 and 1; both μ_2 and v_2 decrease with e_1, while they are non-monotonic functions of v, with μ_2 ranging from 0 to 0.78, and v_2 from 0 to 1.9. Similar graphics have been obtained for M ranging from 0.01 to 100 (not shown). Moreover, provided e_1 and v are both not too small, μ_1 and v_1 (μ_2 and v_2, respectively) decrease (increase, respectively) with M. We also find that μ_2 and v_2 decrease with e_1, while v_1 increases.

The case of conservative migration, which occurs when the relative size of each deme is maintained after migration, corresponds to $v=\frac{1}{2}$, or, equivalently,

$$M_1e_1=M_2e_2. \tag{68}$$

Fig. 2 shows numerical evaluations in this case for four different values of $M=M_1e_1$ ranging from 0.01 to 100. The effects of non-conservative migration when the deme sizes are equal ($e_1=\frac{1}{2}$) are illustrated in Fig. 3.

Note that, if we let M go to 0 so that, in the limit, deme 2 does not contribute to deme 1, then (61) leads to

$$C_0=(\mathbf{p}_A-\mathbf{p}_B)\cdot W_1\mathbf{p}_B+\tfrac{1}{3}(\mathbf{p}_A-\mathbf{p}_B)\cdot W_1(\mathbf{p}_A-\mathbf{p}_B). \tag{69}$$

This result corresponds to the first-order approximation of the fixation probability in the case of a linear game in a panmictic population (Lessard, 2005; Lessard and Ladret, 2007).

On the other hand, in the completely symmetric case, that is, when $M_1=M_2=2M$, $e_1=e_2=\frac{1}{2}$ and $W_1=W_2=W$, it follows from (61) that

$$\begin{aligned}C_0={}&(\mathbf{p}_A-\mathbf{p}_B)\cdot W\mathbf{p}_B\\&+\left(\frac{1}{3}+\frac{1}{12(M+1)}\right)(\mathbf{p}_A-\mathbf{p}_B)\cdot W(\mathbf{p}_A-\mathbf{p}_B).\end{aligned} \tag{70}$$

This result shows that the approximation for the probability of fixation of a newly introduced single mutant in the case of Wright's island model for demes of equal size N, and with the same game matrix W, given in Ladret and Lessard (2007) for $D\geqslant 3$ demes, still holds for $D=2$ demes.

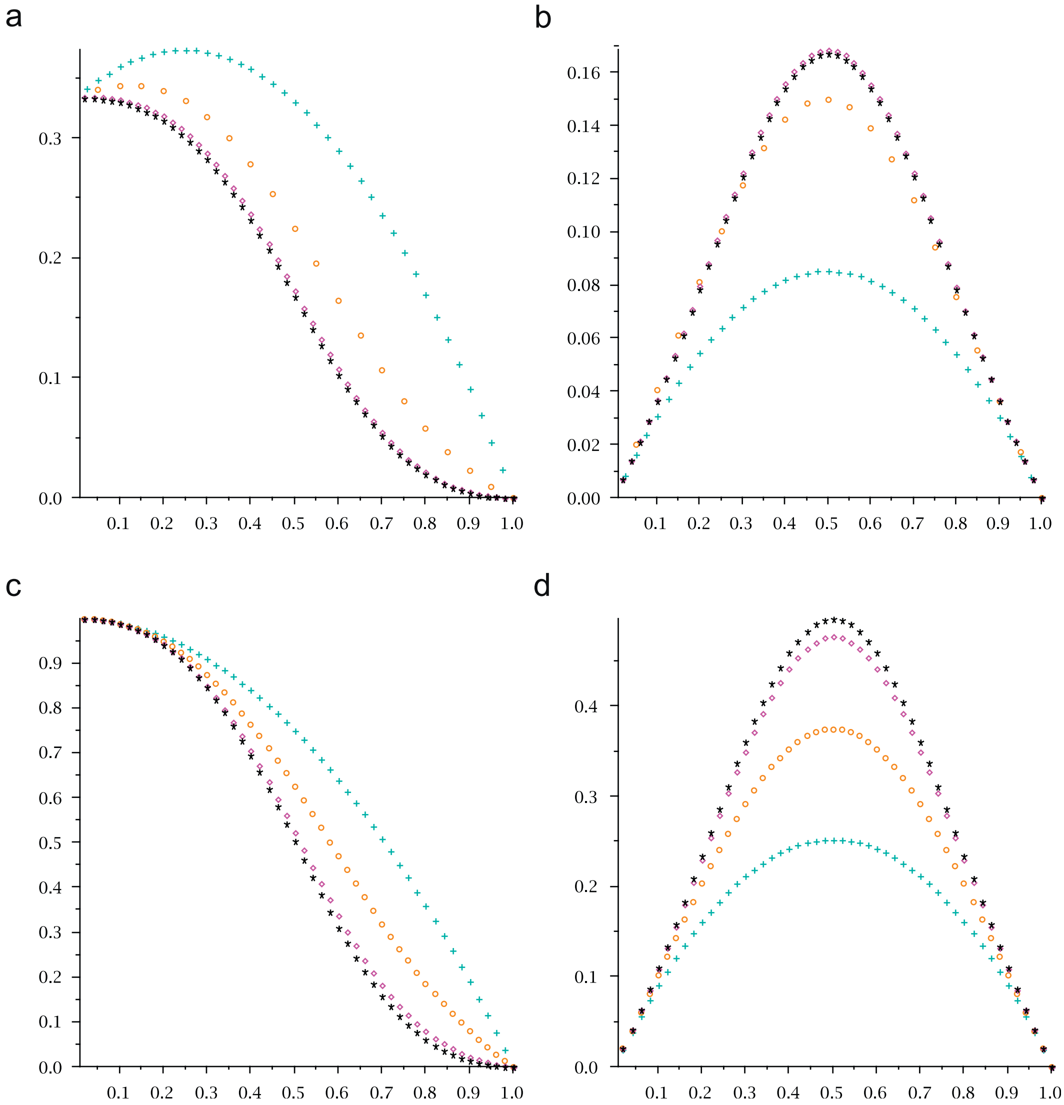

Fig. 3. Effect of non-conservative migration. Coefficients ν_1, ν_2, μ_1 and μ_2 as functions of ν (horizontal axis) in the case of equal deme sizes ($e_1 = \frac{1}{2}$) for different values of M: $M = 0.01$ (green crosses), $M = 1$ (orange circles), $M = 10$ (magenta diamonds), $M = 100$ (black asterisks). Parameter ν ranges from 0 to 1: (a) $\mu_1(\nu)$, (b) $\mu_2(\nu)$, (c) $\nu_1(\nu)$, and (d) $\nu_2(\nu)$.

5. Game dynamics in an infinite two-deme population

The case where the backward migration matrix is constant and the selection intensity $s \geqslant 0$ is of order $1/N$ as N goes to infinity, corresponds to a strong-migration limit. In this case, it follows from Nagylaki (1980) that, up to a rescaling of time with respect to the effective population size, which depends on the pattern of migration, the frequency of the mutant type A in each deme converges in probability to the frequency of A in the whole population averaged with respect to the stationary distribution of the migration matrix, denoted by Z (see Eq. (14)), and this averaged frequency converges in distribution to the usual diffusion process in a panmictic population.

Here, we consider the case where the deme sizes are infinite, with the relative size of deme 1 satisfying $0 < e_1 < 1$. Moreover, we assume that the migration rates, m_1 and m_2, are kept constant as the selection intensity s goes to 0, while time is measured in units of $1/s$ generations. Then, denoting the frequency vector of the mutant type A in demes 1 and 2 at time $\tau = ts$ by $\mathbf{x}(\tau) = (x_1(\tau), x_2(\tau))$, it follows from (7) that

$$\mathbf{x}(\tau + s) = \mathbf{M}\mathbf{x}(\tau) + s\Phi(\mathbf{M}\mathbf{x}(\tau)) + o(s), \tag{71}$$

where

$$\Phi(\mathbf{x}) = \begin{bmatrix} \Phi_1(\mathbf{x}) \\ \Phi_2(\mathbf{x}) \end{bmatrix}, \tag{72}$$

in which

$$\Phi_i(\mathbf{x}) = x_i(1 - x_i)\{x_i(\mathbf{p}_A - \mathbf{p}_B) \cdot W_i\mathbf{p}_A + (1 - x_i)(\mathbf{p}_A - \mathbf{p}_B) \cdot W_i\mathbf{p}_B\} \tag{73}$$

for $\mathbf{x} = (x_1, x_2)$, with $0 \leqslant x_i \leqslant 1$. Letting s go to 0 and assuming continuity yield

$$\mathbf{x}(\tau) = \mathbf{M}\mathbf{x}(\tau). \tag{74}$$

This implies that

$$\mathbf{x}(\tau) = z(\tau)\begin{bmatrix} 1 \\ 1 \end{bmatrix}, \tag{75}$$

where

$$z(\tau) = u_1x_1(\tau) + u_2x_2(\tau)$$

is the averaged frequency of A with respect to the stationary distribution (u_1, u_2) for the backward migration matrix $\mathbf{M}$. Moreover, taking the scalar product with (u_1, u_2) on both sides of (71) gives

$$\begin{aligned} z(\tau+s) &= z(\tau) + sz(\tau)(1-z(\tau)) \\ &\quad \times \{(1-z(\tau))(\mathbf{p}_A - \mathbf{p}_B)\cdot(u_1W_1+u_2W_2)\mathbf{p}_B \\ &\quad + z(\tau)(\mathbf{p}_A-\mathbf{p}_B)\cdot(u_1W_1+u_2W_2)\mathbf{p}_A\} + o(s). \end{aligned} \tag{76}$$

Thus, dividing by s and letting s go to 0 lead to the differential equation

$$\begin{aligned} \frac{\mathrm{d}z(\tau)}{\mathrm{d}\tau} &= z(\tau)(1-z(\tau))\{(\mathbf{p}_A-\mathbf{p}_B)\cdot(u_1W_1+u_2W_2)\mathbf{p}_B \\ &\quad + z(\tau)(\mathbf{p}_A-\mathbf{p}_B)\cdot(u_1W_1+u_2W_2)(\mathbf{p}_A-\mathbf{p}_B)\}. \end{aligned} \tag{77}$$

This is the analogue of the replicator equation for two types in the more general case of an infinite two-deme population. Actually, this corresponds to the classical replicator equation (see, e.g., Hofbauer and Sigmund, 1998, and references therein) for a linear game with game matrix $u_1W_1 + u_2W_2$ in an infinite panmictic population with $z(\tau)$ interpreted as the frequency of A in the population.

According to the original definition of evolutionary stability (Maynard Smith and Price, 1973; Maynard Smith, 1974), a strategy $\mathbf{p}$ is evolutionarily stable if it cannot be invaded by any mutant strategy, $\mathbf{p}' \neq \mathbf{p}$, provided the initial frequency of the mutant strategy is sufficiently small. In other words, $\mathbf{p}$ is an evolutionarily stable strategy (ESS) if the replicator equation that describes the population dynamics leads ultimately to the elimination of the mutant strategy. Thus, owing to (77), we find that the strategy $\mathbf{p}_B$ will be evolutionarily stable for the current two-deme linear-game model, with game matrices W_1, W_2 and stationary distribution (u_1, u_2) with respect to the backward migration matrix, if and only if

$$\text{(i)}\quad (\mathbf{p}_A-\mathbf{p}_B)\cdot(u_1W_1+u_2W_2)\mathbf{p}_B \leqslant 0, \tag{78}$$

or, in case of equality in (i),

$$\text{(ii)}\quad (\mathbf{p}_A-\mathbf{p}_B)\cdot(u_1W_1+u_2W_2)(\mathbf{p}_A-\mathbf{p}_B) < 0 \tag{79}$$

for every $\mathbf{p}_A \neq \mathbf{p}_B$. This means that $\mathbf{p}_B$ is an ESS for the game matrix $W = u_1W_1 + u_2W_2$ (Maynard Smith and Price, 1973; Maynard Smith, 1974). It is also convergence stable in the sense that if $\mathbf{p}_C$ is close enough to $\mathbf{p}_B$, then a rare mutant A increases initially in frequency if $\mathbf{p}_A$ lies between $\mathbf{p}_B$ and $\mathbf{p}_C$ (Christiansen, 1991, and references therein).

6. Conditions against replacement in a finite two-deme population

In this section, we go back to the finite two-deme population model under weak selection. Following Nowak et al. (2004), selection favors (opposes, respectively) A replacing B if the fixation probability of a single mutant A is greater (lower, respectively) than its value under neutrality, that is, $u(s) > u_1/N_1$ ($u(s) < u_1/N_1$, respectively) for $s > 0$. Owing to (61), provided selection is weak enough and $\mathbf{p}_A$ is different but close enough to $\mathbf{p}_B$, selection opposes A replacing B if and only if either

$$\text{(i)}\quad (\mathbf{p}_A-\mathbf{p}_B)\cdot(v_1W_1+v_2W_2)\mathbf{p}_B \leqslant 0, \tag{80}$$

or, in the case of equality in (i),

$$\text{(ii)}\quad (\mathbf{p}_A-\mathbf{p}_B)\cdot(\mu_1W_1+\mu_2W_2)(\mathbf{p}_A-\mathbf{p}_B) < 0. \tag{81}$$

If the twofold condition (80) and (81) is met for every $\mathbf{p}_A \neq \mathbf{p}_B$, close enough to $\mathbf{p}_B$, it will hold for every $\mathbf{p}_A \neq \mathbf{p}_B$. On the other hand, if condition (80) and (81) holds for every $\mathbf{p}_A \neq \mathbf{p}_B$, this does not imply that the probability of fixation of A is necessarily less than u_1/N_1, for $\mathbf{p}_A$ not close enough to $\mathbf{p}_B$. This will be the case, however, if $\mathbf{p}_B$ has all positive components, since then, we have an equality in (i) for all $\mathbf{p}_A \neq \mathbf{p}_B$. But, if $\mathbf{p}_B$ has some null components, then a strict inequality in (i) is possible for some $\mathbf{p}_A \neq \mathbf{p}_B$, with at least one positive component corresponding to a null component of $\mathbf{p}_B$. Thus, if inequality (ii) is reversed, $\mathbf{p}_A$ has to be close enough to $\mathbf{p}_B$ to ensure that

$$\begin{aligned} &(\mathbf{p}_A-\mathbf{p}_B)\cdot(v_1W_1+v_2W_2)\mathbf{p}_B \\ &\quad + (\mathbf{p}_A-\mathbf{p}_B)\cdot(\mu_1W_1+\mu_2W_2)(\mathbf{p}_A-\mathbf{p}_B) < 0. \end{aligned} \tag{82}$$

To sum-up, provided selection is weak enough, a resident strategy $\mathbf{p}_B$ is selectively favored against replacement by any alternative mutant strategy $\mathbf{p}_A$, if $\mathbf{p}_B$ meets condition (80) and (81) and makes use of all pure strategies; or by any alternative mutant strategy $\mathbf{p}_A$ using the same subset of pure strategies as $\mathbf{p}_B$ and any mutant strategy $\mathbf{p}_A$ close enough to $\mathbf{p}_B$ using some new pure strategies, if $\mathbf{p}_B$ satisfies (80) and (81) and uses a strict subset of pure strategies.

Note that, if condition (80) and (81) is met for every $\mathbf{p}_A \neq \mathbf{p}_B$, this does not mean that $\mathbf{p}_B$ is an ESS for some game matrix, since, in general, $\mu_1W_1 + \mu_2W_2$ differs from $v_1W_1 + v_2W_2$. In particular, this does not imply that $\mathbf{p}_B$ is an ESS for the two-infinite-deme linear-game model with game matrices W_1, W_2 and stationary distribution of the backward migration matrix (u_1, u_2), or equivalently, for the linear-game model with game matrix $u_1W_1 + u_2W_2$ in a panmictic population. Thus, unlike what happens in the case of an infinite panmictic population (Lessard, 2005; Lessard and Ladret, 2007) or in the case of a finite island model with identical game matrices, deme sizes and migration rates (Ladret and Lessard, 2007), conditions for strategies to be favored against replacement by weak selection in an asymmetric two-deme linear-game model with distinct linear games for a finite population, even large, do not reduce to classical ESS conditions based on a single game matrix.

Consider, for instance, symmetric demographic parameters ($e_1 = e_2 = \frac{1}{2}$, $M_1 = M_2 = 2M$), with $M = 1$, and game matrices, $W_1 \neq W_2$, given by

$$W_1 = \begin{pmatrix} a_1 & b_1 \\ c_1 & d_1 \end{pmatrix}, \quad W_2 = \begin{pmatrix} a_2 & b_2 \\ c_2 & d_2 \end{pmatrix}. \tag{83}$$

Then, we have $u_1 = u_2 = \frac{1}{2}$, $v_1 = \frac{5}{8}$, $v_2 = \frac{3}{8}$, $\mu_1 = \frac{9}{40}$, $\mu_2 = \frac{3}{20}$. Now, assume that $b_1 - d_1 = -(b_2 - d_2)(3/5) < 0$, and $3(a_1 - b_1 - c_1 + d_1) + 2(a_2 - b_2 - c_2 + d_2) < 0$. Then, the resident strategy $\mathbf{p}_B = (0, 1)$ is such that $(\mathbf{p}_A - \mathbf{p}_B)\cdot(v_1W_1 + v_2W_2)\mathbf{p}_B = 0$, $(\mathbf{p}_A - \mathbf{p}_B)\cdot(\mu_1W_1 + \mu_2W_2)(\mathbf{p}_A - \mathbf{p}_B) < 0$, and $(\mathbf{p}_A - \mathbf{p}_B)\cdot(u_1W_1 + u_2W_2)\mathbf{p}_B > 0$, for every $\mathbf{p}_A \neq \mathbf{p}_B$. Therefore, weak selection opposes any $\mathbf{p}_A \neq \mathbf{p}_B$ replacing $\mathbf{p}_B$ in the finite two-deme population model, even though $\mathbf{p}_B$ is not an ESS for the game matrix $(u_1W_1 + u_2W_2)$. Conversely, if $b_1 - d_1 = -(b_2 - d_2) > 0$ and $a_1 - c_1 < a_2 - c_2$, then strategy $\mathbf{p}_B$ is an ESS for $(u_1W_1 + u_2W_2) = (W_1 + W_2)/2$, but fails to meet condition (80) and (81), since $(\mathbf{p}_A - \mathbf{p}_B)\cdot(v_1W_1 + v_2W_2)\mathbf{p}_B > 0$, for all $\mathbf{p}_A \neq \mathbf{p}_B$.

Unless special relationships are satisfied as identical game matrices ($W_1 = W_2 = W$), condition (80) and (81) for a strategy to be selectively favored against replacement by any close enough mutant in a finite two-deme population does not directly translate into the standard concept of ESS based on a single game matrix. In the case of different game matrices, selection may even oppose the fixation of mutants that would bring the population closer to such a strategy in the spirit of the convergence stability concept (Christiansen, 1991). Indeed, one might have (80) and (81) with an equality in (80) for all $\mathbf{p}_A \neq \mathbf{p}_B$ and

$$\begin{aligned} &(\mathbf{p}_A-\mathbf{p}_C)\cdot(v_1W_1+v_2W_2)\mathbf{p}_C \\ &\quad = -r(\mathbf{p}_C-\mathbf{p}_B)\cdot(v_1W_1+v_2W_2)(\mathbf{p}_C-\mathbf{p}_B) < 0, \end{aligned} \tag{84}$$

where $\mathbf{p}_A = (1-r)\mathbf{p}_C + r\mathbf{p}_B$ for $0 < r < 1$ and $\mathbf{p}_C$ close enough to $\mathbf{p}_B$ such that

$$(\mathbf{p}_C-\mathbf{p}_B)\cdot(\mu_1W_1+\mu_2W_2)(\mathbf{p}_C-\mathbf{p}_B) < 0. \tag{85}$$

This is the case, for instance, with $a_1 = d_1 = 10$, $b_1 = c_1 = 5$, $a_2 = d_2 = 0$, $b_2 = c_2 = 8$ and $\mathbf{p}_B = (\frac{1}{2}, \frac{1}{2})$.

Similarly, if $\mathbf{p}_B$ is an ESS for the game matrix $(v_1 W_1 + v_2 W_2)$, then weak selection will favor a mutant $\mathbf{p}_A$ a little closer to $\mathbf{p}_B$, replacing $\mathbf{p}_C$ close enough to $\mathbf{p}_B$, while it may favor $\mathbf{p}_A$ replacing $\mathbf{p}_B$. This occurs, for instance, with $a_1 = d_1 = 0$, $b_1 = c_1 = 3$, $a_2 = d_2 = 10.8$, $b_2 = c_2 = 6$ in (83) and $\mathbf{p}_B = (\frac{1}{2}, \frac{1}{2})$. Note that this cannot occur for $\mathbf{p}_B = (0, 1)$ when $d_1 > b_1$ and $d_2 > b_2$, in which case weak selection will always favor the strategy closer to $\mathbf{p}_B$ replacing another closeby strategy.

7. Extension of the one-third law

In the following, we are interested in conditions under which the replacement of a resident strategy by a mutant strategy is selectively favored when both strategies are best replies to themselves (that is, when they are strict Nash equilibria) with respect to the two game matrices. In particular, we will investigate how the one-third law (Nowak et al., 2004) can be extended to include the case of the asymmetric two-deme linear-game model.

7.1. Coordination games

Consider two pure strategies, $\mathbf{p}_A = (1, 0)$ and $\mathbf{p}_B = (0, 1)$, and two 2×2 game matrices, W_1 and W_2, in the form (83), with $a_1 > c_1, a_2 > c_2, d_1 > b_1$, and $d_2 > b_2$, which means that $\mathbf{p}_A$ and $\mathbf{p}_B$ are best replies to themselves for both W_1 and W_2. From the deterministic replicator equation in an infinite population given by (77), we know that a unique unstable equilibrium exists at a frequency of A averaged with respect to the stationary distribution (u_1, u_2) of the backward migration matrix, given by

$$z^* = \frac{u_1(d_1 - b_1) + u_2(d_2 - b_2)}{u_1(a_1 - b_1 - c_1 + d_1) + u_2(a_2 - b_2 - c_2 + d_2)}. \tag{86}$$

In the context of a finite population, selection favors A replacing B for selection weak enough if inequality (82) is reversed, which is equivalent to

$$\tilde{z} = \frac{v_1(d_1 - b_1) + v_2(d_2 - b_2)}{\mu_1(a_1 - b_1 - c_1 + d_1) + \mu_2(a_2 - b_2 - c_2 + d_2)} < 1. \tag{87}$$

This condition corresponds to the extension of the one-third law to the two-deme linear-game model.

Note that

$$\frac{v_1(a_1 - c_1) + v_2(a_2 - c_2)}{\mu_1(a_1 - b_1 - c_1 + d_1) + \mu_2(a_2 - b_2 - c_2 + d_2)} = \frac{v_1(a_1 - b_1 - c_1 + d_1) + v_2(a_2 - b_2 - c_2 + d_2)}{\mu_1(a_1 - b_1 - c_1 + d_1) + \mu_2(a_2 - b_2 - c_2 + d_2)} - \tilde{z}$$

and this always exceeds $2 - \tilde{z}$, which exceeds 1 if $\tilde{z} < 1$. Therefore, if weak selection favors A replacing B, then it opposes B replacing A. Moreover, if this is the case for $\mathbf{p}_B = (0, 1)$, then it is also the case for $\mathbf{p}_B = (1 - r, r)$ for any $0 < r < 1$, since

$$\left(\frac{\tilde{z}}{1 - r}\right) - \left(\frac{r}{1 - r}\right)\left(\frac{v_1(a_1 - b_1 - c_1 + d_1) + v_2(a_2 - b_2 - c_2 + d_2)}{\mu_1(a_1 - b_1 - c_1 + d_1) + \mu_2(a_2 - b_2 - c_2 + d_2)}\right) < 1$$

if $\tilde{z} < 1$.

Note also that, unlike what happens in the context of a panmictic population (see Nowak et al., 2004, for the case of a Moran model; Lessard, 2005; Imhof and Nowak, 2006, for the case of a Wright–Fisher population model; Lessard, 2007, for a more general model of reproduction in which a fraction of the population is replaced at discrete-time steps; Traulsen et al., 2006, for pairwise comparison updating; Lessard and Ladret, 2007, for an extended Cannings exchangeable model), or in the framework of a symmetric island model with identical game matrices (Ladret and Lessard, 2007), inequality (87) cannot be written in the form $z^* < C$, where z^* represents the unstable frequency of A in an infinite population.

Thus, in general, in the case of a population subdivided into two demes with different game matrices, $W_1 \neq W_2$, and two strategies $\mathbf{p}_A$ and $\mathbf{p}_B$ that are best replies to themselves with respect to both W_1 and W_2, the conditions for a single mutant A to be selectively advantageous in a finite population do not translate into conditions on the unstable equilibrium frequency of A in an infinite population.

7.2. Coordination games with identical game matrices

If the game matrices are identical, that is,

$$W_1 = W_2 = W = \begin{pmatrix} a & b \\ c & d \end{pmatrix}, \tag{88}$$

and if $\mathbf{p}_A = (1, 0)$ and $\mathbf{p}_B = (0, 1)$ are best replies to themselves for W ($a > c$ and $d > b$), then z^* is equal to $x^* = (d - b)/(a - b - c + d)$, the equilibrium frequency of A in an infinite panmictic population with game matrix W. Moreover, z^* is proportional to $\tilde{z}$ and (87) reduces to

$$z^* = x^* = \frac{d - b}{a - b - c + d} < \frac{\mu_1 + \mu_2}{v_1 + v_2} = \Lambda < \frac{1}{2}. \tag{89}$$

If this inequality holds, then a single mutant A takes over the whole population with a selective advantage.

Note that, in the particular case of a symmetric population structure with identical deme sizes ($e_1 = e_2 = \frac{1}{2}$) and migration rates ($M_1 = M_2 = 2M$), (89) reduces to

$$x^* = \frac{d - b}{a - b - c + d} < \frac{1}{3} + \frac{1}{12(M + 1)}, \tag{90}$$

which, as already noticed, can be derived from Ladret and Lessard (2007).

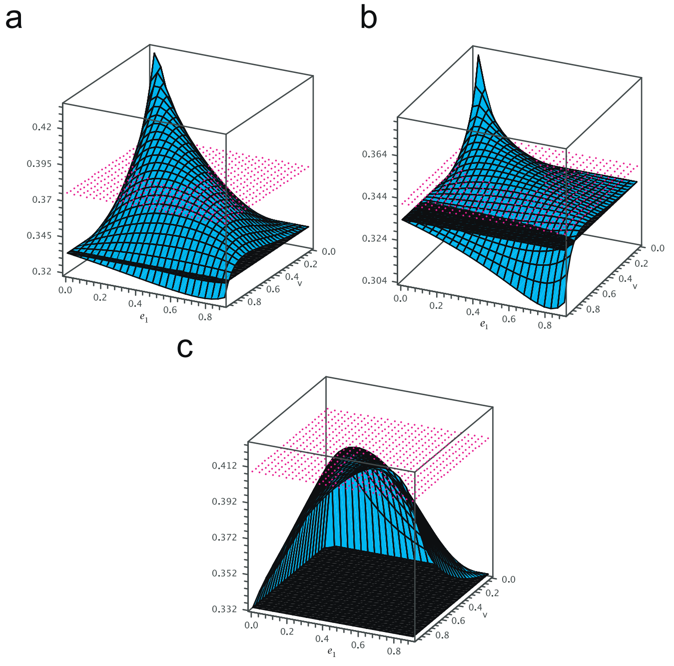

Fig. 4. Threshold Λ as a function of e_1 and v (patch blue surface) versus $\Lambda = \frac{1}{3} + 1/(12(M+1))$ (magenta dots) in the case of equal deme sizes and conservative migration ($e_1 = v = \frac{1}{2}$), and $\Lambda = \frac{1}{3}$ (solid black surface) in the panmictic scenario, when e_1 and v range from 0 to 0.9: (a) $M = 1$, (b) $M = 10$, and (c) $M = 0.1$.

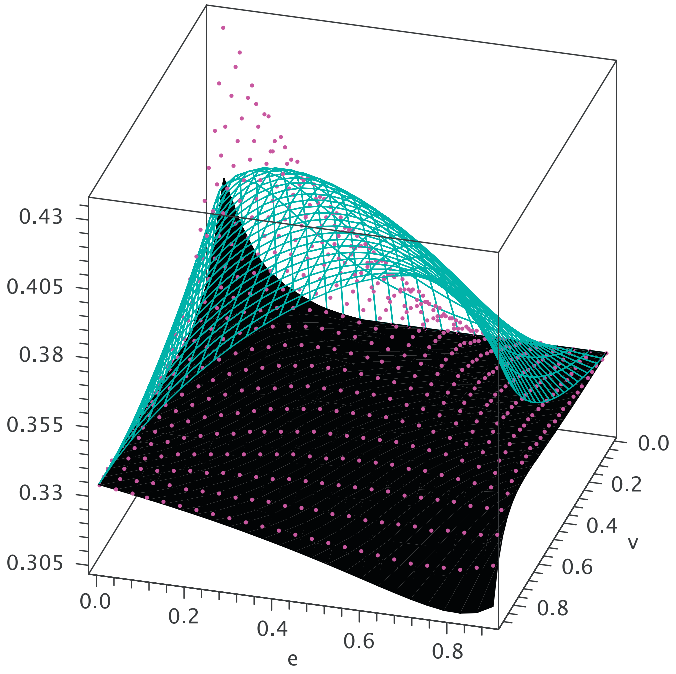

Fig. 5. Threshold Λ as a function of e_1 and v for different values of M: $M = 0.1$ (green lines), $M = 1$ (magenta dots), $M = 10$ (solid black surface). Parameters e_1 and v range from 0 to 0.9.

7.3. Numerical comparisons

In the case where condition (87) takes the form $x^* < \Lambda$ as in (89), comparisons are possible with the symmetric model counterpart, (90), and the one-third law, $x^* < \frac{1}{3}$, which holds when the population is panmictic.

Fig. 4 shows numerical evaluations of the threshold frequency Λ as a function of e_1, the proportion of individuals in deme 1, and v, the expected proportion of migrant offspring in deme 1 among all migrant offspring in both demes after population regulation, for three different values of the average expected number of migrant offspring in both demes after population regulation ($M = 0.1, 1$ and 10), versus the reference value of $\frac{1}{3}$ for a panmictic population and the special value $\frac{1}{3} + 1/(12(M+1))$ in the symmetric case corresponding to $e_1 = v = \frac{1}{2}$. We see that Λ decreases with M provided e_1 and v are both not too small (Fig. 5). On the other hand, Fig. 7 plots projections of Fig. 4 (a), which corresponds to the case where $M = 1$, when either $e_1 = \frac{1}{2}$ or $v = \frac{1}{2}$. When the deme sizes are equal ($e_1 = \frac{1}{2}$), the value of Λ increases with v from $\frac{1}{3}$ to 0.377, until v reaches some intermediate value close to $\frac{1}{2}$, but below this value, and then decreases to 0.3. When v is held equal to $\frac{1}{2}$, which means that migration is conservative, the value of Λ increases with e_1 from $\frac{1}{3}$ to 0.38, until e_1 reaches an intermediate value close to, but below, $\frac{1}{2}$, and then decreases back to $\frac{1}{3}$. Numerical evaluations show that similar projections are obtained when M varies between 0.1 and 10 (not shown). In the following, since Λ depends on the population parameters M, v and e_1, we shall denote it by $\Lambda(M, v, e_1)$.

7.3.1. Comparisons with the symmetric model

Let us focus first on the case $M = 1$ (Fig. 7). Under this scenario, when the population structure is entirely symmetric, we find that $\Lambda = \Lambda(1, \frac{1}{2}, \frac{1}{2}) = \frac{3}{8}$ and then condition (89) reduces to

$$x^* < \frac{3}{8}. \tag{91}$$

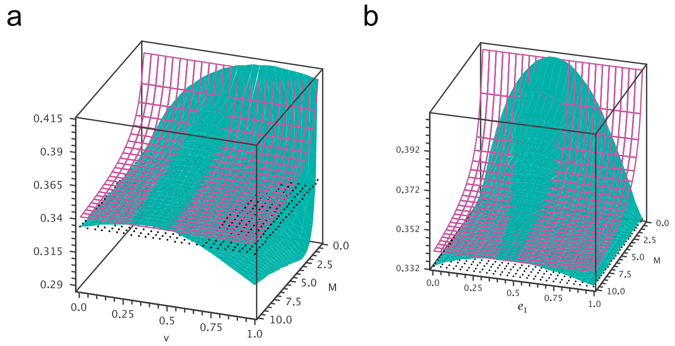

Fig. 6. Effect of unequal deme sizes and non-conservative migration on the threshold Λ (solid green surface) as a function of v, M and e_1: (a) $e_1 = \frac{1}{2}$ with M ranging from 0.1 to 10 and v from 0 to 0.99; (b) $v = \frac{1}{2}$ with M ranging from 0.1 to 10 and e_1 from 0 to 0.99. The value $\Lambda = \frac{1}{3} + 1/(12(M+1))$ (magenta lines) is for the symmetric case ($e_1 = v = \frac{1}{2}$) and $\Lambda = \frac{1}{3}$ (black dots) for the panmictic scenario.

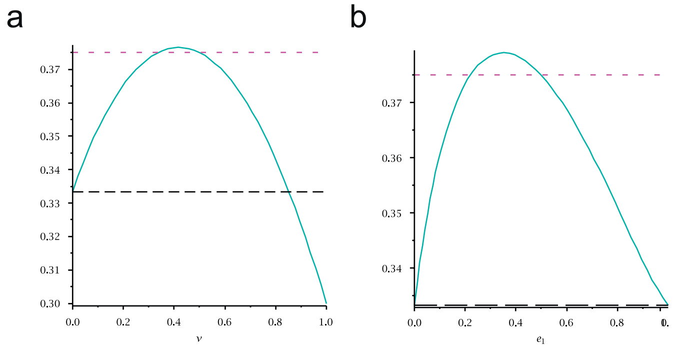

Fig. 7. Effect of unequal deme sizes and non-conservative migration on the threshold Λ (green line): (a) $e_1 = \frac{1}{2}$ with v ranging from 0 to 0.99; (b) $v = \frac{1}{2}$ with e_1 ranging from 0 to 0.99. The value $\Lambda = \frac{1}{3} + 1/(12(M+1))$ (dashed magenta line) is for the symmetric case ($e_1 = v = \frac{1}{2}$) and $\Lambda = \frac{1}{3}$ (dashed black line) for the panmictic scenario. Parameter M is taken equal to 1.

When the deme sizes are equal ($e_1 = \frac{1}{2}$) but $v < \frac{1}{2}$, we find that $\Lambda(1, v, \frac{1}{2}) > \frac{3}{8}$, which means a higher threshold value for x^*, if and only if $0.3376 < v < \frac{1}{2}$. Similarly, when migration is conservative ($v = \frac{1}{2}$) but $e_1 < \frac{1}{2}$, we have $\Lambda(1, \frac{1}{2}, e_1) > \frac{3}{8}$, and therefore we get a wider range for x^*, if and only if $0.22 < e_1 < \frac{1}{2}$.

More generally, for M ranging from 0.1 to 10, numerical evaluations of Λ (Figs. 4 and 6) suggest that the condition for the replacement of the resident strict Nash equilibria $\mathbf{p}_B$ by the other mutant strict Nash equilibria $\mathbf{p}_A$ is less stringent in an asymmetric model ($(v, e_1) \neq (\frac{1}{2}, \frac{1}{2})$), in which the size of deme 2 is equal to, or exceeds, the size of deme 1, provided it is not too much larger, and in which the proportion v is less or equal to $\frac{1}{2}$, provided it is not too small.

In the case of TFT with cooperation in the first round versus AllD for the IPD (see, e.g., Nowak et al., 2004), the frequency x^* decreases with the number of rounds. In this case, for a fixed M and provided e_1 and v are not too small and remain below $\frac{1}{2}$, an asymmetric two-deme population model will require less rounds of the game than the symmetric model to ensure that cooperation fixates in the population with a selective advantage.

7.3.2. Comparisons with the one-third law

Let us first consider the case $M = 1$ (Fig. 7). Under this hypothesis, we find that $\Lambda(1, v, \frac{1}{2}) > \frac{1}{3}$ if $v < 0.852$, and $\Lambda(1, \frac{1}{2}, e_1) > \frac{1}{3}$, for every $0 < e_1 < 1$. These are conditions that weaken the one-third law.

Similar results are obtained when M ranges from 0.1 to 10 (Figs. 4 and 6), that is: (89) is less stringent than the one-third law, if v is not too close to 1.

In the context of TFT versus AllD, provided the proportion v is not too close to 1, a two-deme linear-game model with identical game matrices will require less rounds of the game than a panmictic model to ensure that cooperation takes over the whole population with a selective advantage.

8. Discussion

The probability of fixation of a single mutant in a finite population can be studied using a diffusion approximation, in the context of a Wright–Fisher panmictic population of large size, N, under weak frequency-dependent selection determined by a linear game with game matrix W (Lessard, 2005). In this case, a first-order approximation, with respect to an intensity of selection $s \ll 1/N \ll 1$, is

$$u(s) = \frac{1}{N} + s\left\{(\mathbf{p}_A - \mathbf{p}_B)\cdot W\mathbf{p}_B + \frac{1}{3}(\mathbf{p}_A - \mathbf{p}_B)\cdot W(\mathbf{p}_A - \mathbf{p}_B)\right\} + O(s/N). \tag{92}$$

In the framework of a fixed total population size, N, and a selection intensity, s, small enough, a more precise approximation, derived from a direct Markov chain method used by Rousset (2003) allowing to express the first-order effect of selection on the probability of fixation in terms of expected coalescence times, under neutrality, of samples of two and three individuals, is (Lessard and Ladret, 2007)

$$u(s) = \frac{1}{N} + s\left(1 - \frac{1}{N}\right)\left\{(\mathbf{p}_A - \mathbf{p}_B)\cdot W\mathbf{p}_B + \frac{N}{3N-2} \times(\mathbf{p}_A - \mathbf{p}_B)\cdot W(\mathbf{p}_A - \mathbf{p}_B)\right\} + o(s). \tag{93}$$

See also Imhof and Nowak (2006) for an alternative approach under the Wright–Fisher scenario.

In the case of a Moran model, an exact explicit formula can be derived for the fixation probability and approximated for an intensity of selection small enough (Nowak et al., 2004; Lessard, 2005). We also refer to Lessard (2007) for more general discrete-time reproduction schemes; and to Lambert (2006) for a general branching process approach based on stochastic calculus.

Considering an island model with $D \geqslant 3$ demes of equal size, N, with the same game matrix in each deme, W, and the same backward migration rate, m, the direct Markov chain method has been extended to show that the fixation probability can be approximated as (Ladret and Lessard, 2007)

$$u(s) = \frac{1}{ND} + s\left\{\left(1 - \frac{1}{ND}\right)(\mathbf{p}_A - \mathbf{p}_B)\cdot W\mathbf{p}_B + \left(\frac{1}{3} + \frac{\gamma}{\delta}\right)(\mathbf{p}_A - \mathbf{p}_B)\cdot W(\mathbf{p}_A - \mathbf{p}_B)\right\} + o(s), \tag{94}$$

in which the coefficient γ/δ, whose value ranges from 0 to $\frac{1}{6}$, depends on the population structure parameters, N, m, and D. Moreover, under the additional structured-coalescent assumptions, which hold when the deme size, N, is large and the backward migration probability, m, is of order $1/N$ such that $M = mND/(D-1)$ is of order 1, this approximation, if $s \ll 1/(ND) \ll 1$, reduces to (Ladret and Lessard, 2007)

$$u(s) = \frac{1}{ND} + s\left\{(\mathbf{p}_A - \mathbf{p}_B)\cdot W\mathbf{p}_B + \left(\frac{1}{3} + \frac{D-1}{6D(M+1)}\right) \times(\mathbf{p}_A - \mathbf{p}_B)\cdot W(\mathbf{p}_A - \mathbf{p}_B)\right\} + o(s). \tag{95}$$

Assuming a two-deme linear-game model, in the context of a population subdivided into two demes of sizes N_1 and N_2, with game matrices W_1 and W_2, backward migration rates m_1 and m_2, in the form $m_1 = M_1/(4N)$ and $m_2 = M_2/(4N)$, where N is defined as half the total population size, that is, $2N = N_1 + N_2$, we have shown that, in the case where N is large, with N_1, N_2 of order N and M_1, M_2 of order 1, which stands for the structured-coalescent assumptions (Notohara, 1990; Herbots, 1994, 1997; Wilkinson-Herbots, 1998) and selection is weak ($s \ll 1/N \ll 1$), a first-order approximation for the probability of fixation of a single mutant A, initially introduced in deme 1, is given by

$$u(s) = \frac{u_1}{N_1} + s\{(\mathbf{p}_A - \mathbf{p}_B)\cdot(v_1 W_1 + v_2 W_2)\mathbf{p}_B + (\mathbf{p}_A - \mathbf{p}_B)\cdot(\mu_1 W_1 + \mu_2 W_2)(\mathbf{p}_A - \mathbf{p}_B)\} + o(s),$$

where u_1 denotes the first coordinate of the stationary distribution of the backward migration matrix $\mathbf{M}$, and the coefficients μ_i, v_i, for $i = 1, 2$, are functions of the population parameters via the migration parameters, M_1, M_2, and the proportion of individuals in deme 1, $e_1 = N_1/(2N)$. The proof is an extension of the direct Markov chain approach and expresses the derivative of $u(s)$ evaluated at $s = 0$, denoted by $u'(0)$, as a function of the quantities $\sum_{t\geqslant 0} E_0(X_i^2(t)(1 - X_i(t)))$ and $\sum_{t\geqslant 0} E_0(X_i(t)(1 - X_i(t))^2)$, where $X_i(t)$ represents the frequency of A in deme i at time t and E_0 an expectation under neutrality. These are computed using the coalescent approach (Kingman, 1982) for a structured population (Notohara, 1990), assuming that the population size is large enough.

In the case of an infinite population subdivided into two demes, assuming a constant backward migration matrix, $\mathbf{M}$, and weak selection, we have derived a modified replicator equation that models the dynamics of the frequency of a mutant in the whole population averaged with respect to (u_1, u_2), the stationary distribution of the backward migration matrix. We have shown that evolutionarily stable strategies (ESS) in the context of the two-deme linear-game model correspond in this case to ESS in the context of a linear-game model for an infinite panmictic population with game matrix $u_1 W_1 + u_2 W_2$. This should give a good approximation of the dynamics in the case $1/N \ll s \ll 1$.

According to the definition of an advantageous mutation in a finite population introduced by Nowak et al. (2004), we have derived a condition for a resident strategy to be selectively favored against replacement by a mutant strategy, under weak selection. In the case of identical game matrices ($W_1 = W_2 = W$), similarly to what happens in the panmictic version of the model (Lessard, 2005; Lessard and Ladret, 2007) or of its symmetric population counterpart (Ladret and Lessard, 2007), we have shown that this condition can be translated in terms of the standard ESS concept in an infinite population, with the additional requirement that the mutant strategy does not exceed some threshold value if it uses some new pure strategies. In the general case of non-identical game matrices, however, we have given an example which shows that the standard condition for a strategy to be evolutionarily stable in an infinite population is neither necessary nor sufficient for a strategy to be selectively advantageous against replacement in the case of a finite population. Moreover, conditions for evolutionary stability and convergence stability based on the fixation probability may be in opposition in the asymmetric case contrary to what happens in a random mating population (Wild and Taylor, 2004).

When the resident and mutant strategies are strict Nash equilibria with respect to the two game matrices W_1 and W_2, we have given a condition under which the resident strict Nash equilibrium is selectively favored against replacement by the other strict Nash equilibrium, in the general setting of an asymmetric two-deme linear-game model. In the context of identical game matrices, we have proved that this condition can be expressed in terms of the unstable equilibrium frequency of the mutant and then, extends the one-third law to take into account the asymmetry in the population structure. Note that the condition is less stringent than the one-third law when migration is conservative and in the case of non-conservative migration, provided the expected fraction of migrant offspring in deme 1 among all migrant offspring after population regulation is not too close to 1. Moreover, when the model is asymmetric, the condition is less stringent than in its symmetric model counterpart, provided both the latter fraction and the relative proportion of deme 1 are not too small and remain less or equal to $\frac{1}{2}$. In the context of the IPD with strategies TFT with cooperation in the first round versus AllD, these results, which translate into conditions for the TFT strategy to be favored by weak selection, indicate that the asymmetric population structure of the two-deme linear-game model can facilitate the emergence of cooperation compared to both its symmetric and panmictic population counterparts.

Where will the population evolve under recurrent mutation? It will depend not only on the selection parameters, but also on the mutation process, the demographic parameters, and the initial state of the population. Convergence stability may address the evolution of cooperation once it is already widespread in the population. The one-third law and its extensions can provide some clues for its evolution from a non-cooperative state.

Let us recall the definition of convergence stability from Christiansen (1991): the convergence stability is the requirement that a population initially [at a monomorphic state] close to [a value] m^* should move closer to m^*. Therefore, convergence stability is a local property. In the case of the IPD with enough rounds of the game in a panmictic population, TFT and AllD are both convergence stable with respect to nearby variant strategies mixing TFT and AllD. This holds with both reproductive fitness and fixation probability used as a measure of fitness (Wild and Taylor, 2004). However, this cannot explain the evolution of cooperation in a population of AllD individuals. The one-third law tells us when TFT fixation is favored by selection as long as selection is weak enough. Once TFT is fixed, it is favored against replacement not only by AllD, but also by any strategy mixing TFT and AllD; if the population size increases, TFT becomes uninvadable. We have seen that such an evolution scenario toward TFT is more likely to occur in a subdivided population.

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Appendix A

A.1. Transition probabilities

A.1.1. Matrix F

$$F_{111,111} = (1-m_1)^3\left(1-\frac{1}{N_1}\right)\left(1-\frac{2}{N_1}\right),$$

$$F_{111,112} = F_{111,121} = F_{111,211} = (1-m_1)^2 m_1\left(1-\frac{1}{N_1}\right),$$

$$F_{111,122} = F_{111,212} = F_{111,221} = (1-m_1)^2\left(1-\frac{1}{N_2}\right),$$

$$F_{111,222} = m_1^3\left(1-\frac{1}{N_2}\right)\left(1-\frac{2}{N_2}\right),$$

$$F_{112,111} = F_{121,111} = F_{211,111} = (1-m_1)^2 m_2\left(1-\frac{1}{N_1}\right)\left(1-\frac{2}{N_1}\right),$$

$$F_{112,112} = F_{121,121} = F_{211,211} = (1-m_1)^2(1-m_2)\left(1-\frac{1}{N_1}\right),$$

$$F_{112,121} = F_{112,211} = F_{121,112} = F_{121,211} = F_{211,112} = F_{211,121} = m_1 m_2(1-m_1)\left(1-\frac{1}{N_1}\right),$$

$$F_{112,122} = F_{112,212} = F_{121,122} = F_{121,221} = F_{211,212} = F_{211,221} = (1-m_1)m_1(1-m_2)\left(1-\frac{1}{N_2}\right),$$

$$F_{112,211} = F_{121,212} = F_{211,122} = m_2 m_1^2\left(1-\frac{1}{N_2}\right),$$

$$F_{112,222} = F_{121,222} = F_{211,222} = m_1^2(1-m_2)\left(1-\frac{1}{N_2}\right)\left(1-\frac{2}{N_2}\right),$$

$$F_{122,111} = F_{212,111} = F_{221,111} = (1-m_1)m_2^2\left(1-\frac{1}{N_1}\right)\left(1-\frac{2}{N_1}\right),$$

$$F_{122,211} = F_{212,121} = F_{221,112} = m_2^2 m_1\left(1-\frac{1}{N_1}\right),$$

$$F_{122,122} = F_{212,212} = F_{221,221} = (1-m_1)(1-m_2)^2\left(1-\frac{1}{N_2}\right),$$

$$F_{122,212} = F_{122,221} = F_{212,221} = F_{212,122} = F_{221,122} = F_{221,212} = m_1 m_2(1-m_2)\left(1-\frac{1}{N_2}\right),$$

$$F_{122,222} = F_{212,222} = F_{221,222} = (1-m_2)^2 m_1\left(1-\frac{1}{N_2}\right)\left(1-\frac{2}{N_2}\right),$$

$$F_{122,112} = F_{122,121} = F_{212,211} = F_{212,112} = F_{221,121} = F_{221,211} = (1-m_1)m_2(1-m_2)\left(1-\frac{1}{N_1}\right),$$

$$F_{222,111} = m_2^3\left(1-\frac{1}{N_1}\right)\left(1-\frac{2}{N_1}\right),$$

$$F_{222,112} = F_{222,121} = F_{222,211} = m_2^2(1-m_2)\left(1-\frac{1}{N_1}\right),$$

$$F_{222,122} = F_{222,212} = F_{222,221} = m_2(1-m_2)^2\left(1-\frac{1}{N_2}\right),$$

$$F_{222,222} = (1-m_2)^3\left(1-\frac{1}{N_2}\right)\left(1-\frac{2}{N_2}\right).$$

A.1.2. Matrix Q

$$\begin{bmatrix}
(1-m_1)^3\frac{1}{N_1}\left(1-\frac{1}{N_1}\right) & m_1(1-m_1)^2\frac{1}{N_1} & m_1^2(1-m_1)\frac{1}{N_2} & m_1^3\frac{1}{N_2}\left(1-\frac{1}{N_2}\right) \\
m_2(1-m_1)^2\frac{1}{N_1}\left(1-\frac{1}{N_1}\right) & (1-m_2)(1-m_1)^2\frac{1}{N_1} & m_2m_1^2\frac{1}{N_2} & \left(1-\frac{1}{N_2}\right)m_1^2(1-m_2)\frac{1}{N_2} \\
m_2(1-m_1)^2\frac{1}{N_1}\left(1-\frac{1}{N_1}\right) & m_1m_2(1-m_1)\frac{1}{N_1} & m_1(1-m_1)(1-m_2)\frac{1}{N_2} & m_1^2(1-m_2)\frac{1}{N_2}\left(1-\frac{1}{N_2}\right) \\
m_2^2(1-m_1)\frac{1}{N_1}\left(1-\frac{1}{N_1}\right) & m_2(1-m_1)(1-m_2)\frac{1}{N_1} & m_1m_2(1-m_2)\frac{1}{N_2} & m_1(1-m_2)^2\frac{1}{N_2}\left(1-\frac{1}{N_2}\right) \\
m_2(1-m_1)^2\frac{1}{N_1}\left(1-\frac{1}{N_1}\right) & m_1m_2(1-m_1)\frac{1}{N_1} & m_1(1-m_1)(1-m_2)\frac{1}{N_2} & m_1^2(1-m_2)\frac{1}{N_2}\left(1-\frac{1}{N_2}\right) \\
m_2^2(1-m_1)\frac{1}{N_1}\left(1-\frac{1}{N_1}\right) & m_1(1-m_1)(1-m_2)\frac{1}{N_1} & m_1m_2(1-m_2)\frac{1}{N_2} & m_1(1-m_2)^2\frac{1}{N_2}\left(1-\frac{1}{N_2}\right) \\
m_2^2(1-m_1)\frac{1}{N_1}\left(1-\frac{1}{N_1}\right) & m_1m_2^2\frac{1}{N_1} & (1-m_1)(1-m_2)^2\frac{1}{N_2} & m_1(1-m_2)^2\frac{1}{N_2}\left(1-\frac{1}{N_2}\right) \\
m_2^3\frac{1}{N_1}\left(1-\frac{1}{N_1}\right) & m_2^2(1-m_2)\frac{1}{N_1} & m_2(1-m_2)^2\frac{1}{N_2} & (1-m_2)^3\frac{1}{N_2}\left(1-\frac{1}{N_2}\right)
\end{bmatrix}.$$

A.1.3. Matrix P

$$\begin{bmatrix}
(1-m_1)^2\left(1-\frac{1}{N_1}\right) & (1-m_1)m_1 & (1-m_1)m_1 & m_1^2\left(1-\frac{1}{N_2}\right) \\
(1-m_1)m_2\left(1-\frac{1}{N_1}\right) & (1-m_1)(1-m_2) & m_1m_2 & m_1(1-m_2)\left(1-\frac{1}{N_2}\right) \\
(1-m_1)m_2\left(1-\frac{1}{N_1}\right) & m_1m_2 & (1-m_1)(1-m_2) & m_1(1-m_2)\left(1-\frac{1}{N_2}\right) \\
m_2^2\left(1-\frac{1}{N_1}\right) & m_2(1-m_2) & m_2(1-m_2) & (1-m_2)^2\left(1-\frac{1}{N_2}\right)
\end{bmatrix}.$$

A.2. Approximations for the structured coalescent

$$\begin{aligned}
\alpha_1 = {} & [12M_1^2+4M_2^2+38e_1e_2M_1^2M_2^2+2e_1^2e_2M_1^4M_2 \\
& +2M_2^3e_1+4e_1e_2^2M_1^4M_2+28e_1e_2M_1^3M_2 \\
& +2e_2^3M_2^5+3e_1e_2^3M_1^2M_2^4+3e_1e_2^3M_1M_2^5+16M_1M_2 \\
& +6e_1^2e_2M_1^3M_2^2+3e_1^2e_2^2M_1^4M_2^2+16e_1e_2^2M_1^3M_2^2 \\
& +8e_2^2M_2^4+e_1^2e_2^2M_1^5M_2+12M_1^3e_1+25e_1e_2M_1M_2^3 \\
& +10e_2M_2^3+e_1e_2^3M_1^3M_2^3+3e_1^2e_2^2M_1^3M_2^3+6e_2M_1^3 \\
& +3e_1^2e_2M_1^2M_2^3+22e_1e_2^2M_1^2M_2^3+16e_1e_2^2M_1M_2^4 \\
& +e_1^2e_2^2M_1^2M_2^4+2M_1^2M_2^2e_1^2+6e_1e_2M_1^4+5e_1e_2M_2^4 \\
& +32e_2M_1^2M_2+4e_1e_2^2M_2^5+6e_2^3M_1M_2^4+21e_2^2M_1^2M_2^2 \\
& +38e_2M_1M_2^2+e_1e_2^3M_2^6+3e_2^2M_1^3M_2+3e_2^3M_1^2M_2^3 \\
& +28e_2^2M_1M_2^3+20M_1^2M_2e_1+12M_1M_2^2e_1 \\
& +4M_1^3M_2e_1^2][3(2M_2^2e_2^2+M_1e_1M_2^2e_2^2+M_2^3e_1e_2^2 \\
& +2M_1e_2+3M_1^2e_1e_2+M_1^3e_1^2e_2+6M_2e_2 \\
& +6M_1e_1M_2e_2+M_1^2e_1^2M_2e_2+3M_2^2e_1e_2+4 \\
& +6M_1e_1+2M_1^2e_1^2+2M_2e_1)(M_1+M_2) \\
& \times(M_1^2e_1+M_1+M_2^2e_2+M_2)]^{-1},
\end{aligned}$$

$$\begin{aligned}
\alpha_2 = {} & [e_2M_2(4M_1+10M_1^2e_1+8M_2^2e_2+4M_2 \\
& +6M_1^3e_1^3M_2+2M_1M_2^2e_2^2+10M_2^3e_1e_2+M_2^5e_1^2e_2^2 \\
& +20M_1e_1M_2+15M_1e_1^2M_2^2+4M_2^4e_1^2e_2 \\
& +16M_2^3e_1^2e_2M_1+M_1^3e_1^2M_2^2e_2^2+3M_1^2e_1M_2^2e_2^2 \\
& +3M_1^2e_1^2M_2^3e_2^2+16M_1^3e_1^2e_2M_2+26M_1e_1M_2^2e_2 \\
& +25M_2M_1^2e_1e_2+3M_2^4e_1^2e_2^2M_1+3M_2e_2e_1^3M_1^4 \\
& +4M_2^3e_2^2+8M_1^3e_1^2+6M_2^3e_1e_2^2M_1+e_2M_2^3e_1^3M_1^2 \\
& +22M_1^2e_1^2M_2^2e_2+3M_2^2e_2e_1^3M_1^3+5M_1^3e_1e_2 \\
& +22M_1^2e_1^2M_2+8M_2^2e_1+2M_1^2e_2+3M_2^3e_1^2 \\
& +2M_1^4e_1^3+2M_2^4e_1e_2^2+M_1^5e_1^3e_2+12M_1M_2e_2 \\
& +4M_1^4e_1^2e_2+3M_1^2e_1^3M_2^2)][3e_1(2M_2^2e_2^2+M_1e_1M_2^2e_2^2 \\
& +M_2^3e_1e_2^2+2M_1e_2+3M_1^2e_1e_2+M_1^3e_1^2e_2 \\
& +6M_2e_2+6M_1e_1M_2e_2+M_1^2e_1^2M_2e_2+3M_2^2e_1e_2 \\
& +4+6M_1e_1+2M_1^2e_1^2+2M_2e_1)(M_1+M_2) \\
& \times(M_1^2e_1+M_1+M_2^2e_2+M_2)]^{-1}.
\end{aligned}$$

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