



**HAL**  
open science

# Evolutionary game dynamics in a finite continental island population model and emergence of cooperation

Véronique Ladret

► **To cite this version:**

Véronique Ladret. Evolutionary game dynamics in a finite continental island population model and emergence of cooperation. 2022. hal-00921092v4

**HAL Id: hal-00921092**

**<https://hal.science/hal-00921092v4>**

Preprint submitted on 28 Mar 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



# Evolutionary Game Dynamics in a Finite Continental Island Population Model and Emergence of Cooperation

Véronique Ladret<sup>1</sup>

Accepted: 23 March 2022

© The Author(s), under exclusive licence to Springer Science+Business Media, LLC, part of Springer Nature 2022

## Abstract

We consider the continental island model for a finite haploid population with a total number of  $n$  demes consisting of one continent and  $n - 1$  islands. We assume viability differences in the population captured by a linear game within each deme as a result of pairwise interactions. Assuming weak selection, conservative migration and the limit case of the structured coalescent assumptions, we derive the first-order approximation for the fixation probability of a single mutant, initially introduced in the continent, with respect to the intensity of selection. This result is applied to the case of the iterated Prisoner's Dilemma, when the resident strategy is always defect and the mutant cooperative strategy is tit-for-tat. In this context, we investigate the condition under which selection favors the emergence of cooperation and we derive an extension of the “one-third law” of evolution. When the continent and the islands are of the same size, we compare the continental island model to its Wright's island model counterpart. When the islands have the same size, but this size differs from the size of the continent, we investigate how the asymmetry in the deme sizes can better promote the evolution of tit-for-tat compared to its equal deme sizes model counterpart.

**Keywords** Evolutionary game theory · Finite population · Structured coalescent · Fixation probability · One third law

## 1 Introduction

Evolutionary game theory is a mathematical framework that has originally been considered in the context of infinitely large populations for studying selection of traits with frequency-dependent fitness [30, 34, 37]. Frequency-dependent selection arises whenever the fitness values of the traits (strategies) depend on the relative abundance of the different strategies in the population. The trait of cooperation is a classic example of traits under frequency-dependent selection [36]. In the context of infinite populations, the evolution of the frequencies of the traits in the population is modeled by differential equations like the

---

✉ Véronique Ladret  
veronique.ladret@umontpellier.fr

<sup>1</sup> IMAG, CNRS, Université de Montpellier, Montpellier, France

wide-spread replicator equations [12, 48] and theoretical predictions of the evolution of the system are based on the identification of equilibrium states and the analysis of their stability.

In nature, real populations are always finite and the evolutionary processes are subject to stochastic fluctuations due, in particular, to the finiteness of the population. In this case, the evolution of a mutant trait may differ significantly from its evolutionary outcome predicted by the deterministic replicator dynamics in infinite populations. For instance, in the absence of mutation, any mutant trait will either be eliminated or will take over the whole population due to random drift. And the probability that a single mutant fixes in a finite population is always nonzero, even in the case where this mutant is one that would be wiped out by selection in an infinitely large population.

Besides, real populations, in addition to being finite, are not always well-mixed. They often exhibit some kind of structure. A substantial amount of studies in evolutionary game theory investigate the effect of population structure on the evolutionary process. One way to incorporate structure in a population is to consider group-structured populations models, which include the traditional island model [19, 23] or models with isolation by distance [42, 44]. Evolutionary games on graphs, in which individuals are viewed as nodes on a graph, provide another natural extension to the modeling of structured populations [2, 4, 7, 35, 39, 40, 47, 51].

When analyzing evolutionary dynamics in a finite population, whether structured or not, an interesting quantity is given by the fixation probability of a single mutant. It has been used by Nowak et al. [38] to define an advantageous mutation in a finite population: selection is said to *favor the replacement of a resident strategy by a mutant strategy*, if the fixation probability of a single mutant is greater than it would be under neutral selection.

From this definition, ensues the *one-third law of evolution* which specifies conditions for weak selection to favor the emergence of a wild type strategy in a  $2 \times 2$  coordination game, in the limit of a large finite population.

The one-third law has been introduced by Nowak et al. [38] in the context of a frequency-dependent Moran model. It has also been obtained for the Wright–Fisher model [13, 21], pairwise comparison updating [49], exchangeable models within the domain of Kingman’s coalescence [26] and games on graphs [39–41]. Then, it has been extended to the  $d$ -player two-strategies game in a Moran population [8, 18]. The extension of the one-third law from the 2-player to the  $d$ -player game has been shown to be the same for all exchangeable models in the domain of application of the Kingman coalescent in the limit of a large neutral population [25]. Group structured populations [19, 20, 24] have also been investigated. Note, however, as shown in Traulsen et al. [49] and Sample and Allen [45], that the order in which limits are taken matters for the rule to be valid: one must first take the weak selection limit and then apply an approximation for large population sizes.

When applied to the Iterated Prisoner’s Dilemma (IPD) game [5, 50], with the cooperative “tit-for-tat” (TFT) strategy as a mutant strategy and “always defect” (AllD) as a resident strategy, the one-third law or its extensions enables one to investigate how the evolution of cooperation can be better promoted by selection in a finite population. Indeed, when the number of iterations of this game is large enough, it becomes a coordination game with both TFT and AllD being evolutionarily stable in the traditional sense. The one-third law states that, in the limit of a large finite population size, weak selection favors a single mutant TFT cooperator taking over a population of resident AllD defectors if the proportion of TFT at the unstable equilibrium of the deterministic replicator’s dynamics is smaller than one-third.

Population subdivision can make the one-third law less stringent, as it happens in group-structured populations models such as Wright’s island model with a finite number of demes

of finite sizes [19], in the limit of a large number of small demes [24], as well as in asymmetric two-demes model with unequal deme sizes and different migration rates [20].

The purpose of this paper is to extend the one-third law to a particular group-structured population model: the *Continental Island model*, CI model in short, with  $n$  demes [52], in the limit case of the structured coalescent assumptions [9, 10, 33, 52]. When applied to the case of the IPD game with the two strategies TFT and AllD, this result will allow us to derive conditions under which the topology of the CI model facilitates the emergence of cooperation compared to some other population structures, including Wright's Island model, WI model in short.

We proceed as follows, first we compute an approximation for the first-order effect of selection on the fixation probability of a single mutant under: weak selection, conservative migration and the structured coalescent assumptions [9, 10, 33, 52]; and second, we derive the condition under which a mutant strategy is selectively advantageous. The first step is an extension of the coalescent approach used in [20], which is adapted from a direct Markov chain method proposed by Rousset [43] and ascertained in Lessard and Ladret [26].

Note that these calculations could also be performed using a general method recently developed by McAvoy and Allen [32], which generalizes the approach of Rousset [43] in the framework of "replacement events" models developed by [1, 3]. This method applies to a broad class of stochastic evolutionary models, in which the size and spatial structure of the population are arbitrary, but fixed. But we resorted to a different straightforward extension of the method used in Ladret and Lessard [20] that is directly adapted to fit the CI model.

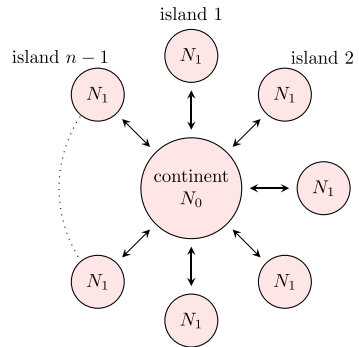
As a consequence of the second step, we obtain an extension of the one-third law when the two strategies are best replies to themselves with respect to the game matrix. Then, for each of the following model comparisons:

- (i) CI model vs panmictic model;
- (ii) CI model with equal deme sizes, called symmetric CI or sCI in short, vs a WI model that has the same deme sizes, the same number of demes,  $n$ , and the same expected total number of migrants per generation after population regulation as the sCI model;
- (iii) CI model vs its sCI model counterpart, which shares the same population parameters as the CI model except for the proportion of individuals living on the continent, which is equal to  $P \neq 1/n$  in the latter model and  $P = 1/n$  in the former;

we establish the conditions under which the extended one-third law is less stringent in the first model compared to the second one. For the IPD game with TFT and AllD, this condition means that the emergence of cooperation is better promoted by the former model compared to the latter. These conditions will be expressed in terms of the population parameters.

This paper is organized as follows. In Sect. 2, we describe the CI model. In Sect. 3, we give a first-order approximation for the fixation probability of a single mutant with respect to the intensity of selection, under weak selection. In Sect. 4, this approximation is derived under the structured coalescent assumptions and conservative migration. In Sect. 5, conditions under which a mutant strategy is favored by selection to replace a resident strategy are derived and links with evolutionarily stable strategies in the traditional sense are given. In Sect. 6, the question of the emergence of cooperation is investigated in the framework of a coordination game. The extended one-third law obtained for the CI model is compared to the one associated with a panmictic population. The results derived for the asymmetric continental island model are compared to their symmetric model counterparts. And comparisons are made between the symmetric continental island model (sCI model) and the WI model. Discussion and conclusions are provided in Sect. 7.

**Fig. 1** Continental Island Model with  $n$  demes. The arrows indicate migration



## 2 The Continental Island Linear Game Model

We consider a CI model [52] in which a haploid population is subdivided into  $n$  demes, or subpopulations: a central deme, “the continent,” surrounded by  $n - 1$  identical islands of equal sizes, with migration only occurring between the continent and each island; see Fig. 1. Deme 0 (resp.  $i = 1, \dots, n - 1$ ) will stand for the continent (resp. the islands). The size of the continent, denoted by  $N_0$ , is possibly different from that of each island, denoted by  $N_1$ , with both sizes remaining fixed. Moreover, we allow for unequal migration rates from the continent to each island and from each island to the continent, but we assume that the migration rate from any particular island to the continent is the same for all the islands. Suppose there are two types of individuals in the population, type  $A$  and type  $B$ , and that, at time  $t = 0$ , a single mutant  $A$  is introduced into the continent.

We assume that the population evolves in discrete, non-overlapping generations represented by time steps  $t = 0, 1, 2, \dots$ . The iteration  $t$  to  $t + 1$  is done in four steps:

*Step 1. Reproduction* At the beginning of every generation, each individual in the population produces the same very large number of offspring (treated as if it were infinite).

*Step 2. Migration* These offspring then disperse independently among the  $n$  demes according to the migration pattern of a continental island model (see [52], and references therein), as described below.

An offspring from the continent can migrate to each island, and an offspring from each island can only migrate to the continent. Hence, migration between islands is not possible in one step of the migration process, it implies passing through the continent. Let:

- $m_{0i}$  denote the proportion of offspring in the continent that come from island  $i$  in the previous generation;
- $m_{i0}$  denote proportion of offspring in island  $i$  that come from the continent in the previous generation;
- $m_i$  denote the probability that an individual from deme  $i$  emigrated from another subpopulation in the previous generation ( $0 \leq i \leq n - 1$ ).

For all  $i = 1, \dots, n - 1$ , we assume that  $m_{0i} = m_0/(n - 1)$  and that  $m_{i0} = m_1$  (here,  $m_1$  is the probability that an individual from island  $i$  emigrated from the continent in the previous generation). Moreover, we suppose all the backward migration probabilities to be constant over time.

Let  $x_i$  denote the frequency of  $A$  in deme  $i$  at the beginning of a given generation, and  $\tilde{x}_i$  the frequency of  $A$  in the same deme after migration, then we have:

$$\tilde{x}_0 = (1 - m_0) x_0 + \frac{m_0}{n - 1} \sum_{i=1}^{n-1} x_i, \tag{1}$$

$$\tilde{x}_i = m_1 x_0 + (1 - m_1) x_i, \quad i = 1, \dots, n - 1. \tag{2}$$

*Step 3. Selection* Migration is then followed by selection among offspring within the same deme. We consider a linear game scenario with two types of individuals,  $A$  and  $B$ . Each type is associated with a mixed strategy represented as a frequency vector, respectively,  $\mathbf{p}_A$  and  $\mathbf{p}_B$ , whose components give the probabilities of using some pure strategies in a contest against an opponent. Pairwise interactions take place among the individuals within each deme and affect their viabilities (fitnesses) which read, respectively, for types  $A$  and  $B$ :

$$\text{for the continent:} \quad f_{A,0} = 1 + s \mathbf{p}_A \cdot W \bar{\mathbf{p}}_0, \quad f_{B,0} = 1 + s \mathbf{p}_B \cdot W \bar{\mathbf{p}}_0, \tag{3a}$$

$$\text{for island } i : \quad f_{A,i} = 1 + s \mathbf{p}_A \cdot W \bar{\mathbf{p}}_i, \quad f_{B,i} = 1 + s \mathbf{p}_B \cdot W \bar{\mathbf{p}}_i, \tag{3b}$$

where  $W$  is a given game matrix,  $s > 0$  is the selection intensity,  $\mathbf{x} \cdot \mathbf{y}$  is the scalar product of two vectors  $\mathbf{x}$  and  $\mathbf{y}$ , and  $\bar{\mathbf{p}}_i$  is the mean strategy in deme  $i$  before selection, that is:

$$\bar{\mathbf{p}}_i = \tilde{x}_i \mathbf{p}_A + (1 - \tilde{x}_i) \mathbf{p}_B = \tilde{x}_i (\mathbf{p}_A - \mathbf{p}_B) + \mathbf{p}_B, \quad i = 0, \dots, n - 1. \tag{4}$$

Following selection, the frequency of  $A$  among the individuals in deme  $i$  becomes:

$$x'_i = \frac{\tilde{x}_i f_{A,i}}{\tilde{x}_i f_{A,i} + (1 - \tilde{x}_i) f_{B,i}}. \tag{5}$$

*Step 4. Sampling of a finite population* The next generation is obtained by drawing at random  $N_0$  individuals in the continent and  $N_1$  individuals in each island. The number of  $A$  individuals in the continent follows a binomial distribution with parameters  $N_0$  and  $x'_0$ , and the number of  $A$  individuals in island  $i$ , a binomial distribution with parameters  $N_1$  and  $x'_i$ .

After this population regulation, the frequency of  $A$  in deme  $i$  has mean  $x'_i$ . Note that in the special case when the number of demes is reduced to  $n = 2$ , this model reduces to the asymmetric two-deme model studied in [20].

Throughout the paper, we focus on the weak selection scenario in which the selection intensity  $s$  is small, that is,  $s = o(1)$ .

### 3 Fixation Coefficient

For  $i = 0, \dots, n - 1$ , let  $X_i(t)$  denote the frequency of  $A$  in deme  $i$  at time  $t$  and define:

$$\mathbf{X}(t) := (X_0(t), \dots, X_{n-1}(t)).$$

Since a single mutant  $A$  is introduced into the continent at time  $t = 0$ , it follows that  $\mathbf{X}(0) = \mathbf{x}_0$ , where:

$$\mathbf{x}_0 := (1/N_0, 0, \dots, 0).$$

We are interested in  $u(s)$ , the fixation probability of a single mutant  $A$  introduced at time  $t = 0$  into the continent in a population of  $B$  individuals when selection intensity is  $s$ . More specifically, in the case of weak selection, we consider the first-order development:

$$u(s) = u(0) + s u'(0) + o(s).$$

The term  $u'(0)$ , referred to as the fixation coefficient, is calculated using an adaptation of a method introduced by Rousset [43] and ascertained in [26]. In the case of a panmictic population [21, 22], it allows to calculate the fixation coefficient in terms of expected coalescence times, under neutrality, that is when  $s = 0$ , of samples of individuals. This method has been applied to the case of exchangeable selection models extending the neutral [6] model in a finite well-mixed population [26]. It has also been used in frequency-dependent selection models in finite structured populations in the case of an asymmetric two-deme structure [20] and in the case of Wright’s island structure [53] with a finite number of demes of finite sizes [19] in the limit of large deme sizes [16, 17] and in the limit of a large number of demes [24]. It has also been adapted to the case of a frequency-dependent viability and fertility selection model with a finite population with a fixed age-structure in the limit of a large population size [46]. Here, we adapt this method to the CI model.

Let  $\mathbb{E}_0$  (resp.  $\mathbb{P}_0$ ) denote the expectation (resp. probability) in the case of neutrality and let  $\mathbb{E}$  (resp.  $\mathbb{P}$ ) denote the expectation (resp. probability), in the case of an unspecified selection intensity  $s$ . Let  $\mathbf{M}$  be the matrix of the backward migration probabilities of this CI model:

$$\mathbf{M} = \begin{bmatrix} 1 - m_0 & m_0/(n - 1) & m_0/(n - 1) & \dots & m_0/(n - 1) & m_0/(n - 1) & m_0/(n - 1) \\ m_1 & 1 - m_1 & 0 & \dots & 0 & 0 & 0 \\ m_1 & 0 & 1 - m_1 & \dots & 0 & 0 & 0 \\ m_1 & 0 & 0 & 1 - m_1 & 0 & \dots & 0 \\ \vdots & & & & & & \vdots \\ m_1 & 0 & \dots & & 0 & 1 - m_1 & 0 \\ m_1 & 0 & \dots & & 0 & 0 & 1 - m_1 \end{bmatrix}.$$

The stationary distribution  $\mathbf{u} = (u_0, \dots, u_{n-1})$  of  $\mathbf{M}$  is defined by:

$$[u_0, \dots, u_{n-1}] \mathbf{M} = [u_0, \dots, u_{n-1}] \tag{6}$$

with  $u_i \geq 0$  and  $\sum_{i=0}^{n-1} u_i = 1$ . We can easily check that:

$$u_0 = \frac{m_1}{m_1 + m_0} \quad \text{and} \quad u_1 = u_2 = \dots = u_{n-1} = \frac{m_0}{(m_0 + m_1)(n - 1)}.$$

**Proposition 1** *The fixation coefficient for the CI model is given by:*

$$u'(0) = (\mathbf{p}_A - \mathbf{p}_B) \cdot \kappa_\lambda W(\mathbf{p}_A - \mathbf{p}_B) + (\mathbf{p}_A - \mathbf{p}_B) \cdot \kappa_\delta W \mathbf{p}_B, \tag{7}$$

with

$$\begin{aligned} \kappa_\lambda &:= u_0 \sum_{t \geq 0} \lambda_0(\mathbf{m}_0, \mathbf{X}(t)) + (1 - u_0) \sum_{t \geq 0} \lambda_1(\mathbf{m}_1, \mathbf{X}(t)), \\ \kappa_\delta &:= u_0 \sum_{t \geq 0} \delta_0(\mathbf{m}_0, \mathbf{X}(t)) + (1 - u_0) \sum_{t \geq 0} \delta_1(\mathbf{m}_1, \mathbf{X}(t)), \end{aligned}$$

where  $\lambda_0(\mathbf{m}_0, \mathbf{X}(t))$ ,  $\lambda_1(\mathbf{m}_1, \mathbf{X}(t))$ ,  $\delta_0(\mathbf{m}_0, \mathbf{X}(t))$ , and  $\delta_1(\mathbf{m}_1, \mathbf{X}(t))$  can be explicitly written in terms of the total number  $n$  of demes, migration probabilities  $m_0, m_1$  and coefficients  $\mathbb{E}_0[X_i(t)X_j(t)(1 - X_k(t))]$  and  $\mathbb{E}_0[X_i(t)(1 - X_j(t))]$ , with  $i, j, k \in \{0, \dots, 3\}$  according to Eqs. (A.3)–(A.4) in Appendix A.

The proof is given in Appendix A.

From Proposition 1, it follows that the calculation of coefficient  $u'(0)$  requires the calculation of:

$$\sum_{t \geq 0} \mathbb{E}_0 \left( X_i(t) X_j(t) (1 - X_k(t)) \right) \quad \text{and} \quad \sum_{t \geq 0} \mathbb{E}_0 \left( X_i(t) (1 - X_j(t)) \right),$$

for  $i, j, k \in \{0, 1, 2, 3\}$ .

In order to calculate those expressions, we shall first introduce an ancestral process,  $(\sigma(t))_{t \geq 0}$ . For  $t \geq 0$ ,  $\sigma(t)$  will describe the locations of the ancestors of three individuals, labeled 1, 2 and 3,  $t$  generations back, by accounting for the number of distinct ancestors they have (describing whether they have three distinct ancestors, two distinct ancestors, in which case whether one is common to individuals 1 and 2, 2 and 3 or 1 and 3, or just a single common ancestor) and by telling whether these ancestors live on the continent or on an island, and in the case where at least two of these ancestors live on an island, whether these islands differ or not. We will partition the state space,  $S$ , of this process into 5 ordered subsets as follows:

$$S_{1,2,3} = (000, 001, 010, 100, 011, 101, 110, 111, 012, 102, 120, 123, 112, 121, 122),$$

$$S_{12,3} = (00, 01, 10, 11, 12),$$

$$S_{13,2} = (00, 01, 10, 11, 12),$$

$$S_{23,1} = (00, 01, 10, 11, 12),$$

$$S_{123} = (0, 1).$$

The subset  $S_{1,2,3}$  is for the case when the ancestors of individuals 1, 2, 3 are all different. Subsets  $S_{12,3}$ ,  $S_{13,2}$  and  $S_{23,1}$  are for the case when the number of distinct ancestors is reduced to two: subset  $S_{12,3}$  means that individuals 1, 2 have a common ancestor which is different from the ancestor of individual 3; subset  $S_{13,2}$  means that individuals 1, 3 have a common ancestor which is different from the ancestor of individual 2; subset  $S_{23,1}$  means that individuals 2, 3 have a common ancestor which is different from the ancestor of individual 1. And subset  $S_{123}$  is for the case when individuals 1, 2 and 3 have a single common ancestor left.

Any element in  $S_{1,2,3}$  is represented by a 3-digits string as follows:

First digit:

- we assign 0 (resp. 1), as the first digit if the ancestor of individual 1 lives on the continent (resp. on an island).

Second digit:

- if the first digit is 0, then again, we assign 0 (resp. 1) as the second digit if the ancestor of individual 2 lives on the continent (resp. on an island).
- If the first digit is 1, the second digit will be assigned 0 (resp. 1; 2), as the second digit if the ancestor of individual 2 lives on the continent (resp. on the same island as the one occupied by the ancestor of individual 1; on a different island than the one occupied by the ancestor of individual 1).

Third digit:

- if the first two digits are 00, then we assign 0 (resp. 1) as the third digit if the ancestor of individual 3 lives on the continent (resp. on an island).
- If the first two digits are 01, 10 or 11, which means that the total number of islands occupied by the ancestors of individuals 1 and 2 is reduced to one, we assign 0, 1 or 2, respectively, as the third digit if the ancestor of individual 3 lives on the continent, on the same island as the one already occupied by the ancestors of individual 1 and 2 (whether it is occupied by one or the other or by both of them), or on a different island than the one already occupied by the ancestors of individual 1 and 2, respectively.
- Finally, if the first two digits are 12, which means that the ancestors of individuals 1 and 2 live on two different islands, we assign 0, 1, 2, or 3, respectively, as the third digit if



the ancestor of individual 3 lives on the continent, on the same island as the one already occupied by the ancestor of individual 1, on the same island as the one already occupied by the ancestor of individual 2, or on a different island than the two ones already occupied by the ancestors of individual 1 and 2, respectively.

The element 102 in  $S_{1,2,3}$ , for instance, means that the ancestors of individuals 1, 2, 3 are all different, and the ancestor of individual 2 is on the continent, while the ancestors of individual 1 and 2 are on two different islands.

Similarly, elements in  $S_{12,3}$  (resp.  $S_{13,2}$ ;  $S_{23,1}$ ) are represented by 2-digits strings. They are assigned the same way the first two digits of elements of  $S_{1,2,3}$  are assigned, with the first digit coding for the location of the ancestor common to individual 1 and 2 (resp. 1 and 3; 2 and 3), and the second digit coding for the location of the ancestor of individual 3 (resp. 2; 1).

For example, element 01 in  $S_{12,3}$  means that individuals 1, 2 have a common ancestor in the continent different from the ancestor of individual 3, whose ancestor is on an island.

Finally, subset  $S_{123}$  has two elements 0, and 1. Element 0 (resp. 1) means that individuals 1, 2, 3 have a common ancestor, and this ancestor lives on the continent (resp. on an island).

For  $t \geq 0$ , let  $\sigma(t)$  denote the state in  $S$  the ancestors of three individuals are in,  $t$  generations back.  $(\sigma(t))_{t \geq 0}$  is a Markov chain and its transition matrix takes a block form with respect to the above ordered subsets in the corresponding order. Without loss of generality, let:

$$K = \begin{bmatrix} F & Q & W & J & R_1 \\ 0 & L & 0 & 0 & R \\ 0 & 0 & L & 0 & R \\ 0 & 0 & 0 & L & R \\ 0 & 0 & 0 & 0 & R_0 \end{bmatrix} \tag{8}$$

be this transition matrix under neutrality. The submatrices  $F$ ,  $Q$ ,  $L$  and  $R$  are given in Appendix D. Note that the states in  $S_{123}$  are absorbing for this chain, while all other states are transient. The Perron–Frobenius theory for non-negative matrices ascertains in particular that the eigenvalues of  $F$  and  $L$  are all less than 1 in modulus.

**Proposition 2** *Expression  $\sum_{t \geq 0} \mathbb{E}_0(X_0(t)^2 (1 - X_0(t)))$  can be written in terms of the continent size,  $N_0$ , and submatrices  $F$ ,  $Q$ ,  $L$ , as follows :*

$$\begin{aligned} & \sum_{t \geq 0} \mathbb{E}_0(X_0(t)^2 (1 - X_0(t))) \\ &= \left(1 - \frac{1}{N_0}\right) \left(1 - \frac{2}{N_0}\right) \left((I - F)^{-1} Q (I - L)^{-1} u\right)_{000} \\ &+ \frac{1}{N_0} \left(1 - \frac{1}{N_0}\right) \left((I - L)^{-1} u\right)_{00}, \end{aligned}$$

where  $u$  is the column vector  $(1/N_0, 1/N_0, 0, 0, 0)$  and index 000, for example, refers to the vector’s component that corresponds to the chain starting in state 000. Similar formulae are obtained for  $\sum_{t \geq 0} \mathbb{E}_0(X_i(t) X_j(t) (1 - X_k(t)))$  and  $\sum_{t \geq 0} \mathbb{E}_0(X_i(t) (1 - X_j(t)))$ , for  $i, j, k \in \{0, \dots, 3\}$  [see Eq. (A.8)].

The proof, which makes use of the ancestral process  $\sigma(t)$  and its transition matrix  $K$ , is given in Appendix B

### 4 Fixation Coefficient in the Limit Case of the Structured-Coalescent Scenario and Conservative Migration

In this section, we focus on the limit case of the structured coalescent assumptions [9, 10, 33, 52], in which the total population size,  $cN$ , is assumed to be large, with deme sizes  $N_1 = \dots = N_{n-1} = c_1N$  and  $N_0 = c_0N$  of order  $N$  and  $c = c_0 + (n - 1)c_1$ , and backward migration rates of order inversely proportional to  $N$ ,  $m_{01} = M_0/(2N(n - 1))$ ,  $m_0 = M_0/2N$  and  $m_1 = \dots = m_{n-1} = M_1/2N$ , so that  $c_0, c_1, c, M_0$  and  $M_1$  are all of order 1. Throughout the rest of this article, it will be assumed that  $s \ll 1/(cN)$ .

Using these notations, the stationary distribution  $(u_0, \dots, u_{n-1})$  of migration matrix  $\mathbf{M}$  [see (6)] can be written as follows:

$$u_0 = \frac{M_1}{M_0 + M_1}$$

$$u_i = \frac{M_0}{(M_0 + M_1)(n - 1)} = \frac{(1 - u_0)}{n - 1}, \quad i = 1, \dots, n - 1.$$

In the remainder of this article, we restrict to the case of conservative migration, which takes place when the relative size of each deme is maintained after migration (which means that the deme sizes remain constant, or, equivalently, that the emigration exactly balances the immigration for every deme). Thus, in this model, this requires that:

$$c_0 M_0 = c_1 (n - 1) M_1.$$

Let  $P = c_0/c$  denote the proportion of the total population that lives in the continent, and let  $M$  be the “migration rate” defined as:

$$M := c_1 M_1 = \frac{c_0 M_0}{n - 1}.$$

Consequently, under the conservative migration assumptions, we have:

$$M_0 = \frac{(n - 1) M}{c P}, \quad M_1 = \frac{M (n - 1)}{c (1 - P)},$$

$$c_0 = c P, \quad c_1 = \frac{c (1 - P)}{n - 1}, \quad \text{and } u_0 = P.$$

Let  $C_0$  denote the constant term of  $u'(0)$  as  $N$  goes to infinity so that:

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

By (7), (A.3) and (A.4), we find that  $C_0$  can be written as:

$$C_0 = (u_0 \gamma_0 + (1 - u_0) \gamma_1) (\mathbf{p}_A - \mathbf{p}_B) \cdot W (\mathbf{p}_A - \mathbf{p}_B) + (u_0 \delta_0 + (1 - u_0) \delta_1) (\mathbf{p}_A - \mathbf{p}_B) \cdot W \mathbf{p}_B,$$

where:

$$\gamma_i := \lim_{N \rightarrow +\infty} \sum_{t \geq 0} \mathbb{E}_0 \left( X_i^2(t) (1 - X_i(t)) \right),$$

$$\delta_i := \lim_{N \rightarrow +\infty} \sum_{t \geq 0} \mathbb{E}_0 \left( X_i(t) (1 - X_i(t)) \right) \tag{9}$$

for  $i = 0, 1$ , since all the other terms in (7) are multiplied by migration rates of order  $1/N$  and are thus, of order  $1/N$  of smaller.

From (A.8a) and (A.8b), we obtain:

$$\begin{aligned} \gamma_i &= \lim_{N \rightarrow +\infty} \left(1 - \frac{1}{N_i}\right) \left(1 - \frac{2}{N_i}\right) \left((I - F)^{-1} Q (I - L)^{-1} u\right)_{iii} \\ &\quad + \frac{1}{N_i} \left(1 - \frac{1}{N_i}\right) \left((I - L)^{-1} u\right)_{ii}, \quad i = 0, 1, \end{aligned}$$

and from (A.8c) and (A.8d):

$$\delta_i = \lim_{N \rightarrow +\infty} \left(1 - \frac{1}{N_i}\right) \left((I - L)^{-1} u\right)_{ii}, \quad i = 0, 1.$$

The calculation of these limits as functions of the population parameters  $M$ ,  $n$  and  $P$ , which cannot be done by hand because of the size of the matrices, are performed using a symbolic computing software like `Maple` and are given by (A.9)–(A.11) in Appendix. We find that:

$$u_0 \delta_0 + (1 - u_0) \delta_1 = 1,$$

and we get the following result.

**Proposition 3** *Consider the CI model under the structured coalescent assumptions and conservative migration described in this section. Ignoring terms of order  $1/N$  or higher, the fixation coefficient  $u'(0)$  can be approximated by:*

$$C_0 = (u_0 \gamma_0 + (1 - u_0) \gamma_1) (\mathbf{p}_A - \mathbf{p}_B) \cdot W (\mathbf{p}_A - \mathbf{p}_B) + (\mathbf{p}_A - \mathbf{p}_B) \cdot W \mathbf{p}_B \quad (10)$$

where  $\gamma_i$  is given by (9).

In (10), we define explicitly:

$$\Lambda(M, n, P) := u_0 \gamma_0 + (1 - u_0) \gamma_1 \quad (11)$$

as a function of the migration rate,  $M$ , the total number of demes,  $n$ , and the proportion of the total population living on the continent,  $P$ . An explicit expression, derived using `Maple`, is given by (A.12) in Appendix. As we will see in Sect. 6, coefficient  $\Lambda(M, n, P)$  will show up in the generalization of the one-third law that holds for the CI model.

Note that when  $n = 2$ , using the proper parameter rescalings, the values of  $C_0$  and  $\Lambda$  are already known since, in this case, the model corresponds to the asymmetric two-deme linear game model [20]. Moreover, still in the case  $n = 2$ , assuming identical deme sizes ( $P = 1/2$ ), Proposition 3 tells us that  $C_0 = \left(\frac{1}{3} + \frac{1}{12(M+1)}\right) (\mathbf{p}_A - \mathbf{p}_B) \cdot W (\mathbf{p}_A - \mathbf{p}_B) + (\mathbf{p}_A - \mathbf{p}_B) \cdot W \mathbf{p}_B$  in accordance with the first-order approximation of the fixation probability of a single mutant in a (symmetric) finite island linear game model with 2 demes [19, 20].

## 5 Conditions Against Replacement in a Finite Continental Island Model Population

In the context of a finite population, Nowak et al. [38] specified a natural definition of an advantageous mutation: selection is said to favor  $A$  replacing  $B$  if the fixation probability of a single mutant  $A$  is greater than its value in the absence of selection, that is,  $u(s) > u(0) = u_0/N_0$ , where  $u_0$  denotes the first coordinate of the stationary distribution of migration matrix  $\mathbf{M}$  [see (6)]; whereas it is said to oppose  $A$  replacing  $B$ , if  $u(s) < u_0/N_0$ .

From (9), we see that  $\Lambda(M, n, P) \geq 0$ , then it follows from (10) that provided selection is weak enough, selection opposes  $A$  replacing  $B$  if and only if:

$$C_0 = \Lambda(M, n, P) (\mathbf{p}_A - \mathbf{p}_B) \cdot W (\mathbf{p}_A - \mathbf{p}_B) + (\mathbf{p}_A - \mathbf{p}_B) \cdot W \mathbf{p}_B < 0. \quad (12)$$

In the case when  $\mathbf{p}_A$  is different but close enough to  $\mathbf{p}_B$ , (12) is equivalent to:

$$(\mathbf{p}_A - \mathbf{p}_B) \cdot W \mathbf{p}_B < 0, \quad (13a)$$

or:

$$(\mathbf{p}_A - \mathbf{p}_B) \cdot W \mathbf{p}_B = 0, \quad \text{and} \quad (\mathbf{p}_A - \mathbf{p}_B) \cdot W (\mathbf{p}_A - \mathbf{p}_B) < 0. \quad (13b)$$

**Remark 1** (*Links with ESS*) For a fixed  $\mathbf{p}_B$ , suppose there exists a neighborhood of  $\mathbf{p}_B$  such that condition (13) holds for every strategy  $\mathbf{p}_A \neq \mathbf{p}_B$  in that neighborhood. Then, for any strategy  $\mathbf{p}_A \neq \mathbf{p}_B$  (not necessarily in that neighborhood), there exist  $\epsilon > 0$ , provided it is small enough, such that  $\mathbf{p}_{A'}$  defined as  $\mathbf{p}_{A'} = \mathbf{p}_B + \epsilon(\mathbf{p}_A - \mathbf{p}_B)$  is also a strategy which, in addition, falls in that particular neighborhood. Thus, (13) is met for  $\mathbf{p}_{A'}$ . It follows that since  $(\mathbf{p}_A - \mathbf{p}_B) = (\mathbf{p}_{A'} - \mathbf{p}_B)/\epsilon$  with  $\epsilon > 0$ , (13) is also met for  $\mathbf{p}_A$ . As a consequence, for a fixed  $\mathbf{p}_B$ , if condition (13) holds for every  $\mathbf{p}_A$  close enough but different from  $\mathbf{p}_B$ , then condition (13) will be met for every  $\mathbf{p}_A \neq \mathbf{p}_B$ ; this implies that  $\mathbf{p}_B$  is an evolutionary stable strategy (ESS) for the game matrix  $W$  [29, 31], which means that when almost fixed in the population,  $\mathbf{p}_B$  cannot be invaded by any alternative mutant strategy, when in a low enough frequency, in the context of an infinite population. Conversely, suppose that  $\mathbf{p}_B$  is an ESS, that is (13) is met for every  $\mathbf{p}_A \neq \mathbf{p}_B$ . In this case, we do not necessarily have that  $C_0 < 0$ , but:

1. if  $\mathbf{p}_B$  has all positive components, then  $C_0 < 0$  for all  $\mathbf{p}_A \neq \mathbf{p}_B$ ;
2. if  $\mathbf{p}_B$  has some null components, then  $C_0 < 0$  either for all  $\mathbf{p}_A \neq \mathbf{p}_B$  that share the same null components as  $\mathbf{p}_B$  or for all  $\mathbf{p}_A \neq \mathbf{p}_B$  close enough to  $\mathbf{p}_B$ .

Indeed, if  $\mathbf{p}_B$  has all positive components, then we have an equality in (13a) for all  $\mathbf{p}_A \neq \mathbf{p}_B$ . Suppose it were not the case, then there would exist a strategy  $\mathbf{p}_A \neq \mathbf{p}_B$  for which  $(\mathbf{p}_A - \mathbf{p}_B) \cdot W \mathbf{p}_B < 0$ . Since  $\mathbf{p}_B$  has all positive components, provided we choose  $\epsilon > 0$  small enough, the vector whose components sum to one defined as  $\mathbf{p}_{A'} = \mathbf{p}_B - \epsilon(\mathbf{p}_A - \mathbf{p}_B)$  will have all non-negative components and hence will also be a strategy. Then,  $(\mathbf{p}_{A'} - \mathbf{p}_B) \cdot W \mathbf{p}_B = -\epsilon(\mathbf{p}_A - \mathbf{p}_B) \cdot W \mathbf{p}_B > 0$ , which contradicts the fact that every strategy must meet condition (13). As a consequence, if  $\mathbf{p}_B$  has all positive components, then we have an equality in (13a) for all  $\mathbf{p}_A \neq \mathbf{p}_B$ , which implies (13b) and  $C_0 < 0$  for all  $\mathbf{p}_A \neq \mathbf{p}_B$ . Whereas, if  $\mathbf{p}_B$  has some null components: for all  $\mathbf{p}_A \neq \mathbf{p}_B$  that share the same null components as  $\mathbf{p}_B$ , using a dimension reduction in the space of strategies, we are brought back to the previous case and then  $C_0 < 0$ ; while a strict inequality in (13a) can hold for some  $\mathbf{p}_A \neq \mathbf{p}_B$  which has at least one positive component corresponding to a null component of  $\mathbf{p}_B$ , therefore, in case where  $(\mathbf{p}_A - \mathbf{p}_B) \cdot W (\mathbf{p}_A - \mathbf{p}_B)$  is positive,  $\mathbf{p}_A$  has to be close enough to  $\mathbf{p}_B$  to make sure that  $C_0 < 0$ .

In other words, as long as selection is weak enough, a resident strategy  $\mathbf{p}_B$  is selectively favored against replacement

- by any alternative mutant strategy  $p_A$ , if  $\mathbf{p}_B$  makes use of all pure strategies and satisfies (13);
- (i) by any mutant strategy  $\mathbf{p}_A$  using the same subset of pure strategies as  $\mathbf{p}_B$ , and (ii) by any mutant strategy  $\mathbf{p}_A$  close enough to  $\mathbf{p}_B$  using some new pure strategies, if  $\mathbf{p}_B$  satisfies (13) and uses a strict subset of pure strategies.

## 6 Extension of the One-Third Law

Suppose the two strategies  $\mathbf{p}_A$  and  $\mathbf{p}_B$  associated with type  $A$  and  $B$ , respectively, are pure strategies of the form  $\mathbf{p}_A = (1, 0)$  and  $\mathbf{p}_B = (0, 1)$ , respectively, with respect to the  $2 \times 2$  game matrix

$$W = \begin{pmatrix} a & b \\ c & d \end{pmatrix},$$

and assume  $W$  is a coordination game, i.e.,  $a > c$  and  $d > b$ , which means that  $\mathbf{p}_A$  and  $\mathbf{p}_B$  are best replies to themselves for  $W$  (i.e., they are strict Nash equilibria). The deterministic replicator equation in an infinite panmictic population [11, 48] with game matrix  $W$  implies that there exists a unique unstable equilibrium at a frequency of  $A$ , which is equal to:

$$x^* := \frac{d - b}{a - c - b + d}. \tag{14}$$

In a finite population, Nowak et al. [38] proved in the context of a frequency-dependent Moran process that weak selection favors a single type  $A$  mutant replacing a population of type  $B$  individuals in the limit of a large finite well-mixed population, if  $x^*$  is smaller than  $1/3$ . In other words, for a coordination game, provided selection is weak enough and the population size is large enough, the fixation probability of a single mutant strategy is larger than under neutrality if the basin of attraction of the wild type strategy in the traditional replicator dynamics is less than one-third.

In this section, in the context of a CI model with a total number of  $n$  demes in which both strategies are best replies to themselves with respect to the game matrix, we investigate conditions under which the replacement of a resident strategy by a mutant strategy is selectively favored. In particular, we find that in this case, the one-third law [38] can be generalized as follows.

**Proposition 4** *When the population is finite, selection, provided it is weak enough, will favor  $A$  replacing  $B$  if:*

$$x^* < \Lambda(M, n, P). \tag{15}$$

This stems from the fact that selection, as long as it is weak enough, will favor  $A$  replacing  $B$  if inequality (12) is reversed, which is equivalent to (15). This result extends the one-third law to the case of a continental island linear game model with  $n$  demes. In the special case  $n = 2$ , (15) reduces to the extended one-third law for an asymmetric two-deme linear game model [20]. Inequality (15) means that if it is met, then selection favors a single mutant  $A$  taking over the whole population.

In the remainder of this section, we derive analytical results for the symmetric CI model, i.e., a CI model in which the deme sizes are equal ( $P = 1/n$ ) and we present numerical results in the general case of an asymmetric CI model (a CI model with  $P \neq 1/n$ ).

### 6.1 Analytical Comparisons in the Symmetric Case

Let us consider the symmetric CI model, sCI in short, as the particular case of a symmetric population structure with identical deme sizes, i.e.:

$$P = 1/n$$

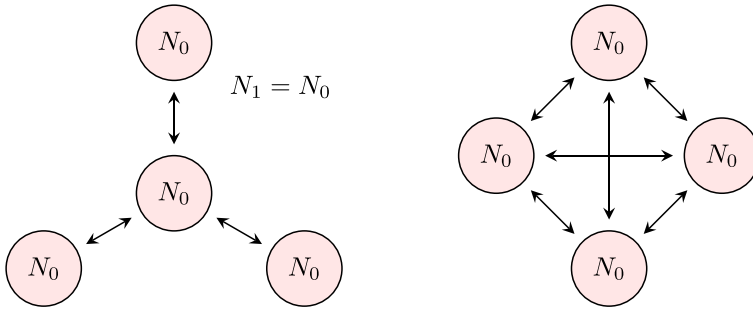


Fig. 2 sCI model (left) vs WI model (right) for  $n = 4$

which also means that  $N_0 = N_1$ , i.e., the size  $N_0$  of the continent is the same as the size  $N_1$  of each island.

In this case, for any island  $i \in \{1, \dots, n - 1\}$ , the backward migration probabilities  $m_{0i}$  and  $m_{i0}$  are identical and satisfy  $m_{0i} = m_{i0} = \frac{nM}{2cN}$ .

In this context, combining (11) with (A.12) leads to the following extended one-third law for an sCI model:

$$x^* < \Lambda_{\text{sCI}}(M, n) := \Lambda(M, n, 1/n) = \frac{1}{3} + \frac{(n - 1)}{3n^2} \frac{f(M, n)}{g(M, n)}, \tag{16}$$

where:

$$\begin{aligned} f(M, n) &:= n^2(n + 2)(n - 1)M^3 + n(5n^2 + 4n + 4)M^2 \\ &\quad + (10n^2 + 8n + 8)M + 8n, \\ g(M, n) &:= n^2(n + 2)M^4 + 2(n^3 + 5n^2 + 4n + 4)M^3 \\ &\quad + 4(n + 2)(3n + 2)M^2 + 8(4 + 3n)M + 16. \end{aligned}$$

Since  $\Lambda_{\text{sCI}} \geq \frac{1}{3}$ , the modified one-third law for the sCI model is always less stringent than the one-third law.

Expression (16) is known when  $n = 2$ , where  $\Lambda_{\text{sCI}} = \frac{1}{3} + \frac{1}{12(M+1)}$  [19, 20]. It is also known when  $n = 1$ , which corresponds to a panmictic population, where  $\Lambda_{\text{sCI}} = 1/3$  [13, 21].

We now compare the sCI model to the Wright’s island linear game model, WI model in short, given in Ladret and Lessard [19] (see Fig. 2): the sCI model will be considered to outperform the WI model if the condition for selection to favor a mutant  $A$  taking over the population of  $B$  is less stringent in the sCI model than in the WI model, i.e.,  $\Lambda_{\text{sCI}} > \Lambda_{\text{WI}}$ .

The two models share the same game matrix  $W$  and the same geographic structure ( $n$  demes of equal sizes equal to  $cN/n$ ). They only differ in the migration scenario, which, in the latter model, occurs according to a Wright’s island scenario. More precisely, in the WI model:  $m_{ij, \text{WI}} = m_{\text{WI}}/(n - 1)$  where  $m_{\text{WI}}$  denotes the probability that an individual from any given deme emigrated from a different deme in the previous generation and  $m_{ij, \text{WI}}$  denotes the probability that an individual from deme  $i$  emigrated from deme  $j \neq i$ , in the previous generation.

Additionally, we suppose that the WI model and the sCI model have the same average expected number of migrants per generation after population regulation. Since in the sCI model this number is  $(n - 1)M$ , this implies that  $m_{\text{WI}} = (n - 1)M/(Nc)$ . In the context of

the WI model, the condition for selection to favor a mutant strategy  $A$  replacing a resident strategy  $B$  takes the form:

$$x^* < \Lambda_{\text{WI}}(M, n), \tag{17}$$

where:

$$\Lambda_{\text{WI}}(M, n) := \frac{1}{3} + \frac{1}{6(M+1)} \left(1 - \frac{1}{n}\right),$$

as shown in [19] (after a suitable rescaling of  $M$ ). From (16) and (17), we find that:

$$\Lambda_{\text{sCI}}(M, n) - \Lambda_{\text{WI}}(M, n) = (n-1)(n-2) \left( n - \frac{1 + \sqrt{1 + 4M^2}}{M^2} \right) \gamma(M, n), \tag{18}$$

where:

$$\gamma(M, n) = \frac{M^3 (2M + 2 + Mn) \left( n + \frac{\sqrt{1+4M^2}-1}{M^2} \right)}{6n^2 (M+1) \psi(M, n)},$$

and

$$\begin{aligned} \psi(M, n) = & 2M^3 n^3 + M^4 n^3 + 10M^3 n^2 + 12M^2 n^2 + 2M^4 n^2 \\ & + 24Mn + 32M^2 n + 8M^3 n + 16 + 16M^2 + 32M + 8M^3. \end{aligned}$$

Since  $\gamma(M, n) \geq 0$ , from (18),  $\Lambda_{\text{sCI}}(M, n) - \Lambda_{\text{WI}}(M, n)$  has the same sign as  $(n-1)(n-2) \left( n - \frac{1 + \sqrt{1 + 4M^2}}{M^2} \right)$ , hence:

- (i) When  $n = 1$  or  $2$ ,  $\Lambda_{\text{sCI}}(M, n) = \Lambda_{\text{WI}}(M, n)$ .
- (ii) When  $n \geq 3$ , let  $n_0(M) := \frac{1 + \sqrt{1 + 4M^2}}{M^2}$ , then for any given  $M > 0$ , we have:

$$\begin{cases} \Lambda_{\text{sCI}}(M, n) > \Lambda_{\text{WI}}(M, n) \iff n > n_0(M), \\ \Lambda_{\text{sCI}}(M, n) = \Lambda_{\text{WI}}(M, n) \iff n = n_0(M). \end{cases}$$

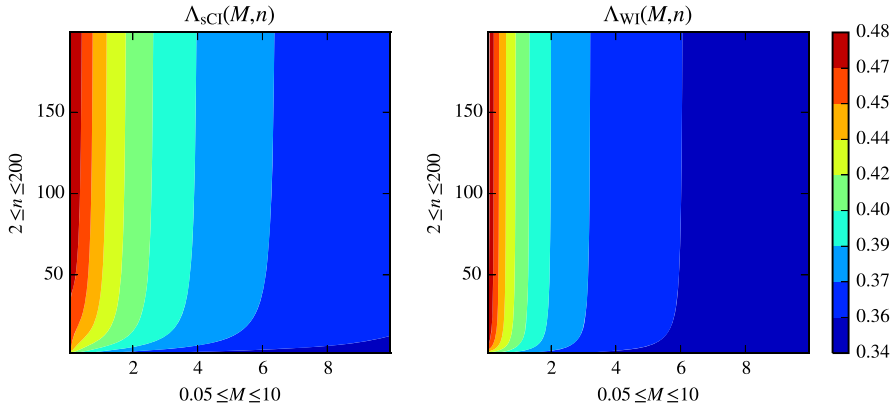
Note that condition  $n > n_0(M)$  (resp.  $n = n_0(M)$ ) can be explicitly rewritten  $M > n_0^{-1}(n)$  (resp.  $M = n_0^{-1}(n)$ ) where  $n_0^{-1}(n) = \sqrt{2n + 4}/n$ .

The case (i) is not surprising, since in both cases, the sCI and WI model coincide: when  $n = 1$ , they correspond to a linear game in a panmictic population and  $\Lambda_{\text{sCI}} = \Lambda_{\text{WI}} = \frac{1}{3}$  [13, 21, 26]; while when  $n = 2$ , the CI model with two demes and the WI model with two demes are identical and  $\Lambda_{\text{sCI}} = \Lambda_{\text{WI}} = \frac{1}{3} + \frac{1}{12(M+1)}$  [19, 20].

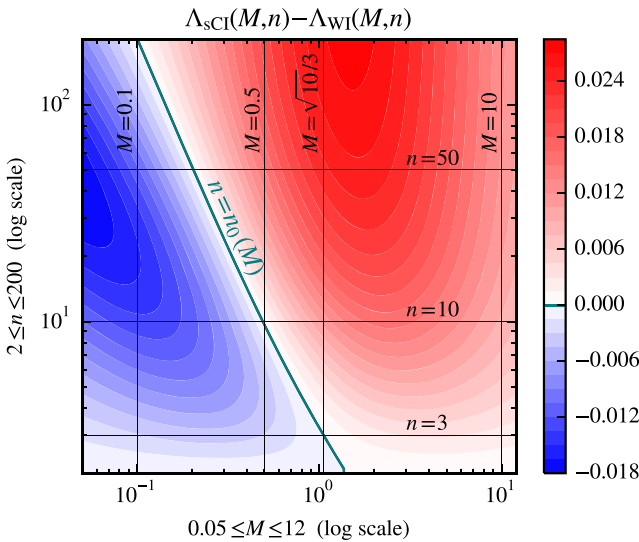
Note that in case (ii), when  $M > \sqrt{10}/3 \simeq 1.054$ :  $\Lambda_{\text{sCI}} > \Lambda_{\text{WI}}$  for any  $n \geq 3$ .

For example, when  $M = 1$ ,  $n_0(M) \simeq 3.236$ , thus  $\Lambda_{\text{sCI}} > \Lambda_{\text{WI}}$  as soon as  $n \geq 4$ . When  $M = 0.5$ ,  $n_0(M) \simeq 9.657$ , thus  $\Lambda_{\text{sCI}} > \Lambda_{\text{WI}}$  provided  $n \geq 10$ . Similarly, when  $M = 0.1$ ,  $n_0(M) \simeq 201.98$  and  $\Lambda_{\text{sCI}} > \Lambda_{\text{WI}}$  provided  $n \geq 202$ . On the other hand, when  $n = 3$ ,  $\Lambda_{\text{sCI}} > \Lambda_{\text{WI}}$ , as soon as  $M > n_0^{-1}(n) \simeq 1.0541$ . For  $n = 10$  (resp.  $n = 100$ ),  $\Lambda_{\text{sCI}} > \Lambda_{\text{WI}}$  provided  $M > n_0^{-1}(n) \simeq 0.4899$  (resp.  $M > n_0^{-1}(n) \simeq 0.1428$ ).

These results are illustrated in Figs. 3, 4. Figure 3 represents numerical evaluations of the threshold frequencies  $\Lambda_{\text{sCI}}$  (left figure) and  $\Lambda_{\text{WI}}$  (right figure), as functions of the migration rate,  $M$ , and the number of demes,  $n$ . Whereas, Fig. 4 plots the effect of parameters  $M$  and  $n$  on their difference,  $\Lambda_{\text{sCI}} - \Lambda_{\text{WI}}$ . Figure 5 illustrates how  $\Lambda_{\text{sCI}} - \Lambda_{\text{WI}}$  changes with the migration rate,  $M$ , for different fixed values of the number of demes  $n$  (left figure) and how it changes with the number of demes,  $n$ , for four fixed values of  $M$  (right figure).



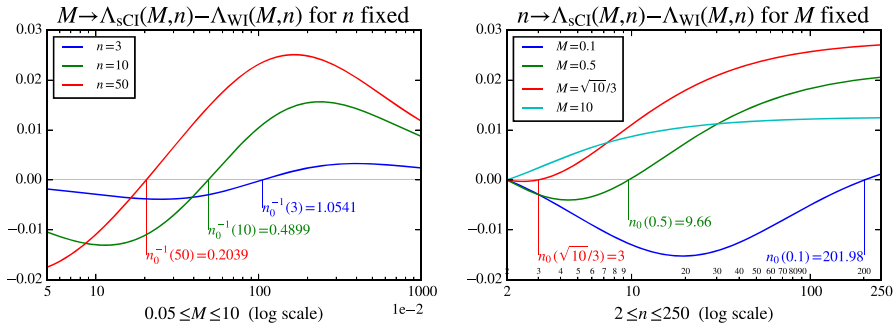
**Fig. 3** Threshold  $\Delta_{sCI}$  (left) and  $\Delta_{wI}$  (right) as functions of  $M$  and  $n$ .  $M$  ranges from 0.1 to 10 and  $n$  from 2 to 200



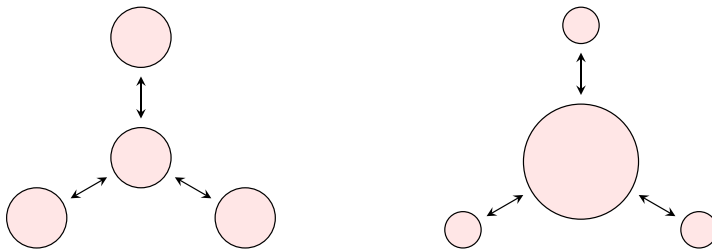
**Fig. 4** Effect of the number of demes,  $n$ , and the migration rate,  $M$ , on the difference  $\Delta_{sCI}(M, n) - \Delta_{wI}(M, n)$  (log-log plot). The green line is for the case when  $n = n_0(M) = (1 + \sqrt{1 + 4M^2})/M^2$ , at which  $\Delta_{sCI}(M, n) - \Delta_{wI}(M, n) = 0$ . When  $M = 0.1$  (resp.  $M = 0.5$ ;  $M = \sqrt{10/3}$ ) (vertical black lines), we find that  $n_0(0.1) \simeq 201.98$  (resp.  $n = n_0(0.5) \simeq 9.66$ ;  $n = n_0(\sqrt{10/3}) = 3$ ); whereas the horizontal black lines corresponding to  $n = 10$  (resp.  $n = 50$ ) cross the green line at  $M = n_0^{-1}(10) \simeq 0.4899$  (resp.  $M = n_0^{-1}(50) \simeq 0.2039$ )

As reminded earlier, in the context of the IPD with TFT versus AIID, the frequency  $x^*$  decreases to zero with the number of rounds [38, see, e.g.]. As a consequence, an sCI model with  $n$  demes and a fixed migration rate  $M$  greater than  $\sqrt{10/3}$  will require less rounds of the game than its WI model counterpart to ensure that cooperation fixes in the population with a selective advantage; whereas, in the case of a fixed migration rate  $M \leq \sqrt{10/3}$ , this will be the case provided the number of demes is large enough (namely,  $n > n_0(M) \geq 3$ ). On the other hand, if the number of demes  $n$  is fixed, an sCI model will require less rounds of the





**Fig. 5** *Left:* effect of the scaled migration rate,  $M$ , on the difference  $\Lambda_{sCI}(M, n) - \Lambda_{WI}(M, n)$  for different values of the number of demes,  $n$ :  $n = 3$  (blue),  $n = 10$  (green),  $n = 50$  (red). The vertical lines correspond to  $M = n_0^{-1}(n)$ . *Right:* effect of the number of demes,  $n$ , on the difference  $\Lambda_{sCI}(M, n) - \Lambda_{WI}(M, n)$  for different values of  $M$ :  $M = 0.1$  (blue),  $n = 0.5$  (green),  $M = \sqrt{10}/3$  (red) and  $M = 10$  (cyan). The vertical lines correspond to  $n = n_0(M)$  (Color figure online)



**Fig. 6** *Left:* sCI model with  $n = 4$ ,  $P = 1/4$ . *Right:* CI model with  $n = 4$ ,  $P \neq 1/4$

game than its WI model counterpart provided  $M$  is not too small (namely,  $M > n_0^{-1}(n)$ ), to ensure that selection favors cooperation taking over the whole population.

### 6.2 Numerical Comparisons in the General Case

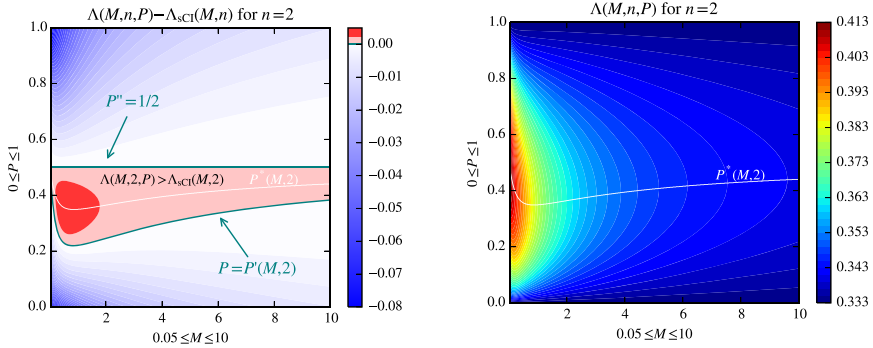
In this section, we compare the asymmetric CI model, in which the size  $N_0$  of the continent differs from the size  $N_1$  of the islands, that will be referred to as the *asymmetric model* (CI), to its symmetric (sCI) model counterpart (see Fig. 6). In other words, for all  $(M, n, P)$ , we compare the CI model with parameters  $(M, n, P \neq 1/n)$ , to the CI model with parameters  $(M, n, P = 1/N)$ , i.e., the sCI model with parameters  $(M, n)$ ; both models sharing the same game matrix  $W$  and the same total population size  $cN$ .

Here again, the two models are compared by comparing their respective threshold value:  $\Lambda(M, n, P)$  given by (11) for the CI model vs  $\Lambda_{sCI}(M, n)$  given by (16) for the sCI model. These threshold values are also compared to  $1/3$ , the threshold value for a panmictic population as given by the one-third law.

For  $M$  and  $n$  fixed, we are interested in determining:

$$\mathcal{P}_{M,n} := \{P \in [0, 1]; \Lambda(M, n, P) \geq \Lambda_{sCI}(M, n)\}$$

the set of  $P$  for which the condition for selection to favor a single mutant  $A$  taking over a population of  $B$  is less stringent in the CI model than in the sCI model. We are also interested



**Fig. 7** Case of  $n = 2$  demes. *Left:*  $(M, P) \mapsto \Lambda(M, 2, P) - \Lambda_{\text{sCI}}(M, 2)$ . The central pink zones correspond to the set  $\mathcal{P}_{M,P}$ . The upper and lower green curves correspond to the roots  $P' = P'(M, 2)$  and  $P'' = 1/2$  of  $\Lambda(M, 2, P) - \Lambda_{\text{sCI}}(M, 2) = 0$ . The central white curve shows  $M \rightarrow P^*(M, 2)$ . *Right:*  $(M, P) \mapsto \Lambda(M, 2, P)$

in determining the values of  $P$  at which the maximum of  $\Lambda(M, n, \cdot)$  is reached:

$$P^*(M, n) := \operatorname{argmax}_{0 \leq P \leq 1} \Lambda(M, n, P) \in \mathcal{P}_{M,n}.$$

**Case  $n = 2$**

In Fig. 7, we consider the case of two demes ( $n = 2$ ), already treated in Ladret and Lessard [20], and we plot  $\Lambda(M, 2, P) - \Lambda_{\text{sCI}}(M, 2)$  as a function of  $M$  and  $P$ . The numerical evaluations suggest that for any fixed value of  $M$  in the considered range, the following equation:

$$\Lambda(M, 2, P) - \Lambda_{\text{sCI}}(M, 2) = 0 \tag{19}$$

has exactly two roots  $P' = P'(M, 2)$  and  $P'' = \frac{1}{2}$ , for some  $0 \leq P'(M, 2) < 1/2$  and  $\mathcal{P}_{M,2} = [P', P'']$ ; moreover,  $P^*(M, 2)$  is unique and  $P^*(M, 2) \in (P', P'')$ . They also suggest, see Fig. 7 (right) and Figs. 12 and 13 (blue curve), that  $P \mapsto \Lambda(M, 2, P)$  increases from  $\frac{1}{3}$  until it reaches its maximum at  $P = P^*(M, 2)$ , and then decreases back to  $1/3$ .

**Case  $n \geq 3$**

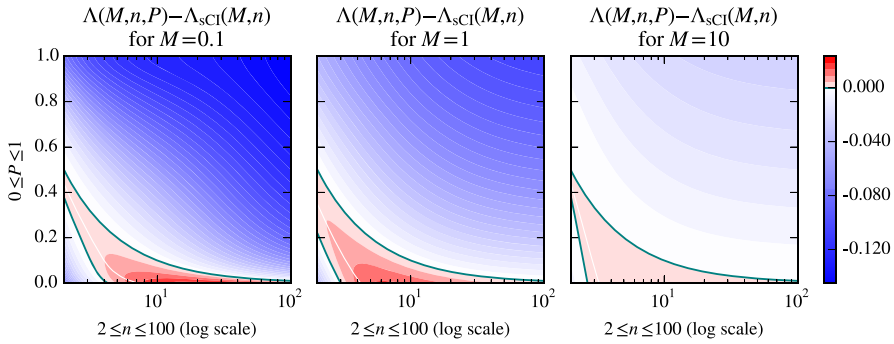
In Fig. 8, we consider  $(n, P) \mapsto \Lambda(M, n, P) - \Lambda_{\text{sCI}}(M, n)$  for fixed values of  $M$ , and in Fig. 9, we consider  $(M, P) \mapsto \Lambda(M, n, P) - \Lambda_{\text{sCI}}(M, n)$  for fixed values of  $n$ .

The numerical evaluations suggest that for any fixed value of  $M$  ranging from 0.01 to 10; there exists an integer  $n^*(M) \geq 2$  such that:

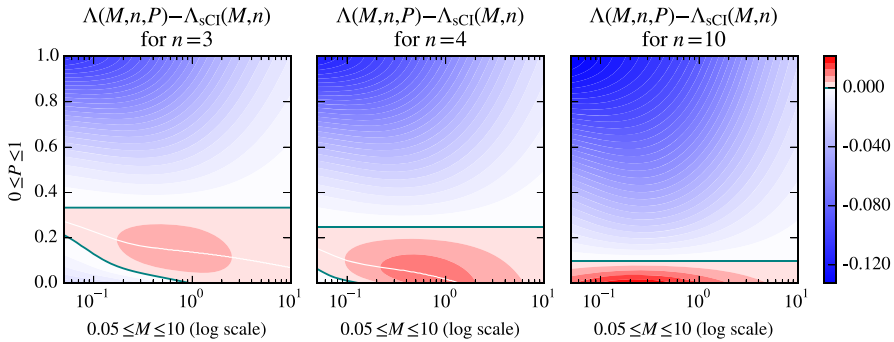
- if  $n \leq n^*(M)$ , the results are similar to the case when  $n = 2$ , in the sense that the following equation:

$$\Lambda(M, n, P) - \Lambda_{\text{sCI}}(M, n) = 0 \tag{20}$$

has exactly two roots  $P' = P'(M, n)$  and  $P'' = \frac{1}{n}$ , for some  $0 \leq P'(M, n) < \frac{1}{n}$ . Moreover,  $\mathcal{P}_{M,n} = [P', P'']$  and  $P^*_{M,n}$  is unique and belongs to  $(P', P'')$ ;



**Fig. 8**  $(n, P) \mapsto \Lambda(M, n, P) - \Lambda_{sCI}(M, n)$  for  $M = 0.1$  (left),  $M = 1$  (center) and  $M = 10$  (right). The red zones correspond to  $\mathcal{P}_{M,n}$ . The upper and lower green curves correspond to the roots  $P' = P'(M, n)$  (lower curve) and  $P'' = 1/n$  (upper curve) of  $\Lambda(M, n, P) - \Lambda_{sCI}(M, n) = 0$ . The central white curve shows  $n \rightarrow P^*(M, n)$  (Color figure online)



**Fig. 9**  $(M, P) \mapsto \Lambda(M, n, P) - \Lambda_{sCI}(M, n)$  for  $n = 3$  (left),  $n = 4$  (center) and  $n = 10$  (right). The red zones correspond to  $\mathcal{P}_{M,n}$ . The upper and lower green curves correspond to the roots  $P' = P'(M, n)$  (lower curve) and  $P'' = 1/n$  (upper curve) of  $\Lambda(M, n, P) - \Lambda_{sCI}(M, n) = 0$ . The central white curve shows  $M \rightarrow P^*(M, n)$  (Color figure online)

- if  $n > n^*(M)$ , Eq. (20) has a single root  $P'' = \frac{1}{n}$  and  $\mathcal{P}_{M,n} = [0, P'']$ . Moreover,  $P_{M,n}^*$  is unique and belongs to  $[0, P'']$ .

Some values of  $n^*(M)$  are:

$M$	0.01	0.1	1	10	100
$n^*(M)$	7	4	2	2	2

In addition, numerical results performed for  $M$  ranging from 0.1 to 10 suggest that  $n^*(M)$  is a decreasing function of  $M$ , with  $2 \leq n^*(M) \leq 4$  (see Figs. 8, 9). Similar results hold when  $M$  ranges from 0.01 to 100, in which case  $2 \leq n^*(M) \leq 7$ .

Regarding the condition for the replacement of the resident strict Nash equilibria  $\mathbf{p}_B$  by the other mutant strict Nash equilibria  $\mathbf{p}_A$ , those results suggest that:

- for  $2 \leq n \leq n^*(M)$ , this condition is less stringent in the CI model than in the sCI model if the size of the islands exceeds the size of the continent provided it is not too much larger ( $P'(M, n) < P < 1/n$ );
- for  $n > n^*(M)$ , this condition is less stringent in CI model than in the sCI model provided the size of the islands exceeds the size of the continent ( $P < 1/n$ ).

Now, let us focus on  $P^*(M, n)$  the optimal relative sizes of the continent at which  $\Lambda(M, n, \cdot)$  is maximized. It emerges from numerical simulations (Figs. 8, 9) that  $P^*(M, n)$  is unique with  $P^*(M, n) < 1/n$  and that for any fixed values of the migration rate,  $M$ , there exists an integer  $n^{**}(M) \geq n^*(M)$  such that:

- if  $n \leq n^{**}(M)$ , then  $P^*(M, n)$  is nonzero and coefficient  $\Lambda(M, n, \cdot)$  increases with  $P$  from  $\Lambda(M, n, 0) = 1/3 + \frac{(n-2)}{3(M+2)(n-1)}$  until it reaches its maximum located at  $P = P^*(M, n)$  and then, decreases back to  $1/3$ .
- if  $n > n^{**}(M)$ , then  $\Lambda(M, n, \cdot)$  is a decreasing function of  $P$  so  $P^*(M, n) = 0$ .

Some values of  $n^{**}(M)$  are given in the following table:

$M$	0.01	0.1	1	10	100
$n^{**}(M)$	17	7	4	3	3

Numerical results, performed for  $M$  ranging from 0.1 to 10, suggest that  $n^{**}(M)$  is a decreasing function of  $M$ , with  $n^{**}(M)$  not exceeding 7 for  $M$  in that range (see also Figs. 12, 13, 14).

As a consequence, we deduce from those numerical evaluations that for any fixed migration rate  $M$ , and any fixed number of demes  $n$ , provided it remains small enough (in the sense that  $n \leq n^{**}(M)$ ), there exists a single “optimal” relative continent size  $P = P^*(M, n) \in (0, 1/n)$  at which 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 the least stringent. In other words, given a migration rate  $M$  and a total number of demes  $n \leq n^{**}(M)$ , the model for which the proportion of individuals living on the continent is equal to  $P = P^*(M, n)$ , is the one for which the threshold value for  $x^*$  is maximized, i.e.,  $\Lambda(M, n, P^*(M, n)) = \max_{P \in [0, 1]} \Lambda(M, n, P)$ . Whereas, if the number of demes,  $n$ , is larger than  $n^{**}(M)$ , then the maximum of  $\Lambda(M, n, \cdot)$  is reached at the limit when  $P$  goes to zero, i.e.,  $P^*(M, n) = 0$ .

Figure 14 (top left) shows numerical evaluations of the maximum threshold frequency  $\Lambda^{**}(M, n) = \max_{P \in [0, 1]} \Lambda(M, n, P) = \Lambda(M, n, P^*(M, n))$  as a function of the number of demes  $n$  for different fixed values of the migration rate,  $M$ , versus  $\Lambda_{sCI}(M, n)$ . Whereas, Fig. 14 (top right) represents  $P^*(M, n)$  as a function of  $n$ , for the same values of  $M$ . Numerical evaluations (Fig. 14) suggest that when the number of demes,  $n$ , is fixed,  $\Lambda^{**}(M, n)$  and  $\Lambda_{sCI}(M, n)$  are both decreasing functions of  $M$ . On the other hand, for any fixed  $M$ , we find that they share the same limit,  $\frac{1}{3} + \frac{1}{3(M+2)}$ , as  $n$  goes to infinity.

As an example, let us see what happens when  $M = 1$  (Figs. 8, 12, 13 and 14 and Table 1). In this context, numerical calculations illustrated in Figs. 8 and 13 suggest that only in the case  $n = 2$  does Eq. (20) have two roots (which are then,  $1/2$  and  $P'(1, 2) < 1/2$ ). Thus,  $n^*(1) = 2$ . In the case of two demes ( $n = 2$ ), it is known [20] that  $\Lambda(1, 2, P) > \Lambda_{sCI}(1, 2) = 3/8$ , which means a larger threshold value for  $x^*$  than in the sCI model if and only if  $P'(1, 2) \simeq 0.224 < P < 0.5$ . Whereas, as soon as  $n \geq 3$ , we find that  $P = 1/n$  is the only root of Eq. (19) and  $\Lambda(1, n, P) > \Lambda_{sCI}(1, n)$  if and only if  $P < 1/n$ .

**Table 1** Approximations of the values taken by  $\Lambda$  at  $P = 0$ , i.e.,  $\Lambda(1, n, 0)$ , and at  $P = 1/n$ , i.e.,  $\Lambda_{sCI}(1, n)$ , at its maximum,  $\Lambda^{**}(1, n)$ , at  $P = P^*(1, n)$ , when the migration rate  $M = 1$  and  $n$  ranges from 2 to 4

$n$	$P^*(1, n)$	$\Lambda(1, n, 0)$	$\Lambda_{sCI}(1, n)$	$\Lambda^{**}(1, n)$
2	0.349	1/3	0.375	0.37904
3	0.395	0.38889	0.38866	0.39528
4	0.0182	0.40741	0.3969	0.40753

Moreover, when  $n$  is held fixed, numerical evaluations show that the optimal relative continent size at which the maximum of  $\Lambda$  is reached,  $P = P^*(1, n)$ , is nonzero as long as  $n$  does not exceed 4. The values of  $\Lambda(1, n, 0)$ ,  $\Lambda_{sCI}(1, n)$ ,  $\Lambda^{**}(1, n)$  and  $P^*(1, n)$  can be found in Table 1, for  $2 \leq n \leq 4$ .

On the other hand, as soon as  $n \geq 5$ , numerical evaluations suggest that  $\Lambda(1, n, P)$  is a decreasing function of  $P$  which decreases from its maximum, which is reached at the limit when  $P$  tends to zero ( $P^*(1, n) = 0$ ), to  $1/3$  (at  $P = 1$ ). This suggests that  $n^{**}(1) = 4$ .

These results are illustrated in Figs. 8, 13, and 14. Figure 8 (central figure) shows the effect of the number of demes,  $n$ , and the relative continent size,  $P$ , on  $\Lambda(1, n, P)$  compared to  $\Lambda_{sCI}(1, n)$ . Figure 13 shows how the difference  $\Lambda(M, n, P) - \Lambda_{sCI}(M, n)$  evolves with  $P$ , for four values of  $n$ :  $2 \leq n \leq 5$ . We also refer to the red curves in Fig. 14 which represent the impact of  $n$  on the evolution of both  $\Lambda^{**}(1, n)$  and  $\Lambda_{sCI}(1, n)$  (left figure) and its effect of  $P^*(1; n)$  (right figure).

Let us go back to the IPD with TFT versus ALLD. Since in this framework,  $x^*$  decreases to zero with the number of rounds [38], we find that for a fixed migration rate,  $M$ , depending on the value of the number of demes,  $n$ , there are two types of conditions, regarding  $P$ , under which an asymmetric (CI) model will require less rounds of the game than its sCI model counterpart to ensure that cooperation will take over the population with a selective advantage : in the case when the number of demes remains small enough (i.e.,  $n \leq n^*(M)$ ), this will happen if  $P$  is not too small and remains below  $1/n$ , as it is already known in the case of a two-deme ( $n = 2$ ) continental island model [20]; whereas for larger values of  $n$  (i.e.,  $n > n^*(M)$ ), it will only require  $P$  to be smaller than  $1/n$  (i.e., it will only require the continent’s size to be smaller than the size of the islands).

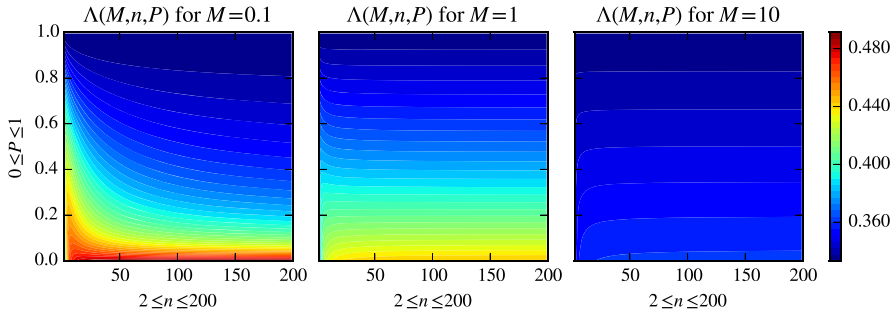
### 6.2.1 Comparisons with the One-Third Law

For a fixed number of demes  $n \geq 2$ , numerical evaluations performed for  $M$  ranging from 0.1 to 10 (Figs. 7, 10, 11 and 14) indicate that  $1/3 < \Lambda(M, n, P) \leq 1/2$  for every  $P \in (0, 1)$ . Similar results hold when  $M$  ranges between 0.01 and 100 (not shown). In particular, this implies that condition (15) is less stringent than the one-third law.

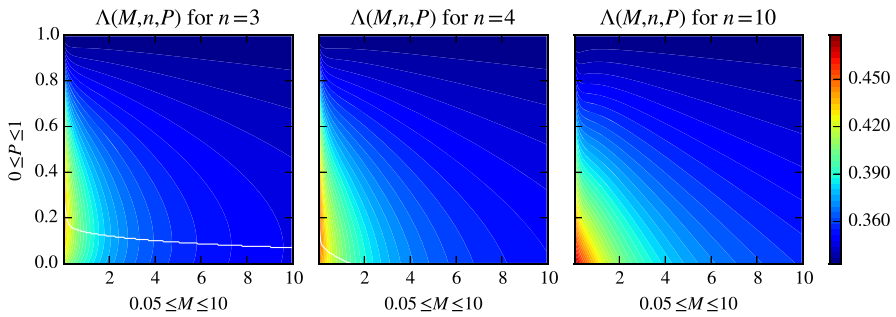
Going back to the case of TFT versus ALLD, a CI model will require less rounds of the game than a panmictic model to ensure that cooperation invades the whole population with a selective advantage.

## 7 Discussion

We have considered an  $n$ -deme continental island linear game model [52], for which we have calculated the first-order approximation of the fixation probability of a single mutant  $A$  initially introduced into the continent, with respect to the intensity of selection, in the

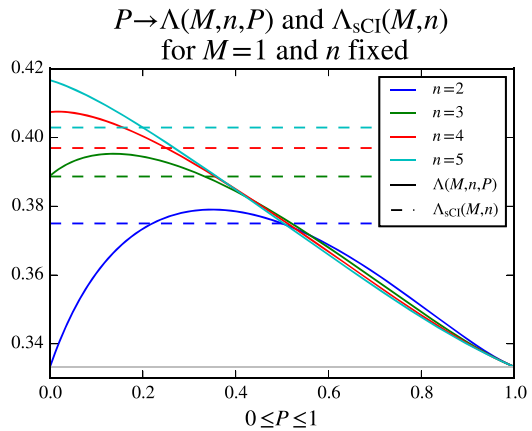


**Fig. 10** Threshold  $\Lambda$  as a function of  $n$  and  $P$  for three different values of  $M$  :  $M = 0.1$  (left);  $M = 1$  (center);  $M = 10$ .  $P$  ranges from 0 to 1 and  $n$  from 2 to 100

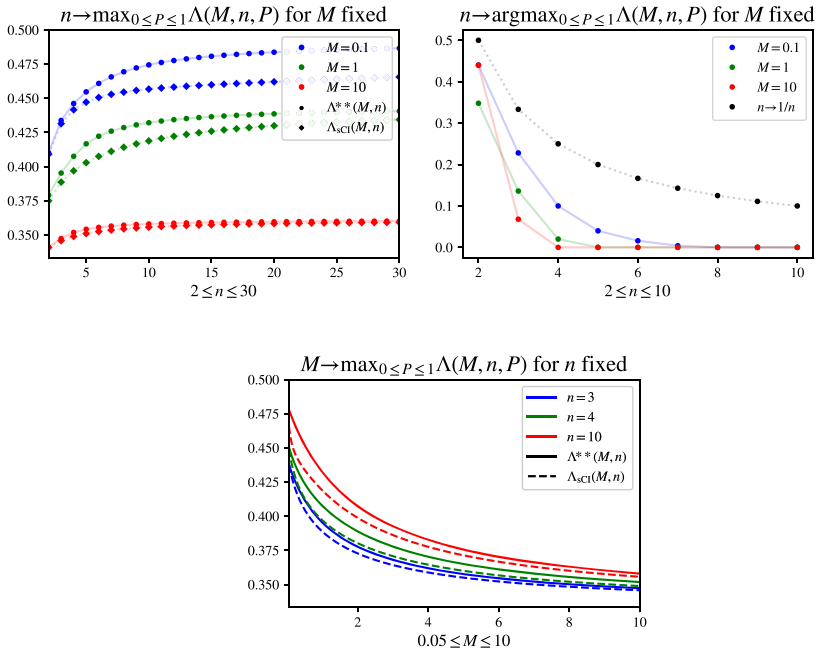
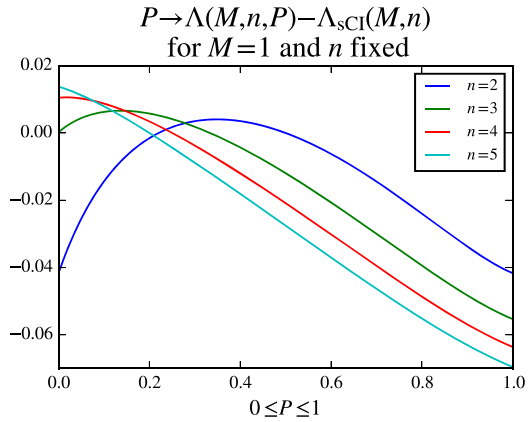


**Fig. 11** Threshold  $\Lambda$  as a function of  $M$  and  $P$  for three different values of  $n$  :  $n = 3$  (left);  $n = 4$  (center);  $n = 10$  (right).  $P$  ranges from 0 to 1 and  $M$  from 0.05 to 10. The white curve corresponds to  $M \mapsto P^*(M, n)$

**Fig. 12** Threshold  $\Lambda$  (solid curve) versus its value in the sCI model (dashed line) as functions of the relative continent size,  $P$ , in the case when  $M = 1$  for different fixed values of  $n$



**Fig. 13** Difference  $\Lambda(M, n, P) - \Lambda_{sCI}(M, n)$  as a function of the relative continent size,  $P$ , in the case when  $M = 1$  for different fixed values of  $n$  (Color figure online)



**Fig. 14** *Top left*: maximum value taken by threshold  $\Lambda$ ,  $\Lambda^{**}(M, n) = \max_{P \in [0, 1]} \Lambda(M, n, P)$ , (dots) versus  $\Lambda_{sCI}(M, n)$  (diamonds), as functions of the number of demes,  $n$ , for 3 different values of the migration rate,  $M$ :  $M = 0.1$  (blue);  $M = 1$  (green);  $M = 10$  (red).  $n$  ranges from 2 to 30. *Top right*:  $P^*(M, n) = \operatorname{argmax}_{0 \leq P \leq 1} \Lambda(M, n, P)$  as a function of the number of demes,  $n$ , for the same values of the migration rate,  $M$ :  $M = 0.1$  (blue);  $M = 1$  (green);  $M = 10$  (red).  $n$  ranges from 2 to 10. The black dots correspond to the value taken by  $P$  in the sCI model ( $P = 1/n$ ). *Bottom*:  $\Lambda^{**}(M, n) = \max_{P \in [0, 1]} \Lambda(M, n, P)$ , (solid curve) versus  $\Lambda_{sCI}(M, n)$  (dashed curve), as functions of the migration rate  $M$  for 3 different values of the number of demes,  $n$ :  $n = 3$  (blue);  $n = 4$  (green);  $n = 10$  (red).  $M$  ranges from 0.05 to 10 (Color figure online)

context of weak selection and conservative migration, in the limit of the structured coalescent assumptions [9, 10, 33, 52].

In this model, the population is subdivided into a continent of size  $N_0 = c_0 N$ , surrounded by  $n - 1$  islands of identical size  $N_1 = c_1 N$ , with symmetric migration occurring between the continent and each island with no direct island-to-island migration in one step of the migration process. The same game matrix  $W$  is assumed within each deme, the continent and the islands. The total population size denoted by  $c N$ , where  $c = c_0 + (n - 1) c_1$ , is assumed to be large, and the backward migration rates are of the form  $m_{0i} = M_0 / (2N(n - 1))$ , for the probability that an individual from the continent emigrated from island  $i$  in the previous generation, and  $m_{i0} = M_1 / (2N)$ , for the backward probability that an individual from island  $i$  emigrated from the continent, and  $M_0$  and  $M_1$  are of order 1, which hold under the structured coalescent assumptions [9, 10, 33, 52]. Moreover, assuming conservative migration, the parameter  $M_0$  is related to  $M_1$  by  $c_1 M_1 = c_0 M_0 / (n - 1) = M$ , where the “migration rate”  $M$  is of order 1. In the context of weak selection ( $s \ll 1 / (cN) \ll 1$ ), we have shown that the fixation probability can be approximated by:

$$\begin{aligned}
 u(s) = & \frac{u_0}{N_0} + s \left\{ (\mathbf{p}_A - \mathbf{p}_B) \cdot (u_0 \gamma_0 + (1 - u_0) \gamma_1) W (\mathbf{p}_A - \mathbf{p}_B) \right. \\
 & \left. + (\mathbf{p}_A - \mathbf{p}_B) \cdot (u_0 \delta_0 + (1 - u_0) \delta_1) W \mathbf{p}_B \right\} + o(s), \tag{21}
 \end{aligned}$$

where  $u_0$  denotes the first coordinate of  $(u_0, u_1, \dots, u_1)$ , the stationary distribution of the backward migration matrix  $\mathbf{M}$ , and coefficients  $\delta_i, \gamma_i, i = 0, 1$ , are explicit functions that depend on the migration rate  $M$ , the proportion of the total population living on the continent,  $P = c_0 / c$ , and the total number of demes,  $n$ .

In the special case when the model is reduced to  $n = 2$  demes, up to the proper parameter rescaling, approximation (21) corresponds to the one obtained for an asymmetric two-deme linear game model [20], since in this particular case the two models coincide. The proof in the case  $n \geq 3$  is a straightforward adaption of the Markov chain method used in Ladret and Lessard [20] to the case of the CI model and is an extension of Rousset [43]. It expresses the first-order effect of selection on the fixation probability as a function of quantities of the form  $\sum_{t \geq 0} E_0(X_i(t) X_j(t) (1 - X_k(t)))$  and  $\sum_{t \geq 0} E_0[X_i(t) (1 - X_j(t))]$ , where  $X_i(t)$  represents the frequency of  $A$  in deme  $i$  at time  $t$  and  $E_0$  an expectation under neutrality. These expressions are then computed using a coalescent [15]-based approach for a structured population [33] that allows to express them as functions of the transition matrix, under neutrality, of the ancestral process that traces the lineages of a set of 3 individuals backwards in time, under a large population and the structured coalescent assumptions.

Note that McAvoy and Allen [32] give a different and unifying method for computing the first-order effect of selection on the fixation probability of a mutant that generalizes the approach of Rousset [43]. This method indeed applies to a broad class of evolutionary models in which the population has an arbitrary fixed size and arbitrary forms of frequency dependence and spatial structure, and into which the CI model fits. They use the framework of “replacement events” [1, 3], and their expressions for the first-order expansion of the fixation probability are written as functions of a set of sojourn times for neutral drift and require the resolution of a system of linear equations.

Their results allow the computation of the first-order expansion of the fixation probability; they nevertheless lead, with different methods, to less explicit expressions.

Also, unlike the present paper, McAvoy and Allen [32] do not conduct a large population analysis; they just point out that their expression requires some care to lend itself to a large



population analysis in that the number of terms in the formulae for the first-order expansion of the fixation probability grows exponentially with the population size.

In the context of the finite population continental island model with  $n \geq 3$  demes under weak selection, we have investigated conditions under which a resident strategy is selectively favored against replacement by a mutant strategy as defined by Nowak et al. [38]. This condition corresponds to the traditional ESS condition in an infinite population, provided the mutant strategy remains close enough to the resident strategy if the mutant strategy uses some new pure strategies. This also holds when the model is reduced to a single deme [21, 26], when the population structure follows a symmetric finite island model with  $n \geq 2$  demes [26], or when the continental island model is reduced to only  $n = 2$  demes, which corresponds to the case of the asymmetric two-deme model [20].

In the case of two pure strategies  $\mathbf{p}_A = (1, 0)$  and  $\mathbf{p}_B = (0, 1)$  that are best replies to themselves with respect to the  $2 \times 2$  game matrix:

$$W = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

which means that  $a > c, d > b$ , we have specified a condition for the resident strategy to be selectively favored against replacement by the mutant strategy. We have shown that this condition translates into a criterion of the form  $x^* < \Lambda$  where  $x^*$  denotes the unstable equilibrium frequency of the mutant, and where the coefficient  $\Lambda$  is an explicit function of the population parameters  $M, n$  and  $P$ . This inequality extends the one-third law to the  $n$ -deme continental island model and when  $n = 2$ , it reduces to the modified one-third law for an asymmetric two-deme model. We have found that this condition is less stringent than the one-third law.

We have compared the modified one-third law for an asymmetric continental island model with unequal deme sizes ( $P \neq 1/n$ ) with its equivalent for its symmetric (in the sense of equal deme sizes, i.e.,  $P = 1/n$ ) model counterpart. The two models share the same population parameters except for the proportion of individuals living on the continent, which is equal to  $P \neq 1/n$  in the latter model and  $P = 1/n$  in the former. We have found that when the migration rate,  $M$ , is fixed, there exists a threshold value,  $n^*(M) \geq 2$ , for the number of demes,  $n$ , such that, if  $n \leq n^*(M)$ , then the condition for the asymmetric model is less stringent than the one for its symmetric model counterpart, provided the relative size of the continent,  $P$ , is not too small and remains less than  $1/n$ , as it is already the case for  $n = 2$  [20]; while, if the number of demes exceeds  $n^*(M)$ , it only requires the relative size of the continent to be less than  $1/n$ . Moreover, we have found that numerical evaluations suggest that  $n^*(M)$  does not exceed 4 when  $M$  ranges from 0.1 to 10 and does not exceed 7 when  $0.01 \leq M \leq 100$ .

On the other hand, we have compared the  $n$ -deme symmetric continental island model with its symmetric finite island model counterpart. In both models, there are  $n$  demes of equal size  $\frac{cN}{n}$  with identical game matrix  $W$  within each deme and both models have the same expected total number of migrants per generation after population regulation, only the migration scenario differs. When the number of demes,  $n$ , is larger than 3 (otherwise both models are equivalent) and the migration rate,  $M$ , is fixed, we have found that as long as  $M$  remains larger than  $\sqrt{10}/3$ , the extended one-third law for the continental island model is always less stringent than the extended one-third law for its island model counterpart. On the other hand, for smaller values of  $M$  (i.e.,  $M \leq \sqrt{10}/3$ ), we have found that this remains true, provided the number of demes is large enough (more precisely, provided it remains larger than  $n_0(M) = 1 + \sqrt{1 + 4M^2/M^2}$ ). Equivalently, when the number of demes,  $n$ , is fixed, we have shown that the extended one-third law for the continental island model is less

stringent than its Wright’s island counterpart, provided the migration rate,  $M$ , remains large enough (namely, larger than  $n_0^{-1}(n) = \sqrt{2n + 4/n}$ ).

Applying these results to the IPD with the strategies TFT versus ALLD, we have found that the condition for the cooperative TFT strategy to fix in the population with a selective advantage is less stringent in a continental island model than in a panmictic model, in the sense that it requires less repetitions of the game. Moreover, the population structure of the symmetric continental island model can facilitate the evolution of cooperation compared to its finite island model counterpart. On the other hand, the asymmetry in the population structure of a continental island model with unequal deme sizes can outperform its symmetric model counterpart when promoting the emergence of cooperation.

Note that while the present paper focuses on the case where the single mutant is initially introduced into the continent, it would be interesting to investigate how a change in its initial location would affect its fixation probability.

Moreover, in addition to the condition for a mutant strategy  $A$  to be favored over a neutral mutation studied in this paper, a second complementary criterion, traditionally used to measure the evolutionary success of a strategic type,  $A$ , would be worth being investigated. It compares the fixation probability of a single  $A$  mutant in an otherwise population of type  $B$ , to the fixation probability of a single  $B$  mutant in a population of all  $A$ ’s: following this criterion, type  $A$  is said to be favored over  $B$  if the former probability exceeds the latter [8, 18, 27, 28, 38]. Note that in the case of the Moran process in evolutionary game theory, Sample and Allen [45] have shown that this latter condition has the advantage of not being affected by the order in which the weak selection and large population size limits are taken, unlike the former condition. It would be interesting to address this second criterion in the specific case of this CI model.

**Acknowledgements** I would like to thank Fabien Campillo for his comments and support.

## Appendix A Proof of Proposition 1

Here, we prove Proposition 1. For  $t = 0, 1, \dots$ , let us define  $Z(t)$ , the weighted frequency of  $A$ , as:

$$Z(t) = u_0 X_0(t) + \dots + u_{n-1} X_{n-1}(t),$$

where  $\mathbf{u} = (u_0, \dots, u_{n-1})$  denotes the stationary distribution of migration matrix  $\mathbf{M}$ . For any given selection intensity  $s \geq 0$ , the discrete-time stochastic process  $(Z(t))_{t \geq 0}$ , is a Markov chain on the finite state space:

$$\left\{ u_0 \frac{k_0}{N_0} + \sum_{i=1}^{n-1} u_i \frac{k_i}{N_i} ; k_0 = 0, \dots, N_0, k_i = 0, \dots, N_1, i = 1, \dots, n - 1 \right\}.$$

Its initial state is  $Z(0) = u_0/N_0$ , and there are two absorbing states  $z = 0$  and  $z = 1$ , which correspond to the fixation of  $B$  and  $A$ , respectively; all the other states being transient.

This process converges in probability to a random variable  $Z(\infty)$ , which takes the value 1 with probability  $u(s)$ , and 0 otherwise. In the neutral scenario ( $s = 0$ ), this process is a bounded martingale. By the stopping time theorem [14], we find that the fixation probability of  $A$ , which occurs when the absorbing state  $z = 1$  is reached, is equal to:

$$u(0) = \mathbb{E}_0(Z(\infty)) = Z(0) = \frac{u_0}{N_0}.$$

In the general case when selection intensity is  $s$ , we can write following [43] that:

$$\mathbb{E}[Z(\infty) - Z(0)] = \sum_{t \geq 0} \mathbb{E}[Z(t + 1) - Z(t)],$$

which is equivalent to:

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

After differentiating with respect to  $s$  and assuming the interchangeability of summation and derivation (for a formal proof under mild regularity conditions see [26]), we get:

$$u'(0) = \sum_{t \geq 0} \frac{d}{ds} \mathbb{E}[Z(t + 1) - Z(t)] \Big|_{s=0}.$$

Conditioning on the values  $\mathbf{x} = (x_0, x_1, \dots, x_{n-1})$  taken by  $\mathbf{X}(t)$ , we can write:

$$\mathbb{E}[Z(t + 1) - Z(t)] = \sum_{\mathbf{x}} \mathbb{E}[Z(t + 1) - Z(t) | \mathbf{X}(t) = \mathbf{x}] \mathbb{P}(\mathbf{X}(t) = \mathbf{x}),$$

which implies that:

$$\begin{aligned} & \frac{d}{ds} \mathbb{E}[Z(t + 1) - Z(t)] \Big|_{s=0} \\ &= \sum_{\mathbf{x}} \frac{d}{ds} \mathbb{E}[Z(t + 1) - Z(t) | \mathbf{X}(t) = \mathbf{x}] \Big|_{s=0} \mathbb{P}_0(\mathbf{X}(t) = \mathbf{x}) \\ &+ \sum_{\mathbf{x}} \mathbb{E}_0[Z(t + 1) - Z(t) | \mathbf{X}(t) = \mathbf{x}] \frac{d}{ds} \mathbb{P}(\mathbf{X}(t) = \mathbf{x}) \Big|_{s=0}. \end{aligned}$$

In the neutral case ( $s = 0$ ), the expected change in  $Z(t)$  from one generation to the next is zero, that is:

$$\mathbb{E}_0[Z(t + 1) - Z(t) | \mathbf{X}(t) = \mathbf{x}] = 0.$$

This leads to:

$$u'(0) = \sum_{t \geq 0} \sum_{\mathbf{x}} \mathbb{P}_0(\mathbf{X}(t) = \mathbf{x}) \frac{d}{ds} \mathbb{E}[Z(t + 1) - Z(t) | \mathbf{X}(t) = \mathbf{x}] \Big|_{s=0}. \tag{A.1}$$

Since the change in the weighted frequency of  $A$  from one generation to the next has conditional expectation :

$$\mathbb{E}[Z(t + 1) - Z(t) | \mathbf{X}(t) = \mathbf{x}] = \sum_{i=0}^{n-1} u_i \left( \mathbb{E}[X_i(t + 1) | \mathbf{X}(t) = \mathbf{x}] - x_i \right),$$

it follows from (3), (4) and (5), that:

$$\begin{aligned} & \frac{d}{ds} \mathbb{E}[Z(t + 1) - Z(t) | \mathbf{X}(t) = \mathbf{x}] \Big|_{s=0} \\ &= \sum_{i=0}^{n-1} u_i \tilde{x}_i^2 (1 - \tilde{x}_i) (\mathbf{p}_A - \mathbf{p}_B) \cdot W (\mathbf{p}_A - \mathbf{p}_B) \\ &+ \sum_{i=0}^{n-1} u_i \tilde{x}_i (1 - \tilde{x}_i) (\mathbf{p}_A - \mathbf{p}_B) \cdot W_i \mathbf{p}_B. \end{aligned} \tag{A.2}$$

If we plug Eqs. (1) and (2) into (A.2), it follows from (A.1) that:

$$\begin{aligned}
 u'(0) &= (\mathbf{p}_A - \mathbf{p}_B) \\
 &\cdot \left\{ u_0 \sum_{t \geq 0} \lambda_0(\mathbf{m}_0, \mathbf{X}(t)) + \sum_{i=1}^{n-1} u_i \sum_{t \geq 0} \lambda_i(\mathbf{m}_1, \mathbf{X}(t)) \right\} W(\mathbf{p}_A - \mathbf{p}_B) \\
 &+ (\mathbf{p}_A - \mathbf{p}_B) \\
 &\cdot \left\{ u_0 \sum_{t \geq 0} \delta_0(\mathbf{m}_0, \mathbf{X}(t)) + \sum_{i=1}^{n-1} u_i \sum_{t \geq 0} \delta_i(\mathbf{m}_1, \mathbf{X}(t)) \right\} W \mathbf{p}_B, \\
 &= (\mathbf{p}_A - \mathbf{p}_B) \cdot \kappa_\lambda W (\mathbf{p}_A - \mathbf{p}_B) + (\mathbf{p}_A - \mathbf{p}_B) \cdot \kappa_\delta W \mathbf{p}_B,
 \end{aligned}$$

where  $\lambda_0(\mathbf{m}_0, \mathbf{X}(t))$ ,  $\lambda_i(\mathbf{m}_1, \mathbf{X}(t))$ ,  $\delta_0(\mathbf{m}_0, \mathbf{X}(t))$ , and  $\delta_i(\mathbf{m}_1, \mathbf{X}(t))$  can be explicitly written in terms of coefficients  $\mathbb{E}_0[X_i(t)X_j(t)(1 - X_k(t))]$  and  $\mathbb{E}_0[X_i(t)(1 - X_j(t))]$ , with  $i, j, k \in \{0, \dots, n - 1\}$ . Due to the interchangeability of the islands, those expressions can be reduced to equations involving coefficients  $\mathbb{E}_0[X_i(t)X_j(t)(1 - X_k(t))]$  and  $\mathbb{E}_0[X_i(t)(1 - X_j(t))]$  only for  $i, j, k \in \{0, 1, 2, 3\}$ , as follows:

$$\begin{aligned}
 \lambda_0(\mathbf{m}_0, \mathbf{X}(t)) &= (1 - m_0)^3 \mathbb{E}_0[X_0(t)^2 (1 - X_0(t))] \\
 &+ m_0 (1 - m_0)^2 \mathbb{E}_0[X_0^2(t) (1 - X_1(t))] \\
 &+ 2 m_0 (1 - m_0)^2 \mathbb{E}_0[X_0(t) (1 - X_0(t)) X_1(t)] \\
 &+ 2 (1 - m_0) m_0^2 \frac{n - 2}{n - 1} \mathbb{E}_0[X_0(t) X_1(t) (1 - X_2(t))] \\
 &+ 2 (1 - m_0) \frac{m_0^2}{n - 1} \mathbb{E}_0[X_0(t) X_1(t) (1 - X_1(t))] \\
 &+ (1 - m_0) \frac{m_0^2}{n - 1} \mathbb{E}_0[X_1^2(t) (1 - X_0(t))] \\
 &+ (1 - m_0) m_0^2 \frac{n - 2}{n - 1} \mathbb{E}_0[X_1(t) X_2(t) (1 - X_0(t))] \\
 &+ \frac{m_0^3}{(n - 1)^2} \mathbb{E}_0[X_1^2(t) (1 - X_1(t))] \\
 &+ \frac{m_0^3 (n - 2)}{(n - 1)^2} \mathbb{E}_0[X_1^2(t) (1 - X_2(t))] \\
 &+ 2 m_0^3 \frac{(n - 2)}{(n - 1)^2} \mathbb{E}_0[X_1(t) X_2(t) (1 - X_1(t))] \\
 &+ m_0^3 \frac{(n - 2) (n - 3)}{(n - 1)^2} \mathbb{E}_0[X_1(t) X_2(t) (1 - X_3(t))], \\
 \delta_0(\mathbf{m}_0, \mathbf{X}(t)) &= (1 - m_0)^2 \mathbb{E}_0[X_0(t) (1 - X_0(t))] \\
 &+ m_0 (1 - m_0) \mathbb{E}_0[X_0(t) (1 - X_1(t))] \\
 &+ m_0 (1 - m_0) \mathbb{E}_0[X_1(t) (1 - X_0(t))] \\
 &+ \frac{m_0^2}{n - 1} \mathbb{E}_0[X_1(t) (1 - X_1(t))] \\
 &+ m_0^2 \frac{n - 2}{n - 1} \mathbb{E}_0[X_1(t) (1 - X_2(t))], \tag{A.3}
 \end{aligned}$$

and for all  $i = 1, \dots, n - 1$ :

$$\begin{aligned}
 \lambda_i(\mathbf{m}_1, \mathbf{X}(t)) &= m_1^3 \mathbb{E}_0[X_0(t)^2 (1 - X_0(t))] \\
 &\quad + m_1^2 (1 - m_1) \mathbb{E}_0[X_0(t)^2 (1 - X_1(t))] \\
 &\quad + 2 m_1^2 (1 - m_1) \mathbb{E}_0[X_0(t) (1 - X_0(t)) X_1(t)] \\
 &\quad + 2 m_1 (1 - m_1)^2 \mathbb{E}_0[X_0(t) X_1(t) (1 - X_1(t))] \\
 &\quad + m_1 (1 - m_1)^2 \mathbb{E}_0[X_1(t)^2 (1 - X_0(t))] \\
 &\quad + (1 - m_1)^3 \mathbb{E}_0[X_1^2(t) (1 - X_1(t))], \\
 \delta_i(\mathbf{m}_1, \mathbf{X}(t)) &= m_1^2 \mathbb{E}_0[X_0(t) (1 - X_0(t))] \\
 &\quad + m_1 (1 - m_1) \mathbb{E}_0[X_0(t) (1 - X_1(t))] \\
 &\quad + m_1 (1 - m_1) \mathbb{E}_0[X_1(t) (1 - X_0(t))] \\
 &\quad + (1 - m_1)^2 \mathbb{E}_0[X_1(t) (1 - X_1(t))].
 \end{aligned} \tag{A.4}$$

### Appendix B Proof of Proposition 2

Here, we calculate  $\mathbb{E}_0[X_i(t) X_j(t) (1 - X_k(t))]$  and  $\mathbb{E}_0[X_i(t) (1 - X_j(t))]$  with  $i, j, k \in \{0, 1, 2, 3\}$ , in terms of the submatrices  $L, F, Q$  of (8) the transition matrix  $K$  of the ancestral process  $\sigma(t)$ , that describes the locations of the ancestors of 3 individuals.

For each  $k \in \{1, \dots, N_1\}$  and  $i \in \{0, \dots, n - 1\}$ , let  $\xi_{k,i}$  denote the random variable that assigns the value 1 to the  $k$ -th individual in deme  $i$  if it is of type  $A$  and the value 0, otherwise:

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

Let us first focus on  $\sum_{t \geq 0} \mathbb{E}_0[X_0^2(t) (1 - X_0(t))]$ . The frequency of  $A$  in the continent at time  $t$  can be written in terms of the  $\xi_{k,0}(t)$  as:

$$X_0(t) = \frac{1}{N_0} \sum_{k=1}^{N_0} \xi_{k,0}(t).$$

Thus, we have:

$$\begin{aligned}
 \mathbb{E}_0[X_0^2(t)(1 - X_0(t))] &= \frac{1}{N_0^3} \mathbb{E}_0 \left[ \left( \sum_{k=1}^{N_0} \xi_{k,0}(t) \right)^2 \left( \sum_{l=1}^{N_0} (1 - \xi_{l,0}(t)) \right) \right] \\
 &= \frac{1}{N_1^3} \sum_{k=1}^{N_1} \sum_{l=1}^{N_1} \sum_{m=1}^{N_1} \mathbb{E}_0[\xi_{k,0}(t) \xi_{l,0}(t) (1 - \xi_{m,0}(t))] \\
 &= \left(1 - \frac{1}{N_0}\right) \left(1 - \frac{2}{N_0}\right) \alpha_0(t) + \frac{1}{N_0} \left(1 - \frac{1}{N_0}\right) \beta_0(t),
 \end{aligned} \tag{A.5}$$

where:

$$\begin{aligned}
 \alpha_0(t) &:= \mathbb{P}_0(\xi_{1,0}(t) = \xi_{2,0}(t) = 1, \xi_{3,0}(t) = 0), \\
 \beta_0(t) &:= \mathbb{P}_0(\xi_{1,0}(t) = 1, \xi_{2,0}(t) = 0).
 \end{aligned}$$

Now, let us calculate  $\sum_{t \geq 0} \alpha_0(t)$ . According to its definition,  $\alpha_0(t)$  is the probability that individuals 1, 2 and 3 from deme 0 at time  $t$  are of respective types  $A$ ,  $A$  and  $B$ . Since a single mutant  $A$  was introduced in the continent at time 0, individuals 1, 2 and 3 in deme 0 at time  $t$  are of types  $A$ ,  $A$  and  $B$ , respectively, if a single coalescence occurs from time  $t$  to time 0, this event being a coalescence between the lineages of individuals 1 and 2, and the two distinct ancestors at time 0 of these three individuals are of respective types  $A$  (for the common ancestor of individuals 1 and 2) and  $B$  (for the ancestor of individual 3). This implies that the state  $\sigma(t)$  in  $S$ , the ancestors of those three individuals are in  $t$  generations back, must either be 00 or 01, while the type of the ancestor common to individuals 1 and 2 is  $A$ . Thus,  $\alpha_0(t)$  is equal to the probability that the process  $\sigma(t)$  is in state 00 or 01 at time  $t$  given that  $\sigma(0)$  is in state 000 in  $S_{1,2,3}$ , times  $1/N_0$ , which is the frequency of  $A$  in the continent at time 0. Using the notations in Eq. (8) for the block form of  $K$ , the transition matrix of  $\sigma(\cdot)$ , this translates as follows:

$$\alpha_0(t) = \sum_{\tau=1}^t \left( F^{\tau-1} Q L^{t-\tau} u \right)_{000},$$

where  $u$  is the column vector  $u = (1/N_0, 1/N_0, 0, 0, 0)$ , and index 000 refers to the vector's component that corresponds to the chain starting in state 000. As a consequence, since matrices  $I - F$  and  $I - L$  are invertible, where  $I$  refers to an identity matrix of appropriate order, if we sum  $\alpha_0(t)$  over  $t \geq 0$ , we find that:

$$\sum_{t \geq 0} \alpha_0(t) = \left( (I - F)^{-1} Q (I - L)^{-1} u \right)_{000}. \tag{A.6}$$

Similarly, we find that:

$$\beta_0(t) := \mathbb{P}_0(\xi_{1,0}(t) = 1, \xi_{2,0}(t) = 0) = (L^t u)_{00},$$

leading to:

$$\sum_{t \geq 0} \beta_0(t) = \left( (I - L)^{-1} u \right)_{00}. \tag{A.7}$$

Let:

$$\mathcal{U} := (I - L)^{-1} u, \quad \text{and} \quad \mathcal{V} := (I - F)^{-1} Q (I - L)^{-1} u.$$

We then derive from (A.5), (A.6) and (A.7) that:

$$\sum_{t \geq 0} \mathbb{E}_0(X_0(t)^2 (1 - X_0(t))) = (1 - \frac{1}{N_0}) (1 - \frac{2}{N_0}) \mathcal{V}_{000} + \frac{1}{N_0} (1 - \frac{1}{N_0}) \mathcal{U}_{00}. \tag{A.8a}$$

In the same way, we find that

$$\begin{aligned} \sum_{t \geq 0} \mathbb{E}_0[X_1(t)^2 (1 - X_1(t))] &= (1 - \frac{1}{N_1}) (1 - \frac{2}{N_1}) \mathcal{V}_{111} + \frac{1}{N_1} (1 - \frac{1}{N_1}) \mathcal{U}_{11}, \\ \sum_{t \geq 0} \mathbb{E}_0[X_0(t)^2 (1 - X_1(t))] &= (1 - \frac{1}{N_0}) \mathcal{V}_{001} + \frac{1}{N_0} \mathcal{U}_{01}, \\ \sum_{t \geq 0} \mathbb{E}_0[X_1(t)^2 (1 - X_0(t))] &= (1 - \frac{1}{N_1}) \mathcal{V}_{110} + \frac{1}{N_1} \mathcal{U}_{10}, \\ \sum_{t \geq 0} \mathbb{E}_0[X_0(t) X_1(t) (1 - X_0(t))] &= (1 - \frac{1}{N_0}) \mathcal{V}_{010}, \\ \sum_{t \geq 0} \mathbb{E}_0[X_0(t) X_1(t) (1 - X_1(t))] &= (1 - \frac{1}{N_1}) \mathcal{V}_{011}, \\ \sum_{t \geq 0} \mathbb{E}_0[X_1(t)^2 (1 - X_2(t))] &= (1 - \frac{1}{N_1}) \mathcal{V}_{112} + \frac{1}{N_1} \mathcal{U}_{12}, \end{aligned}$$

$$\begin{aligned} \sum_{t \geq 0} \mathbb{E}_0[X_1(t) X_2(t) (1 - X_1(t))] &= (1 - \frac{1}{N_1}) \mathcal{V}_{112}, \\ \sum_{t \geq 0} \mathbb{E}_0[X_0(t) X_1(t) (1 - X_2(t))] &= \mathcal{V}_{012}, \\ \sum_{t \geq 0} \mathbb{E}_0[X_1(t) X_2(t) (1 - X_0(t))] &= \mathcal{V}_{120}, \\ \sum_{t \geq 0} \mathbb{E}_0[X_1(t) X_2(t) (1 - X_3(t))] &= \mathcal{V}_{123}, \end{aligned} \tag{A.8b}$$

$$\sum_{t \geq 0} \mathbb{E}_0[X_0(t) (1 - X_0(t))] = (1 - \frac{1}{N_0}) \mathcal{U}_{00}, \tag{A.8c}$$

$$\sum_{t \geq 0} \mathbb{E}_0[X_1(t) (1 - X_1(t))] = (1 - \frac{1}{N_1}) \mathcal{U}_{11},$$

$$\sum_{t \geq 0} \mathbb{E}_0[X_0(t) (1 - X_1(t))] = \mathcal{U}_{01},$$

$$\sum_{t \geq 0} \mathbb{E}_0[X_1(t) (1 - X_0(t))] = \mathcal{U}_{10},$$

$$\sum_{t \geq 0} \mathbb{E}_0[X_1(t) (1 - X_2(t))] = \mathcal{U}_{12}. \tag{A.8d}$$

### Appendix C Approximations under the Structured Coalescent Assumptions

Here, we give the formulae for coefficients  $\gamma_i$  and  $\delta_i$ ,  $i = 0, 1$  as functions of the population parameters  $n, M, P$  and  $\Lambda$  derived using `Maple`.

$$\gamma_0 = \frac{\gamma_{01}}{3(Mn - M + 1 - 2P + nP)\gamma_{02}} \tag{A.9}$$

where

$$\begin{aligned} \gamma_{01} &= 16P^5 + 6M^5 Pn - 71M^2 nP + 29M^2 n^2 P - 39M^2 n^2 P^2 + 11M^2 nP^2 \\ &\quad - 59M^2 n^2 P^3 + 22Mn^2 P + M^4 P^2 - 13M^3 P^2 + 3M^5 n - 2M^5 P + 10M^2 P^2 \\ &\quad + 11M^2 n^2 P^4 + 2M^2 n^2 P^5 - 52Mn^2 P^3 + 4Mn^2 P^4 + 22Mn P^4 + 4Mn^3 P^2 \\ &\quad + 72M P^2 + 56M^3 n P^3 - 28M P^3 - 12P^3 n^2 - 34M^3 n^2 P^2 + 116Mn P^3 \\ &\quad - 11M^3 Pn + 6M^3 n^2 - 10M^4 P^3 + 11M^3 P - 36n P^2 - 15M^3 n - 20M P \\ &\quad - 24P^4 M^2 - 40M^2 P^3 + M^5 n^3 - 3M^5 n^2 - 44M P^4 + 16M P^5 + 2M^3 n^3 \\ &\quad - 4M^3 P^4 + 113M^2 n P^3 + 20M^4 n P^3 - 16P^2 - 4n^2 P^4 + 12n P - 8M^2 n P^5 \\ &\quad + 36n P^4 + 3M^4 n - 20M P^5 n + 8Mn^2 P^2 + 6M^2 n^3 P + 10M^2 n^3 P^2 + 12n^2 P^2 \\ &\quad + 39M^3 n P^2 + 13M^3 n^3 P + 6M P^5 n^2 + 8M^3 n^3 P^2 - 32M^3 n^2 P^3 + 4M^3 n^2 P^4 \\ &\quad - 6M^5 n^2 P + 2M^5 n^3 P - M^5 - 6M^2 + 8M^2 n^2 + 9M^4 n^3 P + 2M^4 n^3 P^2 \\ &\quad - 23M^4 n^2 P - 3M^4 n^2 P^2 - 10M^4 n^2 P^3 + 19M^4 n P + 7M^3 - M^2 n \\ &\quad - 13M^3 n^2 P - 24M^3 P^3 - 5M^4 P + 6Mn - 8Mn P - 104Mn P^2 + 56P^3 - 56P^4 \\ &\quad + 36M^2 P + 8M^2 P^5 + 4M^2 n P^4 + 4n^2 P^5 - 16n P^5 + 3M^4 n^3 - 6M^4 n^2 + 4n P^3, \end{aligned}$$

and

$$\begin{aligned} \gamma_{02} &= 4M + 6M^2 n P + 6M^2 n^2 P + 6M^2 n^2 P^2 - 20M^2 n P^2 + 8P + 16M^2 P^2 - 20M P^2 \\ &\quad - 8M^3 n P^3 + 32M P^3 + 2M^3 n^2 P^2 - 20Mn P^3 - 11M^3 Pn + 2M^3 n^2 + 4M^3 P \\ &\quad + 8n P^2 - M^3 n - 12M P + 16M^2 P^3 - 16M^2 n P^3 - 24P^2 - 2M^4 n + 4Mn^2 P^2 \\ &\quad - 2M^3 n P^2 + M^4 - 4M^2 + 2M^4 n^2 P - 4M^4 n P - M^3 + 6M^2 n + 7M^3 n^2 P \\ &\quad + 8M^3 P^3 + 2M^4 P + 16Mn P - 4Mn P^2 + 16P^3 - 16M^2 P + M^4 n^2 - 8n P^3. \end{aligned}$$

$$\gamma_1 = \frac{\gamma_{11}}{3(n - 1)(Mn - M + 1 - 2P + nP)\gamma_{12}} \tag{A.10}$$

where

$$\begin{aligned} \gamma_{11} = & -16P^5 - 8M - 8M^5Pn + 93M^2nP - 92M^2n^2P - 2M^2n^2P^2 + 47M^2nP^2 \\ & + 96M^2n^2P^3 + 36Mn^2P - 16P - M^4P^2 + 29M^3P^2 + 8M^3n^4P^2 + 2M^5n^4P \\ & - 4M^5n + 2M^5P - 26M^2P^2 - 26M^3n^3P^3 + 4M^3n^3P^4 + 9M^3n^4P \\ & + 29M^2n^2P^4 - 10M^2n^2P^5 + 62Mn^2P^3 + 14Mn^2P^4 - 38Mn^3P^4 + 18Mn^3P^2 \\ & - 100MP^2 - 50M^3nP^3 - 4M^3nP^4 + 36MP^3 - 33M^2n^3P^3 - 28P^3n^2 \\ & + 101M^3n^2P^2 - M^2n^3P^4 + 2M^2n^3P^5 - 58MnP^3 + 42M^3Pn - 20Mn^3P^3 \\ & + 2Mn^3P^4 - 35M^3n^2 + 10M^4P^3 - 17M^3P - 68nP^2 + M^5n^4 + 34M^3n \\ & + 60MP + 32P^4M^2 + 24M^2P^3 - 4M^5n^3 + 6M^5n^2 + 12MP^4 + 12M^3n^3 + 4M^3P^4 \\ & - 87M^2nP^3 - 10M^4n^3P^3 + M^4nP^2 - 30M^4nP^3 + 72P^2 + 20n^2P^4 + 12nP \\ & + 16M^2nP^5 - 76nP^4 + 3M^4n^4 - 3M^4n + 4MP^5n - 110Mn^2P^2 + 33M^2n^3P \\ & - 25M^2n^3P^2 + 12n^2P^2 - 90M^3nP^2 - 10M^3n^3P - 2MP^5n^2 - 48M^3n^3P^2 \\ & + 64M^3n^2P^3 - 4M^3n^2P^4 + 12M^5n^2P - 8M^5n^3P + M^5 + 18M^2 + 15M^2n^2 \\ & - 32M^4n^3P - 5M^4n^3P^2 + 42M^4n^2P + 3M^4n^2P^2 + 30M^4n^2P^3 - 24M^4nP \\ & - 11M^3 + 6M^2n^4P^2 - 33M^2n - 24M^3n^2P + 12M^3P^3 + 5M^4P + 6Mn \\ & - 86MnP + 172MnP^2 - 112P^3 + 72P^4 + 9M^4n^4P + 2M^4n^4P^2 - 34M^2P \\ & - 8M^2P^5 - 60M^2nP^4 - 4n^2P^5 + 16nP^5 - 9M^4n^3 + 9M^4n^2 + 116nP^3 \end{aligned}$$

and

$$\begin{aligned} \gamma_{12} = & 4M + 6M^2nP + 6M^2n^2P + 6M^2n^2P^2 - 20M^2nP^2 + 8P + 16M^2P^2 - 20MP^2 \\ & - 8M^3nP^3 + 32MP^3 + 2M^3n^2P^2 - 20MnP^3 - 11M^3Pn + 2M^3n^2 + 4M^3P \\ & + 8nP^2 - M^3n - 12MP + 16M^2P^3 - 16M^2nP^3 - 24P^2 - 2M^4n + 4Mn^2P^2 \\ & - 2M^3nP^2 + M^4 - 4M^2 + 2M^4n^2P - 4M^4nP - M^3 + 6M^2n + 7M^3n^2P \\ & + 8M^3P^3 + 2M^4P + 16MnP - 4MnP^2 + 16P^3 - 16M^2P + M^4n^2 - 8nP^3. \\ \delta_0 = & \frac{-P + Mn + n - M}{Mn - M + 1 - 2P + nP} ; \delta_1 = \frac{1 - P + Mn - M}{Mn - M + 1 - 2P + nP} \end{aligned} \tag{A.11}$$

$$\begin{aligned} (1 - u_0)\delta_1 + u_0\delta_0 &= 1. \\ \Lambda(M, n, P) &= (1 - u_0)\gamma_1 + u_0\gamma_0 = \rho_1/\rho_2 \end{aligned} \tag{A.12}$$



with:

$$\begin{aligned} \rho_1 = & -8M + 4Mn^3P^2 + 41M^2nP^3 - 12MP^4 + 8MP^5 + M^4n^3 + 12n^2P^2 \\ & - 50MnP + 39M^2nP^2 - 16P + 56P^2 + 12nP - 52nP^2 + 44nP^3 + 4nP^4 \\ & + 24Mn^2P + 6Mn + 5M^3P^2 + 2MnP^2 + 6Mn^2P^5 + 10M^2 \\ & - 21M^3n^2P - 56P^3 - 10M^3n^2P^3 - 23M^2n^2P^2 - 25M^2n^2P^3 \\ & + 8M^2n^2P^4 - 10M^3nP^2 + 20M^3nP^3 + 8M^2n^3P + 4M^2n^3P^2 - M^4 \\ & - 5M^3P + 3M^4n - 10M^3P^3 - 26Mn^2P^3 + 2M^4n^3P - 14Mn^2P^2 \\ & - 2Mn^2P^4 - 5M^2n^2P - 12M^2nP^4 - 13M^2nP - 12P^3n^2 + 8M^3n^3P \\ & - 16MP^3 - 2M^4P + 10M^2P - 7M^3n^2 + 62MP^3n + 4MP^4n \\ & - 12MP^5n - 6M^4Pn^2 + 6M^4Pn + 9M^2n^2 + 5M^3n - 19M^2n + 36MP \\ & - 12MP^2 + 5M^3n^2P^2 - 20M^2P^2 - 16M^2P^3 - M^3 + 16P^4 + 4n^2P^5 \\ & - 8nP^5 + 3M^3n^3 - 3M^4n^2 + 4P^4M^2 + 18M^3nP - 4n^2P^4, \\ \rho_2 = & 3(n-1)(4M - 16M^2nP^3 + 16MnP - 20M^2nP^2 + 8P - 24P^2 \\ & + 8nP^2 - 8nP^3 - 4MnP^2 - 4M^2 + 7M^3n^2P + 16P^3 \\ & + 6M^2n^2P^2 - 2M^3nP^2 - 8M^3nP^3 + M^4 + 4M^3P - 2M^4n \\ & + 8M^3P^3 + 4Mn^2P^2 + 6M^2n^2P + 6M^2nP + 32MP^3 + 2M^4P \\ & - 16M^2P + 2M^3n^2 - 20MP^3n + 2M^4Pn^2 - 4M^4Pn - M^3n \\ & + 6M^2n - 12MP - 20MP^2 + 2M^3n^2P^2 + 16M^2P^2 + 16M^2P^3 \\ & - M^3 + M^4n^2 - 11M^3nP). \end{aligned}$$

### Appendix D Transition Probabilities

Matrix  $K$  is the probability transition matrix, under neutrality, for the ancestral process  $\sigma(t)$  that traces the spatial locations of the ancestors of 3 individuals, labelled individuals 1, 2, 3, over one time step backwards in time. Following Eq. (8),

$$K = \begin{pmatrix} S_{1,2,3} & S_{12,3} & S_{13,2} & S_{23,1} & S_{123} \\ F & Q & W & J & R_1 \\ 0 & L & 0 & 0 & R \\ 0 & 0 & L & 0 & R \\ 0 & 0 & 0 & L & R \\ 0 & 0 & 0 & 0 & R_0 \end{pmatrix} \begin{matrix} S_{1,2,3} \\ S_{12,3} \\ S_{13,2} \\ S_{23,1} \\ S_{123} \end{matrix}$$

For the calculation of the first-order expansion of the fixation probability (see Proposition 2), only submatrices  $F$ ,  $Q$ ,  $R$ , and  $L$  are needed (resp. of sizes  $15 \times 15$ ,  $5 \times 15$ ,  $5 \times 5$ ,  $5 \times 2$ ), so we do not compute the other submatrices. We now give the detailed expressions for  $F$ ,  $Q$ ,  $R$ , and  $L$ . As the square  $15 \times 15$  matrix  $F$  is cumbersome, it is decomposed into three  $5 \times 15$  submatrices:

$$F = (F^{(1)} \ F^{(2)} \ , \ F^{(3)}). \tag{A.13}$$

The computation of these matrices does not present any specific difficulties apart from their size. Before giving their expressions, we shall present how the first line related to transitions from the “000” state (in which the lineages of individuals 1, 2, 3 are not coalesced and on the continent at the given time  $t$ ) is computed, leaving the reader to detail the other lines. For the “000” state, only the terms in the first row of sub-matrices  $F$  and  $Q$  need to be detailed.

From the “000 state” going one generation back in time, the possible transitions are broken down as follows:

- 0 coalescence, corresponding to the matrix  $F$ , in which case there can either be:
  - 0 migration: the 3 parents remain on the continent  $\rightarrow 1$  possibility:  $000 \rightarrow 000$
  - 1 migration (and only 1, this is no longer specified in the following):  $\rightarrow 3$  possibilities:  $000 \rightarrow \{001, 010, 100\}$
  - 2 migrations
    - \* to the same island  $\rightarrow 3$  possibilities:  $000 \rightarrow \{011, 101, 110\}$
    - \* to 2 distinct islands  $\rightarrow 3$  possibilities:  $000 \rightarrow \{012, 102, 120\}$
  - 3 migrations
    - \* to the same island  $\rightarrow 1$  possibility:  $000 \rightarrow 111$
    - \* to 2 distinct islands  $\rightarrow 3$  possibilities:  $000 \rightarrow \{112, 121, 211\}$
    - \* to 3 distinct islands  $\rightarrow 1$  possibility:  $000 \rightarrow 123$
- 1 coalescence (only one is possible: the one of the lineages of individuals 1 and 2) corresponding to matrix  $Q$ , in which case there can either be:
  - 0 migration  $\rightarrow 1$  possibility:  $000 \rightarrow 00$
  - 1 migration (the one of the lineage of individual 3)  $\rightarrow 1$  possibility:  $000 \rightarrow 01$
  - 2 migrations (the one of the lineages of individuals 1 and 2)  $\rightarrow 1$  possibility:  $000 \rightarrow 10$
  - 3 migrations:
    - \* to the same island  $\rightarrow 1$  possibility:  $000 \rightarrow 11$
    - \* to 2 distinct islands  $\rightarrow 1$  possibility:  $000 \rightarrow 12$

In conclusion, we obtain 20 possible transitions for the 000 state (i.e., transitions to states in  $S_{1,2,3} \cup S_{12,3}$ ), corresponding to the 20 terms of the first line of  $F$  and  $Q$ . In each case, the computation of the transition probabilities is immediate.

The expressions for submatrices  $F^{(1)}$ ,  $F^{(2)}$ ,  $F^{(3)}$ ,  $Q$ ,  $L$  and  $R$  are now given below.





$$L = \begin{pmatrix} 00 & 01 & 10 & 11 & 12 \\ (1-m_0)^2(1-\frac{1}{N_0}) & (1-m_0)m_0 & (1-m_0)m_0 & m_0\frac{m_0}{n-1}(1-\frac{1}{N_1}) & m_0m_0(1-\frac{1}{n-1}) \\ (1-m_0)m_1(1-\frac{1}{N_0}) & m_0m_1 & m_0m_1 & (1-m_1)\frac{m_0}{n-1}(1-\frac{1}{N_1}) & (1-m_1)m_0(1-\frac{1}{n-1}) \\ (1-m_0)m_1(1-\frac{1}{N_0}) & m_1m_0 & (1-m_1)(1-m_0) & (1-m_1)\frac{m_0}{n-1}(1-\frac{1}{N_1}) & (1-m_1)m_0(1-\frac{1}{n-1}) \\ m_1^2(1-\frac{1}{N_0}) & m_1(1-m_1) & (1-m_1)m_1 & (1-m_1)^2(1-\frac{1}{N_1}) & 0 \\ m_1^2(1-\frac{1}{N_0}) & (1-m_1)m_1 & (1-m_1)m_1 & 0 & (1-m_1)^2 \end{pmatrix}$$

$$R = \begin{pmatrix} 0 & 1 \\ (1-m_0)\frac{1}{N_0} & m_0\frac{m_0}{n-1}\frac{1}{N_1} \\ (1-m_0)m_1\frac{1}{N_0} & m_0(1-m_1)\frac{1}{N_1} \\ m_1(1-m_0)\frac{1}{N_0} & (1-m_1)\frac{m_0}{n-1}\frac{1}{N_1} \\ m_1^2\frac{1}{N_0} & (1-m_1)^2\frac{1}{N_1} \\ m_1^2\frac{1}{N_0} & 1 \end{pmatrix}$$

## References

1. Allen B, McAvoy A (2019) A mathematical formalism for natural selection with arbitrary spatial and genetic structure. *J Math Biol* 78(4):1147–1210. <https://doi.org/10.1007/s00285-018-1305-z>
2. Allen B, Nowak M (2014) Games on graphs. *EMS Surv Math Sci*. <https://doi.org/10.4171/emss/3>
3. Allen B, Tarnita CE (2014) Measures of success in a class of evolutionary models with fixed population size and structure. *J Math Biol* 68(1):109–143. <https://doi.org/10.1007/s00285-012-0622-x>
4. Allen B, Lippner G, Chen YT et al (2017) Evolutionary dynamics on any population structure. *Nature* 544(7649):227–230. <https://doi.org/10.1038/nature21723>
5. Axelrod R, Hamilton WD (1981) The evolution of cooperation. *Science* 211(4489):1390–1396. <https://doi.org/10.1126/science.7466396>
6. Cannings C (1974) The latent roots of certain Markov chains arising in genetics: a new approach, I. Haploid models. *Adv Appl Probab* 6(2):260–290. <https://doi.org/10.2307/1426293>
7. Chen YT (2013) Sharp benefit-to-cost rules for the evolution of cooperation on regular graphs. *Ann Appl Probab* 23(2):637–664. <https://doi.org/10.1214/12-aap849>
8. Gokhale CS, Traulsen A (2010) Evolutionary games in the multiverse. *Proc Natl Acad Sci* 107(12):5500–5504. <https://doi.org/10.1073/pnas.0912214107>
9. Herbots HM (1994) Stochastic models in population genetics: genealogy and genetic differentiation in structured populations. PhD thesis, University of London
10. Herbots HM (1997) The structured coalescent. In: Donnelly P, Tavaré S (eds) *Progress in population genetics and human evolution*. Springer
11. Hofbauer J, Sigmund K (1988) *The theory of evolution and dynamical systems: mathematical aspects of selection*. Cambridge University Press
12. Hofbauer J, Sigmund K (1998) *Evolutionary games and population dynamics*. Cambridge University Press. <https://doi.org/10.1017/CBO9781139173179>
13. Imhof AL, Nowak AM (2006) Evolutionary game dynamics in a Wright–Fisher process. *J Math Biol* 52(5):667–681. <https://doi.org/10.1007/s00285-005-0369-8>
14. Karlin S, Taylor HM (1975) *A first course in stochastic processes*, 2nd edn. Academic Press
15. Kingman JFC (1982) The coalescent. *Stoch Process Appl* 13(3):235–248. [https://doi.org/10.1016/0304-4149\(82\)90011-4](https://doi.org/10.1016/0304-4149(82)90011-4)
16. Kroumi D, Lessard S (2015a) Conditions for cooperation to be more abundant than defection in a hierarchically structured population. *Dyn Games Appl* 5(2):239–262. <https://doi.org/10.1007/s13235-014-0114-2>
17. Kroumi D, Lessard S (2015b) Strong migration limit for games in structured populations: Applications to dominance hierarchy and set structure. *Games* 6:318–346. <https://doi.org/10.3390/g6030318>
18. Kurokawa S, Ihara Y (2009) Emergence of cooperation in public goods games. *Proc R Soc Lond B: Biol Sci* 276(1660):1379–1384. <https://doi.org/10.1098/rspb.2008.1546>
19. Ladret V, Lessard S (2007) Fixation probability for a beneficial allele and a mutant strategy in a linear game under weak selection in a finite island model. *Theor Popul Biol* 72(3):409–425. <https://doi.org/10.1016/j.tpb.2007.04.001>
20. Ladret V, Lessard S (2008) Evolutionary game dynamics in a finite asymmetric two-deme population and emergence of cooperation. *J Theor Biol* 255(1):137–151. <https://doi.org/10.1016/j.jtbi.2008.07.025>
21. Lessard S (2005) Long-term stability from fixation probabilities in finite populations: new perspectives for ESS theory. *Theor Popul Biol* 68(1):19–27. <https://doi.org/10.1016/j.tpb.2005.04.001>
22. Lessard S (2007) Cooperation is less likely to evolve in a finite population with a highly skewed distribution of family size. *Proc R Soc Lond B: Biol Sci* 274(1620):1861–1865. <https://doi.org/10.1098/rspb.2007.0366>
23. Lessard S (2011a) Effective game matrix and inclusive payoff in group-structured populations. *Dyn Games Appl* 1(2):301. <https://doi.org/10.1007/s13235-011-0014-7>
24. Lessard S (2011b) Evolution of cooperation in finite populations. In: *Proc. sympos. appl. math.*, vol 69. American Mathematical Society, Providence, pp 143–171
25. Lessard S (2011c) On the robustness of the extension of the one-third law of evolution to the multi-player game. *Dyn Games Appl* 1(3):408–418. <https://doi.org/10.1007/s13235-011-0010-y>
26. Lessard S, Ladret V (2007) The probability of fixation of a single mutant in an exchangeable selection model. *J Math Biol* 54(5):721–744. <https://doi.org/10.1007/s00285-007-0069-7>
27. Li A, Wu B, Wang L (2014) Cooperation with both synergistic and local interactions can be worse than each alone. *Sci Rep* 4(1):5536. <https://doi.org/10.1038/srep05536>
28. Li A, Broom M, Du J et al (2016) Evolutionary dynamics of general group interactions in structured populations. *Phys Rev E* 93(2):022407. <https://doi.org/10.1103/PhysRevE.93.022407>
29. Maynard Smith J (1974) The theory of games and the evolution of animal conflicts. *J Theor Biol* 47(1):209–221. [https://doi.org/10.1016/0022-5193\(74\)90110-6](https://doi.org/10.1016/0022-5193(74)90110-6)

30. Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press. <https://doi.org/10.1017/CBO9780511806292>
31. Maynard Smith J, Price GR (1973) The logic of animal conflict. *Nature* 246(5427):15–18. <https://doi.org/10.1038/246015a0>
32. McAvoy A, Allen B (2021) Fixation probabilities in evolutionary dynamics under weak selection. *J Math Biol*. <https://doi.org/10.1007/s00285-021-01568-4>
33. Notohara M (1990) The coalescent and the genealogical process in geographically structured population. *J Math Biol* 29(1):59–75. <https://doi.org/10.1007/BF00173909>
34. Nowak M (2006a) Evolutionary dynamics. Harvard University Press
35. Nowak M, Tarnita C, Antal T (2010) Evolutionary dynamics in structured populations. *Philos Trans R Soc Lond B Biol Sci* 365:19–30. <https://doi.org/10.1098/rstb.2009.0215>
36. Nowak MA (2006b) Five rules for the evolution of cooperation. *Science* 314(5805):1560–1563. <https://doi.org/10.1126/science.1133755>
37. Nowak MA, Sigmund K (2004) Evolutionary dynamics of biological games. *Science* 303(5659):793–799. <https://doi.org/10.1126/science.1093411>
38. Nowak MA, Sasaki A, Taylor C et al (2004) Emergence of cooperation and evolutionary stability in finite populations. *Nature* 428(6983):646–650. <https://doi.org/10.1038/nature02414>
39. Ohtsuki H, Nowak MA (2006) Evolutionary games on cycles. *Proc R Soc Lond B: Biol Sci* 273(1598):2249–2256. <https://doi.org/10.1098/rspb.2006.3576>
40. Ohtsuki H, Hauert C, Lieberman E et al (2006) A simple rule for the evolution of cooperation on graphs and social networks. *Nature* 441(7092):502–505. <https://doi.org/10.1038/nature04605>
41. Ohtsuki H, Pacheco JM, Nowak MA (2007) Evolutionary graph theory: breaking the symmetry between interaction and replacement. *J Theor Biol* 246(4):681–694. <https://doi.org/10.1016/j.jtbi.2007.01.024>
42. Rousset Billiard (2000) A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. *J Evol Biol* 13(5):814–825. <https://doi.org/10.1046/j.1420-9101.2000.00219.x>
43. Rousset F (2003) A minimal derivation of convergence stability measures. *J Theor Biol* 221(4):665–668. <https://doi.org/10.1006/jtbi.2003.3210>
44. Rousset F (2006) Separation of time scales, fixation probabilities and convergence to evolutionary stable states under isolation by distance. *Theor Popul Biol* 69:165–79. <https://doi.org/10.1016/j.tpb.2005.08.008>
45. Sample C, Allen B (2017) The limits of weak selection and large population size in evolutionary game theory. *J Math Biol* 75(5):1285–1317. <https://doi.org/10.1007/s00285-017-1119-4>
46. Soares CD, Lessard S (2020) First-order effect of frequency-dependent selection on fixation probability in an age-structured population with application to a public goods game. *Theor Popul Biol* 133:80–96. <https://doi.org/10.1016/j.tpb.2019.05.001>
47. Szabó G, Fáth G (2007) Evolutionary games on graphs. *Phys Rep* 446(4):97–216. <https://doi.org/10.1016/j.physrep.2007.04.004>
48. Taylor PD, Jonker LB (1978) Evolutionary stable strategies and game dynamics. *Math Biosci* 40(1):145–156. [https://doi.org/10.1016/0025-5564\(78\)90077-9](https://doi.org/10.1016/0025-5564(78)90077-9)
49. Traulsen A, Pacheco JM, Imhof LA (2006) Stochasticity and evolutionary stability. *Phys Rev Lett E* 3:74(2):021,905. <https://doi.org/10.1103/PhysRevE.74.021905>
50. Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46(1):35–57. <https://doi.org/10.1086/406755>
51. van Veelen M, Nowak MA (2012) Multi-player games on the cycle. *J Theor Biol* 292:116–128. <https://doi.org/10.1016/j.jtbi.2011.08.031>
52. Wilkinson-Herbots MH (1998) Genealogy and subpopulation differentiation under various models of population structure. *J Math Biol* 37(6):535–585. <https://doi.org/10.1007/s002850050140>
53. Wright S (1931) Evolution in Mendelian populations. *Genetics* 16(2):97–159

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.