

# EVOLUTION OF COOPERATION IN FINITE POPULATIONS

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**ABSTRACT.** The Iterated Prisoner's Dilemma with an additive effect on viability selection as payoff is used to study the evolution of cooperation in finite populations. A condition for weak selection to favor Tit-for-Tat replacing Always-Defect when introduced as a single mutant strategy in a well-mixed population is deduced from the sum of all future expected changes in frequency. It is shown by resorting to coalescent theory that the condition reduces to the one-third law of evolution in the realm of the Kingman coalescent in the limit of a large population size. The condition proves to be more stringent when the reproductive success of an individual is a random variable having a highly skewed probability distribution. An explanation of the one-third law of evolution based on the notion of projected average excess in payoff is provided. A two-timescale argument is applied for group-structured populations. The condition is found to be less stringent in the case of uniform dispersal of offspring followed by interactions within groups. The condition becomes even less stringent if dispersal occurs after interactions so that there are differential contributions of groups in offspring. On the other hand, the condition is strengthened by a highly skewed probability distribution for the contribution of a group in offspring.

## 1. INTRODUCTION

Al though cooperation is widespread in nature, its evolution is difficult to explain. The main problem is that cooperation did not always exist and before being common in a population it must have been rare. But the advantage of cooperation when rare is not obvious. In order to study the advantage of cooperation and understand its evolution, we will consider a game-theoretic framework based on pairwise interactions.

In the Prisoner's Dilemma (PD) two accomplices in committing a crime are arrested and each one can either defect ( $D$ ) by testifying against the other or cooperate with the other ( $C$ ) by remaining silent. Each of the accomplices receives a light sentence corresponding to some reward ( $R$ ) when both cooperate, compared to a heavy sentence corresponding to a punishment ( $P$ ) when both defect. When one defects and the other cooperates the defector receives a lighter sentence represented by some temptation ( $T$ ), while the cooperator receives a heavier sentence represented by the sucker's payoff ( $S$ ). Therefore, the payoffs in the PD game satisfy the inequalities  $T > R > P > S$ . The situation is summarized in Fig. 1 with some particular values for the different payoffs.

Note that the payoff to strategy  $C$  is smaller than the payoff to strategy  $D$  whatever the strategy of the opponent is. If pairwise interactions occur at random in an infinite population, then the expected payoff to  $C$  can only be smaller than the expected payoff to  $D$ . Moreover, if the reproductive success of an individual is an increasing function of the payoff and true breeding is assumed so that an offspring uses the same strategy as its parent, then  $C$  is not expected to increase in frequency.

In order to find conditions that could favor the evolution of cooperation the PD game is extended by assuming  $n$  rounds of the game between the same players. This is known as

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Cooperate	Reward 5	Sucker's payoff 1
Defect	Temptation 14	Punishment 3
against	Cooperate	Defect

FIGURE 1. Payoffs in the PD game with some particular values.

the Iterated Prisoner's Dilemma (IPD). Then two sequential strategies are considered: Tit-for-Tat, represented by  $A$ , and Always-Defect, represented by  $B$ . Always-Defect consists obviously in defecting in every round, while Tit-for-Tat consists in cooperating in the first round and then using the previous strategy of the opponent in the next rounds. Note that two players using Tit-for-Tat will always cooperate. Moreover, Tit-for-Tat has proved to do better than any other sequential strategy in computer experiments. See, e.g., Axelrod (1984) or Hofbauer and Sigmund (1998, Chap. 9) and references therein for more details and historical perspectives.

Let us assume that the payoffs in the different repetitions of the IPD game are additive. Then the payoffs to  $A$  against  $A$ ,  $A$  against  $B$ ,  $B$  against  $A$ , and  $B$  against  $B$ , denoted by  $a, b, c$ , and  $d$ , respectively, take the expressions given in Fig. 2. What is important is that these payoffs satisfy the inequalities  $a > c > d > b$  as soon as the number of repetitions is large enough, that is,

$$(1.1) \quad n > \frac{T - P}{R - P}.$$

Actually this is a necessary and sufficient condition for the payoff to  $A$  against  $A$  to exceed the payoff to  $B$  against  $A$ . This is the case, for instance, when  $n = 10$  with the payoffs of the PD game given in Fig. 1. The consequence of this is that the expected payoff to  $A$  will exceed the expected payoff to  $B$  in an infinite population with random pairwise interactions if the frequency of  $A$  exceeds some threshold value.

As a matter of fact, if the frequencies of  $A$  and  $B$  in an infinite population are  $x$  and  $1 - x$ , respectively, then the expected payoffs to  $A$  and  $B$  are

$$(1.2) \quad w_A(x) = ax + b(1 - x)$$

and

$$(1.3) \quad w_B(x) = cx + d(1 - x),$$

respectively. Therefore,  $w_A(x) > w_B(x)$  if and only if

$$(1.4) \quad x > \frac{d - b}{a - b - c + d} = x^*.$$

Tit-for-Tat ( <i>A</i> )	$a = Rn$ 50	$b = S + P(n - 1)$ 28
Always-Defect ( <i>B</i> )	$c = T + P(n - 1)$ 41	$d = Pn$ 30
against	<i>A</i>	<i>B</i>

FIGURE 2. Payoffs in the IPD game with particular values in the case  $n = 10$  with the numerical payoffs of the PD game given in Fig. 1.

With the expressions of the different payoffs given in Fig. 2, we find that

$$(1.5) \quad x^* = \frac{P - S}{(P - S) + (R - P) \left( n - \frac{T - P}{R - P} \right)}.$$

This threshold value for  $x$  decreases from 1 to 0 as  $n$  increases from  $(T - P)/(R - P)$  to infinity, but remains always positive. This suggests that the frequency of *A* in an infinite population can increase, but only if the initial frequency is high enough.

## 2. DYNAMICS IN AN INFINITE POPULATION

Consider an infinite haploid population undergoing discrete, non-overlapping generations and suppose random pairwise interactions among the offspring of the same generation. These interactions are assumed to have an additive effect on viability. More precisely the probability for an individual to survive from conception to maturity, and then to contribute to the next generation, is proportional to some fitness given in the form

$$(2.1) \quad \text{fitness} = 1 + s \times \text{payoff}.$$

Here, 1 is an arbitrary reference value and  $s \geq 0$  represents an intensity of viability selection whose coefficient is the payoff to the individual. The intensity of selection will be assumed small throughout the paper. The case  $s = 0$  corresponds to neutrality.

Let  $x(t)$  be the frequency of *A* in generation  $t$  before selection. As a result of random pairwise interactions, the probability for an individual of type *A* to survive will be  $1 + sw_A(x(t))$  compared to  $1 + sw_B(x(t))$  for an individual of type *B*. Then the frequency of *A* in generation  $t$  after selection will be

$$(2.2) \quad \tilde{x}(t) = \frac{x(t)(1 + sw_A(x(t)))}{1 + sw(x(t))},$$

where

$$(2.3) \quad w(x(t)) = x(t)w_A(x(t)) + (1 - x(t))w_B(x(t))$$

is the mean payoff in generation  $t$ . After reproduction and in the absence of mutation, this frequency will be also the frequency of  $A$  in the offspring of generation  $t + 1$ , that is,  $x(t + 1) = \tilde{x}(t)$ . Therefore, the change in the frequency of  $A$  before selection from generation  $t$  to generation  $t + 1$ , represented by  $\Delta x(t) = x(t + 1) - x(t)$ , will be given by

$$(2.4) \quad \Delta x(t)\tilde{x}(t) - x(t) = \frac{sx(t)(1-x(t))(w_A(x(t)) - w_B(x(t)))}{1 + sw(x(t))},$$

where

$$(2.5) \quad w_A(x(t)) - w_B(x(t)) = (a - b - c + d)(x(t) - x^*).$$

We conclude that  $\Delta x(t) = 0$  if and only if  $x(t) = 0, 1$  or  $x^*$ , which are the stationary states. Moreover, since  $a - b - c + d > 0$  and  $0 < x^* < 1$ , we have that  $\Delta x(t) > 0$  if  $x(t) > x^*$ , while  $\Delta x(t) < 0$  if  $x(t) < x^*$ . Therefore,  $x(t)$  increases as  $t \rightarrow \infty$  if  $x(0) > x^*$ , while it decreases if  $x(0) < x^*$ . Actually  $x(t)$  increases to 1 in the former case, while  $x(t)$  decreases to 0 in the latter case, since the limit of  $x(t)$  as  $t \rightarrow \infty$  must be a stationary state by continuity.

Let us summarize.

**Proposition 1.** *Consider the IPD game in Fig. 2 with a number of rounds satisfying  $n > (T - P)/(R - P)$  so that the payoffs satisfy  $a > c > d > b$ . Assume random pairwise interactions in an infinite population undergoing discrete, non-overlapping generations and viability selection of intensity  $s$  with coefficient given by the payoff. The frequency of  $A$  in generation  $t$  before selection,  $x(t)$ , satisfies*

$$(2.6) \quad x(t) \uparrow 1 \text{ if } x(0) > x^* \text{ and } x(t) \downarrow 0 \text{ if } x(0) < x^*,$$

where

$$(2.7) \quad x^* = \frac{d - b}{a - b - c + d}$$

is a stationary state in  $(0, 1)$  for the deterministic dynamics.

Proposition 1 means that  $x^*$  is an unstable polymorphic equilibrium, while 0 and 1 are monomorphic stable equilibria. Unfortunately this cannot explain the spread of  $A$  from an initial low frequency following its introduction as a rare mutant strategy.

### 3. FIXATION PROBABILITY IN A FINITE POPULATION

In a finite population, random drift that results from sampling effects can ultimately bring the frequency of  $A$  to fixation from any low initial frequency. In this section we consider the probability of this event.

Each generation starts with  $N$  parents labeled from 1 to  $N$ . These produce virtually infinite numbers of offspring identical to themselves in the relative proportions  $\pi_1, \dots, \pi_N$ , respectively. The population size  $N$  is assumed to be finite and constant. The proportions  $\pi_1, \dots, \pi_N$  are exchangeable random variables. This means that the joint distribution is invariant under any permutation. Furthermore, they satisfy  $0 \leq \pi_i \leq 1$  for  $i = 1, \dots, N$  and  $\sum_{i=1}^N \pi_i = 1$ . In particular this implies that the expected proportion of offspring produced by each parent is the same. It is given by

$$(3.1) \quad E(\pi_1) = N^{-1} \sum_{i=1}^N E(\pi_i) = N^{-1} E \left( \sum_{i=1}^N \pi_i \right) = N^{-1}.$$

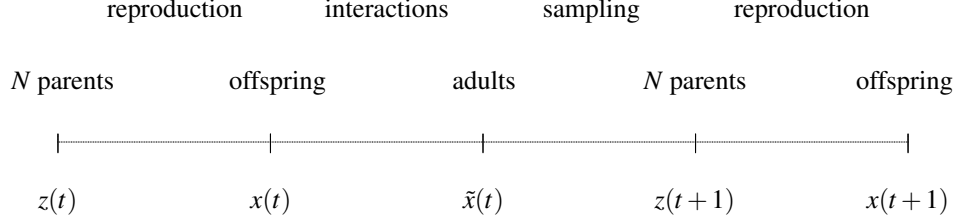


FIGURE 3. Life cycle from generation  $t$  to generation  $t+1$  and notation for the frequency of  $A$  in the whole population at each step.

Moreover, it is assumed that

$$(3.2) \quad c_N = NE(\pi_1^2) = \sum_{i=1}^N E(\pi_i^2) \rightarrow 0$$

as  $N \rightarrow \infty$ . This says that the probability for two offspring chosen at random without replacement to have the same parent tends to 0 as the population size increases.

The Wright-Fisher model (Fisher 1930, Wright 1931) corresponds to the situation where  $\pi_i = N^{-1}$  for  $i = 1, \dots, N$ . In this case, we have  $c_N = N^{-1}$ .

A modified Wright-Fisher model with a skewed distribution of progeny size can be obtained by allowing for  $\pi_i = \psi$  for some  $i$  chosen at random and  $\pi_j = (1 - \psi)(N - 1)^{-1}$  for every  $j \neq i$ , for some fixed  $0 < \psi < 1$ . A combination of this reproduction scheme with probability  $N^{-\alpha}$  and the Wright-Fisher scheme with the complementary probability  $1 - N^{-\alpha}$ , and this for each generation, has been considered and applied to oysters for instance (Eldon and Wakeley 2006). In this case, we find that

$$(3.3) \quad c_N = \frac{1}{N} \left( 1 - \frac{1}{N^\alpha} \right) + \frac{1}{N^\alpha} \left( \psi^2 + \frac{(1 - \psi)^2}{N - 1} \right),$$

whose leading term is  $\psi^2 N^{-\alpha}$  if  $0 < \alpha < 1$ , but  $(1 + \psi)^2 N^{-1}$  if  $\alpha = 1$ , and  $N^{-1}$  if  $\alpha > 1$ .

The general situation of exchangeable proportions of offspring produced by the  $N$  parents each generation corresponds to the Cannings model (Cannings 1974).

The frequency of  $A$  in the parents of generation  $t$  is represented by a random variable  $z(t)$ . This random variable can take only the values  $i/N$  for  $i = 0, 1, \dots, N$ . The frequency of  $A$  in the offspring of generation  $t$  is represented by  $x(t)$ , which has the same expected value as  $z(t)$ . This frequency becomes  $\tilde{x}(t)$  as defined in the previous section in the adults of generation  $t$  after viability selection as a result of random pairwise interactions among the offspring. Then  $N$  adults are chosen at random to be the parents of the offspring of generation  $t+1$ . The frequency of  $A$  in these parents is  $z(t+1)$ . The conditional distribution of  $z(t+1)$  given  $x(t)$  is the distribution of a binomial random variable of parameters  $N$  and  $\tilde{x}(t)$ , divided by  $N$ . In particular, the conditional expected value of  $z(t+1)$  is  $\tilde{x}(t)$ , which is the same as the conditional expected value of  $x(t+1)$ . (See Fig. 3 for a schematic representation of the life cycle.)

Actually  $z(t)$  for  $t \geq 0$  is a Markov chain on the finite state space  $\{i/N : i = 0, 1, \dots, N\}$  with fixation states 0 and 1, all other states being transient. From any initial state  $z(0)$ , the chain will hit 0 or 1 in a finite time with probability 1 owing to the ergodic theorem. Actually as  $t \rightarrow \infty$  the chain  $z(t)$  will converge in probability to a random variable  $z(\infty)$

that takes the value 1 with some probability  $u(s)$ , which is the probability for the chain to hit 1 before 0, and the value 0 with the complementary probability  $1 - u(s)$ . Here,  $u(s)$  represents the probability of ultimate fixation of  $A$  as a function of the intensity of selection.

Note that

$$(3.4) \quad u(s) = E_s[z(\infty)],$$

where  $E_s$  denotes expectation as a function of  $s$ . Moreover  $u(0) = z(0)$ , since one of the offspring in the initial generation will be the ancestor of the whole population in the long run, and it will be one offspring chosen at random in the initial generation by symmetry if no selection takes place.

Being uniformly bounded by 1, the chain will also converge in mean. Therefore, we have

$$(3.5) \quad \begin{aligned} E_s[z(\infty)] &= \lim_{T \rightarrow \infty} E_s[z(T)] \\ &= \lim_{T \rightarrow \infty} E_s \left[ z(0) + \sum_{t=0}^T (z(t+1) - z(t)) \right] \\ &= z(0) + \lim_{T \rightarrow \infty} \sum_{t=0}^T E_s[z(t+1) - z(t)] \\ &= z(0) + \sum_{t=0}^{\infty} E_s[z(t+1) - z(t)]. \end{aligned}$$

On the other hand, the tower property of conditional expectation and (2.4) yield

$$(3.6) \quad \begin{aligned} E_s[z(t+1) - z(t)] &= E_s[x(t+1) - x(t)] \\ &= E_s[E_s[x(t+1) - x(t)|x(t)]] \\ &= E_s[\tilde{x}(t) - x(t)] \\ &= s(a - b - c + d)E_s \left[ \frac{x(t)(1 - x(t))(x(t) - x^*)}{1 + sw(x(t))} \right] \\ &= s(a - b - c + d)E[x(t)(1 - x(t))(x(t) - x^*)] + o(s), \end{aligned}$$

where  $E$  denotes expectation in the absence of selection, that is,  $E_s$  when  $s = 0$ , while  $|o(s)|/s \rightarrow 0$  as  $s \rightarrow 0$ . This leads to the approximation

$$(3.7) \quad u(s) = u(0) + s(a - b - c + d) \sum_{t=0}^{\infty} E[x(t)(1 - x(t))(x(t) - x^*)] + o(s)$$

for the probability of ultimate fixation of  $A$  under weak selection.

The above approach was suggested in Rousset (2003) and ascertained in Lessard and Ladret (2007) under mild regularity conditions on the transition probabilities of the Markov chain. Actually it suffices that these probabilities and their derivatives are continuous functions of  $s$  at  $s = 0$ , which is the case here.

The following definition was introduced in Nowak *et al.* (2004).

**Definition 1.** *Selection favors  $A$  replacing  $B$  if the probability of ultimate fixation of  $A$  is larger in the presence of selection than in the absence of selection.*

The inequality  $u(s) > u(0)$  for  $s > 0$  small enough guarantees that weak selection favors  $A$  replacing  $B$ . This will be the case if  $u'(0) > 0$ , where

$$(3.8) \quad u'(0) = (a - b - c + d) \sum_{t=0}^{\infty} E[x(t)(1-x(t))(x(t) - x^*)]$$

is the derivative of the fixation probability with respect to the intensity of selection evaluated at  $s = 0$ . The condition  $a - b - c + d > 0$  leads to the following conclusion.

**Proposition 2.** *Assume that the offspring of generation  $t$  are produced in infinite numbers in exchangeable proportions by a fixed finite number  $N$  of adults chosen at random in the previous generation and that they undergo viability selection according to the IPD game as in Proposition 1. Weak selection favors  $A$  replacing  $B$  if*

$$(3.9) \quad x^* < \frac{\sum_{t \geq 0} E[x(t)^2(1-x(t))]}{\sum_{t \geq 0} E[x(t)(1-x(t))]} = \hat{x},$$

where  $x(t)$  is the frequency of  $A$  in the offspring of generation  $t$  and  $E$  denotes expectation under neutrality.

Note that the condition for  $A$  to be favored for replacement under weak selection is more stringent if the upper bound  $\hat{x}$  defined in Proposition 2, which satisfies  $0 < \hat{x} < 1$ , is closer to 0.

#### 4. GENERALIZED ONE-THIRD LAW OF EVOLUTION

In this section we calculate the upper bound  $\hat{x}$  in Proposition 2. This is done under the assumption that  $A$  is initially a single mutant, that is,  $u(0) = z(0) = N^{-1}$ . Moreover, all calculations are made under neutrality.

First note that  $E[x(t)(1-x(t))]$  is the probability for two offspring chosen at random without replacement in generation  $t$  to be of types  $A$  and  $B$  in this order. This is a consequence of the tower property of conditional expectation. As a matter of fact, using the indicator random variable  $\xi_i(t) = 1$  if the  $i$ -th offspring chosen at random without replacement in generation  $t$  is of type  $A$ , and 0 otherwise, for  $i = 1, 2$ , we have

$$(4.1) \quad E[x(t)(1-x(t))] = E[E[\xi_1(t)(1-\xi_2(t))|x(t)]] = E[\xi_1(t)(1-\xi_2(t))].$$

Going backwards in time from generation  $t$  to generation 0, we obtain

$$(4.2) \quad E[\xi_1(t)(1-\xi_2(t))] = \frac{p_{22}(t+1)}{N},$$

where  $p_{22}(t+1) = p_{22}^{t+1}$  is the probability that two offspring chosen at random without replacement in generation  $t$  descend from two distinct ancestral parents in generation 0, and  $1/N$  the probability that the ancestral parent of the first offspring is of type  $A$ . Then necessarily the ancestral parent of the second offspring will be of type  $B$ , since  $A$  is represented only once in the initial generation. Here, the quantity  $p_{22}$  denotes the probability for two offspring chosen at random without replacement in the same generation to have different parents. Therefore,

$$(4.3) \quad \sum_{t \geq 0} E[x(t)(1-x(t))] = \frac{p_{22}}{N(1-p_{22})}.$$

Similarly,

$$(4.4) \quad E[x(t)^2(1-x(t))] = E[\xi_1(t)\xi_2(t)(1-\xi_3(t))] = \frac{p_{32}(t+1)}{3N},$$

where  $p_{32}(t+1)$  represents the probability that three offspring chosen at random without replacement in generation  $t$  descend from two distinct ancestral parents in generation 0 and  $1/3$  is the conditional probability that it is then the first two offspring that descend from the same ancestral parent (see Fig. 4.). Here,

$$(4.5) \quad p_{32}(t+1) = \sum_{r=0}^t p_{33}^{t-r} p_{32} p_{22}^r = p_{32} \frac{p_{33}^{t+1} - p_{22}^{t+1}}{p_{33} - p_{22}},$$

where

$$(4.6) \quad p_{ij} = \sum_{\substack{a_1 + \dots + a_j = i \\ a_1, \dots, a_j \geq 1}} E \left( \prod_{r=1}^j \pi_r^{a_r} \right)$$

represents the probability that  $i$  offspring chosen at random without replacement in the same generation have  $j$  distinct parents. This leads to

$$(4.7) \quad \sum_{t \geq 0} E [x(t)^2 (1 - x(t))] = \frac{p_{32}}{3N(1 - p_{22})(1 - p_{33})}.$$

Finally we obtain

$$(4.8) \quad \hat{x} = \frac{p_{32}}{3p_{22}(1 - p_{33})}$$

for the upper bound in Proposition 2. Note that

$$(4.9) \quad p_{22} = 1 - c_N \rightarrow 1,$$

as  $N \rightarrow \infty$ , and

$$(4.10) \quad p_{32} \leq p_{32} + p_{31} = 1 - p_{33},$$

which complete the proof of the following statement.

**Proposition 3.** *In the case of a single initial A, the upper bound  $\hat{x}$  in the condition given in Proposition 2 for weak selection to favor A replacing B satisfies*

$$(4.11) \quad \lim_{N \rightarrow \infty} \hat{x} = \lim_{N \rightarrow \infty} \frac{p_{32}}{3(1 - p_{33})} \leq \frac{1}{3},$$

where  $p_{ij}$  is the probability that  $i$  offspring chosen at random without replacement in the same generation have  $j$  distinct parents.

An equality on the right-hand side of the equation in Proposition 3 gives the weakest condition for A to be favored for replacement under weak selection. This is known as the one-third law of evolution (Nowak *et al.* 2004).

**Definition 2.** *The one-third law of evolution states that weak selection favors a single A replacing B in the limit of a large population size if  $x^* < 1/3$ .*

According to Proposition 3, the one-third law of evolution holds if and only if at most two lineages out of three coalesce at a time backwards in time with probability 1 in the limit of a large population size. This is the necessary and sufficient condition for the limiting backward process of the neutral Cannings model with  $c_N^{-1}$  generations as unit of time to be the Kingman coalescent (Kingman 1982, Möhle 2000, Möhle and Sagitov 2001).

Let us recall that the number of lineages backwards in time under the Kingman coalescent is a death process on the positive integers with death rate from  $k \geq 1$  to  $k - 1$  given by



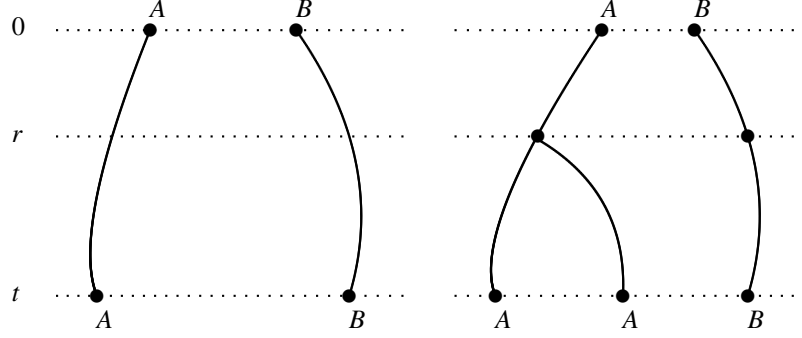


FIGURE 4. Lineages of two offspring of types  $A, B$  and three offspring of types  $A, A, B$  from generation  $t$  to generation  $0$ .

$\lambda_k = k(k-1)/2$ . This means that each pair of lineages coalesces with rate 1 independently of each other.

The above conclusion first drawn in Lessard and Ladret (2007) shows that the one-third law of evolution originally deduced for the Moran model (Nowak *et al.* 2004) and the Wright-Fisher model (Lessard 2005, Imhof and Nowak 2006) holds for a wide class of models. Moreover it shows how the one-third law extends beyond this class. Note that the Moran model (Moran 1958) assumes overlapping generations with one individual replaced at a time, but such models lead to the same conclusion (Lessard and Ladret 2007, Lessard 2007a).

In the case of the Eldon-Wakeley model with probability  $N^{-\alpha}$  for a random parent to produce a fraction  $\psi$  of all offspring (Eldon and Wakeley 2006), we find that

$$(4.12) \quad p_{31} = \frac{1}{N^2} \left(1 - \frac{1}{N^\alpha}\right) + \frac{1}{N^\alpha} \left(\psi^3 + \frac{(1-\psi)^3}{(N-1)^2}\right)$$

and

$$(4.13) \quad p_{32} = \frac{3}{N} \left(1 - \frac{1}{N}\right) \left(1 - \frac{1}{N^\alpha}\right) + \frac{3(1-\psi)}{N^\alpha} \left(\psi^2 + \frac{1-\psi}{N-1} - \frac{(1-\psi)^2}{(N-1)^2}\right).$$

In this case,

$$(4.14) \quad \lim_{N \rightarrow \infty} \frac{p_{32}}{3(1-p_{33})} = \begin{cases} \frac{1}{3} & \text{if } \alpha > 1, \\ \frac{1-\psi}{3-2\psi} & \text{if } \alpha < 1, \\ \frac{1+\psi^2(1-\psi)}{3+\psi^3(3-2\psi)} & \text{if } \alpha = 1. \end{cases}$$

The limit is strictly less than  $1/3$  if and only if  $\alpha \leq 1$ . This means a more stringent condition for  $A$  to be favored for replacement under weak selection when the distribution of progeny size is highly skewed.

Note that  $\alpha \leq 1$  is the condition for the limit backward process of the neutral Eldon-Wakeley model with  $c_N^{-1}$  generations as unit of time to be a  $\Lambda$ -coalescent allowing for multiple mergers involving more than two lineages (Pitman 1999, Sagitov 1999). In the

case  $\alpha < 1$ , the rate of an  $m$ -merger among  $k$  lineages is given by

$$(4.15) \quad \lambda_{k,m} = \binom{k}{m} \psi^{m-2} (1-\psi)^{k-m},$$

for  $m = 2, \dots, k$ .

## 5. EXPLANATION FOR THE ONE-THIRD LAW OF EVOLUTION: PROJECTED AVERAGE EXCESS

The following explanation for the one-third law of evolution in the limit of a large Moran or Wright-Fisher population has been proposed (Ohtsuki *et al.* 2007): in an invasion attempt by a single mutant of type  $A$  up to extinction or fixation in the absence of selection,  $A$ -players effectively interact on average with  $B$ -players twice as often as with  $A$ -players. The argument is based on the mean effective sojourn times in the different population states. These can be obtained exactly for the Moran model and approximated for the Wright-Fisher model (Fisher 1930, p. 90).

In this section, we propose another explanation based on the notion of projected average excess (Lessard and Lahaie 2009). This is an extension of the classical notion of average excess in fitness for a gene substitution (Fisher 1930). Here, we consider the excess in payoff for a mutant strategy not only in the current generation but also in all future generations.

First observe that

$$(5.1) \quad \sum_{t \geq 0} E[x(t)(1-x(t))] = \frac{p_{22}E(S_2)}{N}$$

and

$$(5.2) \quad \sum_{t \geq 0} E[x(t)^2(1-x(t))] = \frac{E(S_2) - E(S_3)}{2N},$$

where  $S_2$  and  $S_3$  represent the numbers of generations spent backwards in time with two and three lineages, respectively, before the first coalescence event occurs. As a matter of fact, we have

$$(5.3) \quad E(S_2) = \frac{1}{1-p_{22}}$$

and

$$(5.4) \quad E(S_3) = \frac{1}{1-p_{33}},$$

so that

$$(5.5) \quad E(S_2) - E(S_3) = \frac{p_{22} - p_{33}}{(1-p_{22})(1-p_{33})}.$$

Moreover, we have

$$(5.6) \quad p_{22} - p_{33} = \frac{2p_{32}}{3},$$

which are two different expressions for the probability that exactly two given offspring out of three chosen at random without replacement have different parents. Therefore, the above equalities agree with the corresponding expressions given in the previous section.

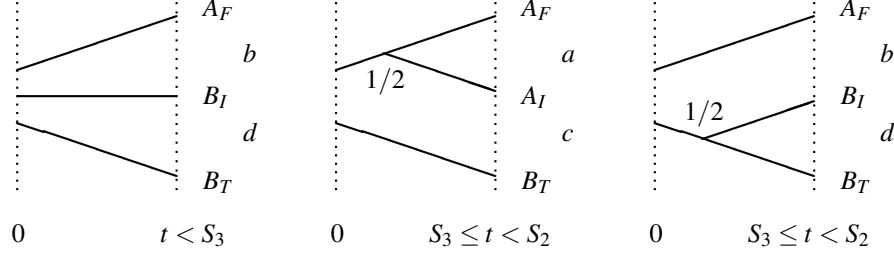


FIGURE 5. Average excess in payoff for  $A$  in generation  $t$ . The indices  $F$ ,  $T$  and  $I$  are used for focal, typical and interacting offspring, respectively. Only typical offspring of type  $B$  have to be considered. The coalescence time  $S_2$  is for  $F$  and  $T$ , while  $S_3$  is for  $F$ ,  $T$  and  $I$ .

On the other hand, the first derivative of the probability of ultimate fixation of  $A$  with respect to the intensity of selection evaluated at  $s = 0$  can be written as

$$(5.7) \quad u'(0) = (a-c) \sum_{t=0}^{\infty} E [x(t)^2(1-x(t))] + (b-d) \sum_{t=0}^{\infty} E [x(t)(1-x(t))^2],$$

where

$$(5.8) \quad E [x(t)(1-x(t))^2] = E [x(t)(1-x(t))] - E [x(t)^2(1-x(t))].$$

Then, the above equalities and the assumption that  $c_N = 1 - p_{22} \rightarrow 0$  as  $N \rightarrow \infty$  lead to the approximation

$$(5.9) \quad u'(0) \approx (a-c) \left( \frac{E(S_2) - E(S_3)}{2N} \right) + (b-d) \left( \frac{E(S_2) + E(S_3)}{2N} \right).$$

This can be written in the form

$$(5.10) \quad u'(0) \approx \frac{1}{N} \left\{ \left( \frac{a-c+b-d}{2} \right) (E(S_2) - E(S_3)) + (b-d)E(S_3) \right\}.$$

The fraction  $N^{-1}$  is the frequency of  $A$  in the initial generation, while the expression in curly brackets represents its projected average excess in payoff. This is the sum of the differences between the marginal payoff to  $A$  and the mean payoff to a competitor in the same generation over all generations  $t \geq 0$  as long as fixation is not reached.

The concept of projected average excess in payoff for  $A$  can be better understood with the help of Fig. 5. Consider a focal offspring ( $F$ ) of type  $A$  in generation  $t \geq 0$ . We want to compare its marginal payoff to the mean payoff in the same generation. This mean will be the expected payoff to a typical offspring ( $T$ ) chosen at random in the same generation. If this offspring has the same ancestor in generation 0 as the focal offspring, then its marginal payoff will also be the same. Therefore, it suffices to consider the case of distinct ancestors for  $F$  and  $T$  in generation 0. Then a third offspring ( $I$ ) is chosen at random in the same generation and it may interact with either  $F$  or  $T$ .

Let  $S_3$  be the number of generations backwards in time for the first coalescence event in the genealogies of the three offspring  $F$ ,  $T$ , and  $I$ , and  $S_2$  be the corresponding number for  $F$  and  $T$  only. If  $t < S_3$ , the three ancestors in generation 0 are all distinct and therefore

$T$  and  $I$  are both of type  $B$ . Then the payoff to  $F$  would be  $b$  compared to  $d$  for  $T$ . On the other hand, if  $S_3 \leq t < S_2$  with  $F$  and  $I$  having a common ancestor in generation 0, whose conditional probability is  $1/2$ , then  $F$  and  $I$  are of type  $A$ , while  $T$  is of type  $B$ . This gives a payoff  $a$  to  $T$  compared to  $c$  to  $T$ . Finally, if  $S_3 \leq t < S_2$  but with  $F$  and  $I$  having a common ancestor in generation 0, whose conditional probability is  $1/2$ , then  $T$  and  $I$  are of type  $B$ , while  $F$  is of type  $A$ . In this case, the payoff to  $F$  is  $b$  compared to  $d$  for  $T$ . In all other cases,  $F$  and  $T$  would be of the same type  $A$ , and then they would have the same payoff.

The final argument for the interpretation follows from the facts that

$$(5.11) \quad \sum_{t=0}^{\infty} P(S_3 > t) = E(S_3)$$

and

$$(5.12) \quad \sum_{t=0}^{\infty} P(S_3 \leq t < S_2) = \sum_{t=0}^{\infty} (P(S_2 > t) - P(S_3 > t)) = E(S_2) - E(S_3).$$

Scaled expected times in the limit of a large population size are obtained by multiplying  $S_2$  and  $S_3$  by  $c_N$  and by letting  $N$  tend to infinity, that is,

$$(5.13) \quad \mu_i = \lim_{N \rightarrow \infty} E(c_N S_i),$$

for  $i = 2, 3$ . Then the sign of the first derivative of the probability of ultimate fixation of  $A$ , and therefore whether or not weak selection favors  $A$  for replacement, is given by the sign of a scaled projected average excess in fitness.

Let us summarize.

**Proposition 4.** *In the case of a single initial  $A$  and in the limit of a large population size, the condition given in Propositions 2 and 3 for weak selection to favor  $A$  replacing  $B$  is equivalent to*

$$(5.14) \quad a_A = \left( \frac{a - c + b - d}{2} \right) (\mu_2 - \mu_3) + (b - d)\mu_3 > 0,$$

where  $\mu_2$  and  $\mu_3$  designate expected times, in number of  $c_N^{-1}$  generations in the limit of a large population size, with two and three lineages, respectively, and  $a_A$  represents a scaled projected average excess in payoff of  $A$ .

Note that

$$(5.15) \quad \mu_2 \geq 3\mu_3,$$

and the one-third law of evolution

$$(5.16) \quad x^* = \frac{d - b}{a - b - c + d} < \frac{1}{3}$$

is obtained when  $\mu_2 = 3\mu_3$ , which occurs with  $\mu_2 = 1$  in the case of the Kingman coalescent.

## 6. ISLAND MODEL WITH DISPERSAL PRECEDING SELECTION

In this section we examine the effect of a group structure on the condition for a single  $A$  to be favored for replacing  $B$ . Actually we consider the Wright (1931) island model for a population subdivided into a finite number of groups of the same size, assuming a Wright-Fisher reproduction scheme within groups and partial uniform dispersal of offspring before selection.

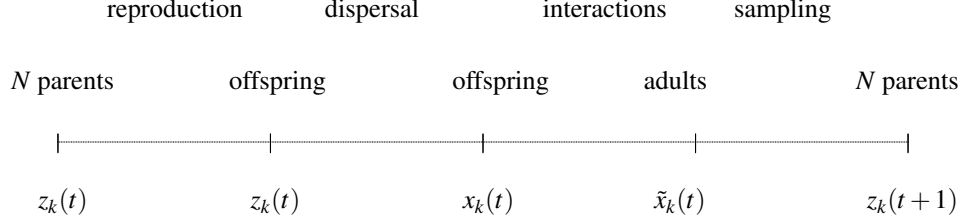


FIGURE 6. Life cycle from generation  $t$  to generation  $t+1$  and notation for the frequency of  $A$  in group  $k$  at each step in the island model with dispersal before selection.

We have  $D$  groups of  $N$  parents producing virtually infinite numbers of offspring in equal relative proportions, that is,  $(ND)^{-1}$  for each parent. We suppose that a fixed proportion  $m$  of offspring disperse uniformly among all groups, while the complementary proportion  $1-m$  stay in their native group. This is followed by random pairwise interactions within groups affecting viability as previously. Finally  $N$  parents are sampled at random in each group to start the next generation.

Under the assumption of a Wright-Fisher reproduction scheme, the frequency of  $A$  in the offspring in group  $k$  in generation  $t$  before dispersal, for  $k = 1, \dots, D$  and  $t \geq 0$ , is the same as the frequency of  $A$  in the parents of group  $k$  at the beginning of generation  $t$ , denoted by  $z_k(t)$ . Then this frequency becomes

$$(6.1) \quad x_k(t) = (1-m)z_k(t) + m\overline{z(t)}$$

in the offspring after dispersal, and

$$(6.2) \quad \tilde{x}_k(t) = \frac{x_k(t)(1 + sw_A(x_k(t)))}{1 + sw(x_k(t))}$$

in the offspring after selection. Here,

$$(6.3) \quad \overline{z(t)} = D^{-1} \sum_{k=1}^D z_k(t) = D^{-1} \sum_{k=1}^D x_k(t) = \overline{x(t)}$$

is the frequency of  $A$  in all parents of generation  $t$ , which is the same as the frequency of  $A$  in all their offspring before dispersal as well as after dispersal, but before selection (see Fig. 6).

Proceeding as previously, we find that the probability of ultimate fixation of  $A$  is

$$(6.4) \quad \begin{aligned} u(s) &= E_s \left[ \overline{z(\infty)} \right] \\ &= \overline{z(0)} + \sum_{t=0}^{\infty} E_s \left[ \overline{z(t+1)} - \overline{z(t)} \right] \\ &= u(0) + D^{-1} \sum_{t=0}^{\infty} \sum_{k=1}^D E_s [\tilde{x}_k(t) - x_k(t)], \end{aligned}$$

where

$$(6.5) \quad E_s [\tilde{x}_k(t) - x_k(t)] = s(a-b-c+d)E [x_k(t)(1-x_k(t))(x_k(t)-x^*)] + o(s).$$

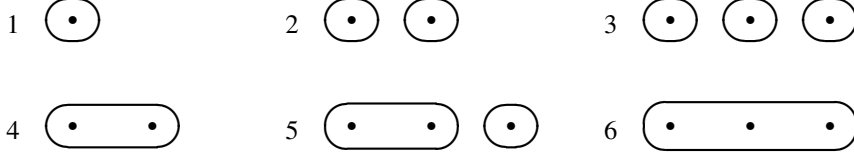


FIGURE 7. States for the ancestors of three offspring in the island model.

Actually the derivative evaluated at  $s = 0$  is given by

$$(6.6) \quad u'(0) = (a - b - c + d)D^{-1} \sum_{t=0}^{\infty} \sum_{k=1}^D E[x_k(t)(1 - x_k(t))(x_k(t) - x^*)].$$

We conclude that  $u'(0) > 0$  if and only if  $x^* < \hat{x}$ , where

$$(6.7) \quad \hat{x} = \frac{\sum_{t \geq 0} E[\overline{x(t)^2(1 - x(t))}]}{\sum_{t \geq 0} E[\overline{x(t)(1 - x(t))}]}.$$

Here, we have

$$(6.8) \quad \overline{x(t)^2(1 - x(t))} = D^{-1} \sum_{k=1}^D x_k(t)^2(1 - x_k(t))$$

and

$$(6.9) \quad \overline{x(t)(1 - x(t))} = D^{-1} \sum_{k=1}^D x_k(t)(1 - x_k(t)).$$

Then the tower property of conditional expectation ascertains the following statement.

**Proposition 5.** *Consider the Wright island model for a finite number of groups of size  $N$  and assume a Wright-Fisher reproduction scheme followed by uniform dispersal of a proportion  $m$  of offspring and viability selection within groups according to the IPD game of Proposition 1. Weak selection favors A replacing B if*

$$(6.10) \quad x^* < \frac{\sum_{t \geq 0} E[\xi_1(t)\xi_2(t)(1 - \xi_3(t))]}{\sum_{t \geq 0} E[\xi_1(t)(1 - \xi_2(t))]} = \hat{x},$$

where  $\xi_1(t), \xi_2(t), \xi_3(t)$  are indicator random variables for type A in offspring chosen at random without replacement in the same group chosen at random in generation  $t$  after dispersal.

## 7. CALCULATION FOR THE ISLAND MODEL WITH DISPERSAL PRECEDING SELECTION

We want to calculate  $\hat{x}$  in Proposition 5 for the island model with dispersal preceding selection in the limit of a large number of groups and in the case where A is initially a single mutant. Without loss of generality, suppose  $z_1(0) = N^{-1}$  and  $z_k(0) = 0$  for  $k = 2, \dots, D$ . See Ladret and Lessard (2007) for the analysis in the case of a fixed number of groups.

We will have to trace backwards in time the ancestors of two or three offspring after dispersal. Actually we will just need to know the number of groups  $d$  containing at least one ancestor and the number of groups  $n_i$  containing  $i$  ancestors for  $i = 1, \dots, d$  with  $1 \leq$

$\sum_{i=1}^d n_i \leq 3$ . There are six possible states in the form  $\mathbf{n} = (n_1, \dots, n_d)$ : (1), (2, 0), (3, 0, 0), (0, 1), (1, 1, 0), (0, 0, 1), and they are labeled from 1 to 6 (see Fig. 7).

The state space  $S$  is partitioned into two subsets,  $S_1 = \{1, 2, 3\}$  with all ancestors in different groups and  $S_2 = \{4, 5, 6\}$  with at least two ancestors in the same group. State 1 is absorbing while all other states are transient. As  $D$  increases, transitions from the other states occur according to two different timescales with expected sojourn times in state 4, 5 or 6 becoming negligible compared to expected sojourn times in state 2 or 3.

As shown in Appendix A1, in the limit  $D \rightarrow \infty$  with  $ND$  generations as unit of time, lineages within the same group either coalesce or migrate instantaneously to different groups, while each pair of lineages in different groups coalesces at rate  $f_{22}$ , which is the probability for two offspring chosen at random without replacement in the same group after dispersal to have ultimately two ancestors in different groups in the case of an infinite number of groups. In other words, after an initial scattering phase during which instantaneous transitions from states in  $S_2$  to states in  $S_1$  take place, there is a collecting phase during which transitions within  $S_1$  occur according to the Kingman (1982) coalescent but with rate  $f_{22}$  instead of 1.

Let  $p_{ij}(t)$  be the probability for the chain to be in state  $j$  and  $v_{ij}(t)$  the probability for the chain to visit state  $j$  for the first time in the  $t$ -th generation backwards in time, given that the chain is in state  $i$  in the current generation. Note that

$$(7.1) \quad v_{ij} = \sum_{t \geq 1} v_{ij}(t)$$

is the probability for the chain to reach state  $j$  from state  $i$  for  $j \neq i$ . Moreover,

$$(7.2) \quad E(T_i) = (ND)^{-1} \sum_{t \geq 0} p_{ii}(t)$$

is the expected value of the time  $T_i$  spent in state  $i$  starting from state  $i$  before absorption into state 1 with  $ND$  generations as unit of time. In particular we have (see Appendix A1)

$$(7.3) \quad \lim_{D \rightarrow \infty} E(T_2) = f_{22}^{-1} \text{ and } \lim_{D \rightarrow \infty} E(T_4) = 0,$$

so that only the time spent in state 2 has to be taken into account in the expected time with two lineages in the limit of a large population size. Moreover,

$$(7.4) \quad \lim_{D \rightarrow \infty} v_{42} = f_{22} = 1 - f_{21} \text{ and } \lim_{D \rightarrow \infty} v_{62} = f_{32} + f_{33} = 1 - f_{31},$$

where  $f_{nk}$  represents the probability for  $n$  offspring chosen at random without replacement in the same group after dispersal to have ultimately  $k$  ancestors in different groups in the case of an infinite number of groups.

Considering all possible transitions from state 4 for two offspring chosen at random without replacement in generation  $t \geq 0$  after dispersal to states in generation 0 so that the two offspring are of types  $A$  and  $B$  in this order, we obtain

$$(7.5) \quad \sum_{t \geq 0} E[\xi_1(t)(1 - \xi_2(t))] = (ND)^{-1} \sum_{t \geq 1} p_{42}(t) + (ND)^{-1} \sum_{t \geq 1} p_{44}(t),$$

since

$$(7.6) \quad \sum_{t \geq 1} p_{42}(t) = \sum_{t \geq 1} \sum_{r=1}^t v_{42}(r) p_{22}(t-r) = \sum_{r \geq 1} \sum_{t \geq 0} v_{42}(r) p_{22}(t).$$

Therefore, we have

$$\sum_{t \geq 0} E[\xi_1(t)(1 - \xi_2(t))] = v_{42}E(T_2) + E(T_4) - (ND)^{-1} \rightarrow 1,$$

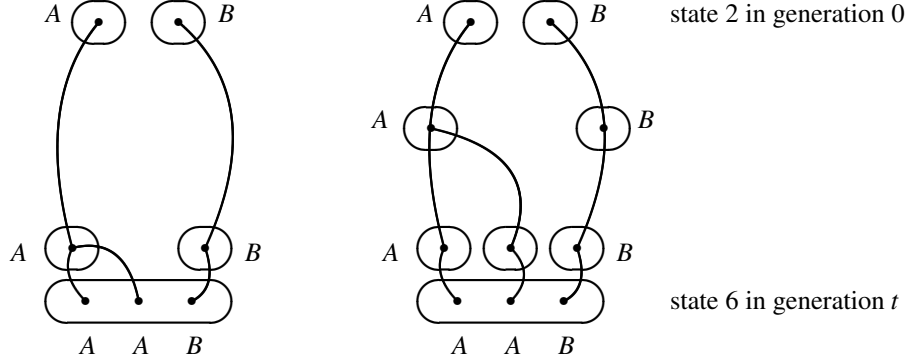


FIGURE 8. Lineages of three offspring of types  $A, A, B$  in the same group in the island model from generation  $t$  to generation 0.

as  $D \rightarrow \infty$ .

For three offspring chosen at random without replacement in state 6 in generation  $t \geq 0$  after dispersal and of types  $A, A$  and  $B$  in this order, we obtain in a similar way

$$(7.7) \quad \sum_{t \geq 0} E[\xi_1(t)\xi_2(t)(1 - \xi_3(t))] = (3ND)^{-1} \sum_{t \geq 1} p_{62}(t) + (3ND)^{-1} \sum_{t \geq 1} p_{64}(t),$$

from which

$$(7.8) \quad \sum_{t \geq 0} E[\xi_1(t)\xi_2(t)(1 - \xi_3(t))] = \frac{v_{62}}{3} E(T_2) + \frac{v_{64}}{3} E(T_4) \rightarrow \frac{1 - f_{31}}{3(1 - f_{21})},$$

as  $D \rightarrow \infty$ . Here,  $1/3$  is the probability that two lineages in particular coalesce given that two lineages out of three coalesce (see Fig. 8).

Exact expressions of  $f_{21}$  and  $f_{31}$  in terms of  $m$  and  $N$  are given in Appendix A1. Note that the inequality  $f_{31} < f_{21}$  always holds.

It remains to plug the above calculations in the upper bound given in Proposition 5. The following conclusion ensues.

**Proposition 6.** *In the case of a single initial  $A$ , the upper bound  $\hat{x}$  in the condition given in Proposition 5 for weak selection to favor  $A$  replacing  $B$  in the island model with dispersal preceding selection satisfies*

$$(7.9) \quad \lim_{D \rightarrow \infty} \hat{x} = \frac{1 - f_{31}}{3(1 - f_{21})} > \frac{1}{3},$$

where  $f_{21}$  and  $f_{31}$  are the probabilities that two and three offspring, respectively, chosen at random without replacement in the same group after dispersal have ultimately a common ancestor in the case of an infinite number of groups.

Proposition 6 means a less stringent condition for a single  $A$  to be favored for replacing  $B$  when the population is subdivided into a large number of small groups.

## 8. ISLAND MODEL WITH DISPERSAL FOLLOWING SELECTION

In this section we consider a variant of the previous island model by assuming that uniform dispersal occurs after selection. The main effect of this assumption is to introduce



differential contributions of groups according to their composition from one generation to the next.

Here, the frequency of  $A$  in the offspring in group  $k$  in generation  $t$  goes from  $x_k(t) = z_k(t)$  before selection to

$$(8.1) \quad \tilde{x}_k(t) = \frac{x_k(t)(1 + sw_A(x_k(t)))}{1 + sw(x_k(t))}$$

after selection, and finally to

$$(8.2) \quad \tilde{\tilde{x}}_k(t) = \frac{(1-m)x_k(t)(1 + sw_A(x_k(t))) + mD^{-1} \sum_{l=1}^D x_l(t)(1 + sw_A(x_l(t)))}{(1-m)(1 + sw(x_k(t))) + mD^{-1} \sum_{l=1}^D (1 + sw(x_l(t)))}$$

after selection and dispersal, since the relative size of group  $k$  after selection is  $1 + sw(x_k(t))$ . (See Fig. 9.)

After some algebraic manipulations, the frequency of  $A$  in generation  $t$  in the whole population after selection and dispersal is found to be

$$(8.3) \quad D^{-1} \sum_{k=1}^D \tilde{\tilde{x}}_k(t) = \overline{x(t)} + s(b-d)\overline{x(t)(1-x(t))} \\ + s(a-b-c+d)\overline{x(t)^2(1-x(t))} \\ + sm(2-m)(b+c-2d)\overline{(x(t))^2 - \overline{x(t)}^2} \\ + sm(2-m)(a-b-c+d)\overline{(x(t))^3 - \overline{x(t)} \overline{x(t)^2}} + o(s).$$

Here,  $\overline{x(t)}$ ,  $\overline{x(t)(1-x(t))}$  and  $\overline{x(t)^2(1-x(t))}$  are defined as in Section 6, while

$$(8.4) \quad \overline{x(t)^2 - \overline{x(t)}^2} = D^{-1} \sum_{k=1}^D x_k(t)^2 - \left( D^{-1} \sum_{k=1}^D x_k(t) \right)^2 \\ = D^{-2} \sum_{k=1}^D \sum_{l=1, l \neq k}^D x_k(t)(1-x_l(t)) - (1-D^{-1})\overline{x(t)(1-x(t))}$$

and

$$(8.5) \quad \overline{x(t)^3 - \overline{x(t)} \overline{x(t)^2}} = D^{-1} \sum_{k=1}^D x_k(t)^3 - \left( D^{-1} \sum_{k=1}^D x_k(t) \right) \left( D^{-1} \sum_{l=1}^D x_l(t)^2 \right) \\ = D^{-2} \sum_{k=1}^D \sum_{l=1, l \neq k}^D x_k(t)^2(1-x_l(t)) - (1-D^{-1})\overline{x(t)^2(1-x(t))}.$$

The tower property of conditional expectation yields

$$(8.6) \quad E[\overline{x(t)(1-x(t))}] = E[\zeta_1(t)(1-\zeta_2(t))]$$

and

$$(8.7) \quad E[\overline{x(t)^2(1-x(t))}] = E[\zeta_1(t)\zeta_2(t)(1-\zeta_3(t))]$$

as before, but with  $\zeta_1(t), \zeta_2(t), \zeta_3(t)$  being indicator random variables for  $A$  in offspring chosen at random without replacement in generation  $t$  in the same group *before dispersal*.

Proceeding as in the previous section, we find that

$$(8.8) \quad \lim_{D \rightarrow \infty} \sum_{t \geq 0} E[\zeta_1(t)(1-\zeta_2(t))] = 1$$

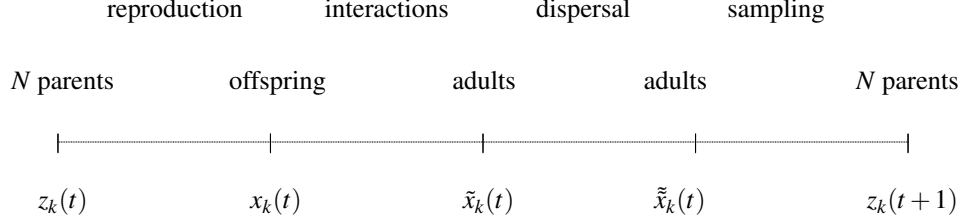


FIGURE 9. Life cycle from generation  $t$  to generation  $t + 1$  and notation for the frequency of  $A$  in group  $k$  at each step in the island model with dispersal after selection.

and

$$(8.9) \quad \lim_{D \rightarrow \infty} \sum_{t \geq 0} E[\zeta_1(t) \zeta_2(t) (1 - \zeta_3(t))] = \frac{1 - \tilde{f}_{31}}{3(1 - \tilde{f}_{21})},$$

where

$$(8.10) \quad \tilde{f}_{n1} = f_{n1}(1 - m)^{-n}$$

represents the probability that  $n$  offspring chosen at random without replacement in the same group *before dispersal* have ultimately a common ancestor in the case of an infinite number of groups.

On the other hand, we have

$$(8.11) \quad E \left[ (D^2 - D)^{-1} \sum_{k=1}^D \sum_{l=1, l \neq k}^D x_k(t) (1 - x_l(t)) \right] = E[\zeta_1(t) (1 - \eta_2(t))]$$

and

$$(8.12) \quad E \left[ (D^2 - D)^{-1} \sum_{k=1}^D \sum_{l=1, l \neq k}^D x_k(t)^2 (1 - x_l(t)) \right] = E[\zeta_1(t) \zeta_2(t) (1 - \eta_3(t))],$$

where  $\eta_2(t)$  and  $\eta_3(t)$  are indicator random variables for  $A$  in offspring chosen at random without replacement in generation  $t$  *before dispersal*, but in a *different group* than the one for the indicator random variables  $\zeta_1(t)$ ,  $\zeta_2(t)$ ,  $\zeta_3(t)$ . In this case, we find that

$$(8.13) \quad \lim_{D \rightarrow \infty} \sum_{t \geq 0} E[\zeta_1(t) (1 - \eta_2(t))] = \frac{1}{1 - \tilde{f}_{21}}$$

and

$$(8.14) \quad \lim_{D \rightarrow \infty} \sum_{t \geq 0} E[\zeta_1(t) \zeta_2(t) (1 - \eta_3(t))] = \frac{1}{3} + \frac{\tilde{f}_{21}}{1 - \tilde{f}_{21}}.$$

These results are obtained by considering all transitions from states 2 and 5, respectively, for offspring sampled at random without replacement in generation  $t \geq 0$  before dispersal to states in generation 0 that are compatible with the sample configuration.

The probability of ultimate fixation of  $A$  as a function of the intensity of selection is given by

$$(8.15) \quad u(s) = u(0) + D^{-1} \sum_{t=0}^{\infty} \sum_{k=1}^D E_s [\tilde{x}_k(t) - x_k(t)].$$

Its derivative evaluated at  $s = 0$  is given by

$$(8.16) \quad \begin{aligned} u'(0) &= (b-d) \sum_{t \geq 0} E[\overline{x(t)(1-x(t))}] \\ &+ (a-b-c+d) \sum_{t \geq 0} E[\overline{x(t)^2(1-x(t))}] \\ &+ m(2-m)(b+c-2d) \sum_{t \geq 0} E[\overline{x(t)^2 - x(t)^2}] \\ &+ m(2-m)(a-b-c+d) \sum_{t \geq 0} E[\overline{x(t)^3 - x(t) x(t)^2}]. \end{aligned}$$

In the limit of a large number of groups and after some algebraic manipulations, we find that

$$(8.17) \quad \begin{aligned} \lim_{D \rightarrow \infty} u'(0) &= (b-d) + (a-b-c+d) \frac{1 - \tilde{f}_{21} + (1-m)^2(\tilde{f}_{21} - \tilde{f}_{31})}{3(1 - \tilde{f}_{21})} \\ &+ (a-d)m(2-m) \frac{\tilde{f}_{21}}{1 - \tilde{f}_{21}}. \end{aligned}$$

Using the exact expressions of  $f_{21} = (1-m)^2 \tilde{f}_{21}$  and  $f_{31} = (1-m)^3 \tilde{f}_{31}$  given in Appendix A1, it can be checked that

$$(8.18) \quad m(2-m) \frac{\tilde{f}_{21}}{1 - \tilde{f}_{21}} = \frac{1}{N-1}$$

and

$$(8.19) \quad \frac{1 - \tilde{f}_{21} + (1-m)^2(\tilde{f}_{21} - \tilde{f}_{31})}{3(1 - \tilde{f}_{21})} > \frac{1 - f_{31}}{3(1 - f_{21})},$$

as soon as  $N > 1$ . Then the condition  $\lim_{D \rightarrow \infty} u'(0) > 0$  yields the following result.

**Proposition 7.** *In the case of dispersal following selection in the Wright island model of Proposition 5 in the limit of a large number of groups of fixed size  $N > 1$ , weak selection favors a single  $A$  replacing  $B$  if*

$$(8.20) \quad x^* < \frac{1 - \tilde{f}_{21} + (1-m)^2(\tilde{f}_{21} - \tilde{f}_{31})}{3(1 - \tilde{f}_{21})} + \frac{a-d}{(N-1)(a-b-c+d)},$$

where  $\tilde{f}_{21}$  and  $\tilde{f}_{31}$  are the probabilities that two and three offspring, respectively, chosen at random without replacement in the same group before dispersal have ultimately a common ancestor in the case of an infinite number of groups.

Note that the upper bound for  $x^*$  given in Proposition 7 is always larger than the upper bound given in Proposition 6. This means an even less stringent condition for  $A$  to be favored for replacing  $B$  in the Wright island model when dispersal follows selection instead of preceding it.

9. MODIFIED ISLAND MODEL WITH SKEWED CONTRIBUTIONS OF GROUPS  
PRECEDING SELECTION

In this section we consider the effect of a skewed distribution for the contribution of a group in offspring in a subdivided population. We assume  $D$  groups of size  $N$  with dispersal of offspring preceding selection in each generation as in the island model of Section 6. However, with a small probability  $D^{-\beta}$  for  $\beta < 1$ , one group chosen at random provides a proportion  $\chi$  of all offspring, produced equally by all members of the group, compared to  $(1 - \chi)(D - 1)^{-1}$  for every other group. With the complementary probability, the proportion is uniformly the same. In all cases, a proportion  $m$  of offspring in each group disperse and are replaced by as many migrants chosen at random among all migrants. This is followed by selection and random sampling within each group to start the next generation. This corresponds to the Eldon-Wakeley model applied to groups instead of parents.

The conclusion of Proposition 5 still holds. Moreover, a two-timescale argument can be applied in the limit of a large number of groups as in Section 7, but with  $ND^\beta$  generations as unit of time (see Appendix A2).

In number of  $ND^\beta$  generations, the expected time spent in state  $i$  before absorption into state 1 is written in the form

$$(9.1) \quad E(T_i) = (ND^\beta)^{-1} \sum_{t \geq 0} p_{ii}(t).$$

It can be shown that

$$(9.2) \quad \lim_{D \rightarrow \infty} E(T_2) = \lambda_{21}^{-1} \text{ and } \lim_{D \rightarrow \infty} E(T_4) = 0,$$

where  $\lambda_{21}$  represents the rate of coalescence of two lineages in different groups backwards in time in the limit of a large number of groups. Moreover, the limiting probabilities of reaching state 2 from states 4 and 6, respectively, are given by

$$(9.3) \quad \lim_{D \rightarrow \infty} v_{42} = f_{22} \text{ and } \lim_{D \rightarrow \infty} v_{62} = f_{32} + \frac{f_{33}\lambda_{32}}{\lambda_{32} + \lambda_{31}},$$

where  $\lambda_{3i}$  represents the rate of transition from 3 to  $i$  lineages, for  $i = 1, 2$ , in different groups backwards in time in the limit of a large number of groups.

Assuming a single initial  $A$ , we find that

$$(9.4) \quad \begin{aligned} D^{1-\beta} \sum_{t \geq 0} E[\xi_1(t)(1 - \xi_2(t))] &= v_{42}E(T_2) + E(T_4) - (ND^\beta)^{-1} \\ &\rightarrow f_{22}\lambda_{21}^{-1}, \end{aligned}$$

and

$$(9.5) \quad \begin{aligned} D^{1-\beta} \sum_{t \geq 0} E[\xi_1(t)\xi_2(t)(1 - \xi_3(t))] &= \frac{v_{62}}{3}E(T_2) + \frac{v_{64}}{3}E(T_4) \\ &\rightarrow \frac{f_{32}}{3\lambda_{21}} + \frac{f_{33}\lambda_{32}}{3\lambda_{21}(\lambda_{32} + \lambda_{31})}, \end{aligned}$$

as  $D \rightarrow \infty$ . Here,  $\xi_1(t), \xi_2(t), \xi_3(t)$  are indicator random variables for type  $A$  in offspring chosen at random without replacement in the same group chosen at random in generation  $t$  after dispersal like in Proposition 5.

This leads to the following result.

**Proposition 8.** *In the case of the Wright island model of Proposition 5 for  $D$  groups with a proportion  $m$  of migrant offspring each generation in each group before selection but a probability  $D^\beta$  for  $\beta < 1$  that they come in proportion  $\chi$  from a same group chosen at random, weak selection favors a single  $A$  replacing  $B$  in the limit of a large number of groups if*

$$(9.6) \quad x^* < \frac{1 - f_{31} - f_{33} \left( \frac{\lambda_{31}}{\lambda_{32} + \lambda_{31}} \right)}{3(1 - f_{21})} < \frac{1 - f_{31}}{3(1 - f_{21})},$$

where  $\tilde{f}_{21}$  and  $\tilde{f}_{31}$  are defined as in Proposition 6, while  $\lambda_{31}$  and  $\lambda_{32}$  are the rates of transition from 3 to 1 and from 3 to 2, respectively, for the number lineages in different groups backwards in time with  $ND^\beta$  generations as unit of time in the limit of a large number of groups.

Proposition 8 means a more stringent condition for a single  $A$  to be favored for replacing  $B$  in an island model with a highly skewed distribution for the contribution of a group in the limit of a large number of groups.

## 10. SUMMARY AND COMMENTS

In conclusion we have shown in this paper that:

- Viability selection determined by the Iterated Prisoner's Dilemma (IPD) in an infinite population predicts the increase in frequency of Tit-for-Tat ( $A$ ) against Always-Defect ( $B$ ), and therefore can explain the spread of cooperation, but only from a frequency  $x > x^*$ , where  $x^*$  is the frequency of  $A$  at an unstable polymorphic equilibrium.
- Weak viability selection determined by the IPD game in a finite population favors a single mutant  $A$  replacing  $B$ , and therefore can explain the advantage for cooperation to go to fixation from a low frequency, but only under the condition  $x^* < \hat{x}$  for some threshold frequency  $\hat{x}$ .
- In the limit of a large population size, we have  $\hat{x} \leq 1/3$ . Actually  $\hat{x} = 1/3$ , which is known as the one-third law of evolution, in a Wright-Fisher model, and more generally in the domain of application of the Kingman coalescent. On the other hand,  $\hat{x} < 1/3$ , which leads to a more stringent condition for the evolution of cooperation, if the contribution of a parent in offspring has a skewed enough distribution.
- In a group-structured population with uniform dispersal of offspring and weak viability selection within groups determined by the IPD game in the limit of a large number of groups of finite size, we have  $\hat{x} > 1/3$ . This means a less stringent condition for cooperation to evolve. Moreover, the condition is weaker if dispersal occurs after selection rather than before selection so that there are differential contributions of groups according to their composition. On the other hand, the condition is stronger if the contribution of a group in offspring has a highly skewed idistribution.

- The first-order effect of selection on the probability of fixation of a single mutant strategy is proportional to a projected average excess in payoff. This is the excess in payoff to the mutant strategy compared to the mean payoff in the population not only in the current generation but in all future generations as long as fixation is not reached.

Our results are based on approximations for the probability of ultimate fixation of a single mutant that are ascertained under the assumption of very weak selection. Actually, the intensity of selection is assumed to be small compared to the intensity of the other evolutionary forces. These are random drift, whose intensity is measured by the inverse of the population size, and dispersal in the case of a group-structured population, whose rate is supposed to be constant as the population size increases. On the other hand, the approach is not limited by restrictive assumptions on the production of offspring by parents or groups.

An alternative approach under the assumption that the intensity of selection is of the same order of magnitude as the other evolutionary forces is a diffusion approximation (see, e.g., Kimura 1984, Nagylaki 1980, 1997, Lessard 2005, 2007b, 2009). In this case, however, the contributions of parents and groups in offspring cannot be too highly skewed in distribution to avoid jump processes.

Our motivation in this paper was the evolution of cooperation and this is the reason for considering the Prisoner's Dilemma and its iterated version with Tit-for-Tat ( $A$ ) and Always-Defect ( $B$ ) as strategies. Of course, the approach used to deduce the first-order effect of selection on the probability of fixation of a single mutant is not limited to this particular game. Indeed, it does not depend on special relationships between the payoffs  $a$ ,  $b$ ,  $c$  and  $d$ .

Actually the approach is not limited to a matrix game, or linear expected payoffs  $w_A(x)$  and  $w_B(x)$  to  $A$  and  $B$ , respectively, with respect to the frequency of  $A$  represented by  $x$ . It can be extended to more general cases of frequency dependence with  $w_A(x) - w_B(x)$  being a polynomial of any degree  $n$  with respect to  $x$ . Then expected backward times with up to  $n + 2$  lineages have to be computed to approximate the fixation probability. Moreover, this can be used to get approximations in the case where the difference  $w_A(x) - w_B(x)$  is any continuous function of  $x$ . (See Lessard and Ladret 2007.)

An approximation for the fixation probability can be obtained also in the case of a matrix game with any number of strategies. Then the approximation depends on the initial state of the population. Moreover, it can be expressed in terms of projected average excess in payoff given any initial frequencies (Lessard and Lahaie 2009).

We have considered pairwise interactions between offspring in infinite numbers. The case of pairwise interactions between adults in finite numbers is also of interest and it can be dealt with in a similar manner (see, e.g., Lessard 2005, Hilbe 2011). The analysis of the more general case of a multi-player game like the Public goods game is more recondite but not out of reach (Kurokawa and Ihara 2009, Gokhale and Traulsen 2010, Lessard 2011a).

Finally it can be shown that a matrix game in a finite group-structured population with uniform dispersal of offspring, or local extinction and recolonization, and payoff matrix  $A$  within groups is formally equivalent in the limit of a large population size to a matrix game in a well-mixed population with some effective game matrix  $A^\circ$  (Lessard 2011b). The entries of this matrix are linear combinations of interaction or competition effects weighted by coefficients of identity-by-descent in an infinite population in the absence of selection. Then what is known about matrix games (see, e.g., Lessard 1990, Hofbauer and Sigmund 1998) can be applied *mutatis mutandis*.

## APPENDIX A1. TWO TIMESCALES FOR THE WRIGHT ISLAND MODEL

Consider the neutral Wright island model for  $D$  groups of size  $N$ . In each generation, infinite numbers of offspring are produced in equal proportions and a fraction  $m$  of these disperse uniformly among all groups. This is followed by random sampling of  $N$  offspring in each group to start the next generation.

The six possible states for the ancestors of three offspring chosen after dispersal are given in Fig. 7. The transition matrix from one generation to the previous one, whose entries are represented by  $p_{ij}(1)$  for  $i, j$  in  $S = \{1, \dots, 6\}$ , takes the form

$$(10.1) \quad \mathbf{P} = \mathbf{R} + (ND)^{-1}\mathbf{M}(D),$$

where  $\mathbf{R}$  is the transition matrix in the case of an infinite number of groups. See Lessard and Wakeley (2004) for exact expressions of  $\mathbf{R}$  and  $\mathbf{M}(D)$ .

Since all states in  $S_1 = \{1, 2, 3\}$  are absorbing and all states in  $S_2 = \{4, 5, 6\}$  transient in the case  $D = \infty$ , the ergodic theorem guarantees that

$$(10.2) \quad \lim_{t \rightarrow \infty} \mathbf{R}^t = \mathbf{H} = \begin{pmatrix} \mathbf{I} & \mathbf{0} \\ \mathbf{F} & \mathbf{0} \end{pmatrix},$$

where  $\mathbf{I}$  designates the  $3 \times 3$  identity matrix and  $\mathbf{0}$  the  $3 \times 3$  zero matrix. Moreover,

$$(10.3) \quad \mathbf{F} = \begin{pmatrix} f_{21} & f_{22} & 0 \\ 0 & f_{21} & f_{22} \\ f_{31} & f_{32} & f_{33} \end{pmatrix},$$

with  $f_{nk}$  denoting the probability for  $n$  offspring chosen at random without replacement in the same group after dispersal to have ultimately  $k$  ancestors in different groups in the case of an infinite number of groups. On the other hand, it can be checked that

$$(10.4) \quad \lim_{D \rightarrow \infty} \mathbf{M}(D) = \mathbf{M} = \begin{pmatrix} \mathbf{M}_{11} & \mathbf{M}_{12} \\ \mathbf{M}_{21} & \mathbf{M}_{22} \end{pmatrix},$$

where

$$(10.5) \quad \mathbf{M}_{11} = \begin{pmatrix} 0 & 0 & 0 \\ m(2-m) & -Nm(2-m) & 0 \\ 0 & 3m(2-m) & -3Nm(2-m) \end{pmatrix}$$

and

$$(10.6) \quad \mathbf{M}_{12} = \begin{pmatrix} 0 & 0 & 0 \\ (N-1)m(2-m) & 0 & 0 \\ 0 & 3(N-1)m(2-m) & 0 \end{pmatrix}.$$

Applying a lemma due to Möhle (1998) to the transition matrix from time 0 to time  $\tau$  in the past with  $ND$  generations as unit of time, we obtain

$$(10.7) \quad \lim_{D \rightarrow \infty} \mathbf{P}^{\lfloor ND\tau \rfloor} = \mathbf{H}e^{\tau\mathbf{H}\mathbf{M}\mathbf{H}} = \begin{pmatrix} e^{\tau\mathbf{G}} & \mathbf{0} \\ \mathbf{F}e^{\tau\mathbf{G}} & \mathbf{0} \end{pmatrix} = \mathbf{Q}(\tau),$$

where  $\lfloor \cdot \rfloor$  denotes the integer value and

$$(10.8) \quad \mathbf{G} = \mathbf{M}_{11} + \mathbf{M}_{12}\mathbf{F} = f_{22} \begin{pmatrix} 0 & 0 & 0 \\ 1 & -1 & 0 \\ 0 & 3 & -3 \end{pmatrix}.$$

This uses the equality

$$(10.9) \quad f_{22} = Nm(2-m) \left[ \frac{1}{N} + \left(1 - \frac{1}{N}\right) f_{21} \right],$$

which can be deduced from the exact expressions of  $f_{21}$  and  $f_{22} = 1 - f_{21}$  (see below).

The matrix  $\mathbf{G}$  is the generator of the death process of the Kingman (1982) coalescent with rate  $f_{22}$  instead of 1. The matrix  $\mathbf{Q}(\tau)$ , whose entries are denoted by  $q_{ij}(\tau)$  for  $i, j$  in  $S$ , is a transition matrix from time 0 to time  $\tau$  for a continuous-time Markov chain with initial instantaneous transitions from states in  $S_2$  to states in  $S_1$  and generator  $\mathbf{G}$  for transitions within  $S_1$ .

The expected time in state 2 in number of  $ND$  generations is

$$(10.10) \quad E(T_2) = (ND)^{-1} \sum_{t=0}^{\infty} p_{22}(t) = \int_0^{\infty} p_{22}(\lfloor ND\tau \rfloor) d\tau,$$

from which

$$(10.11) \quad \lim_{D \rightarrow \infty} E(T_2) = \int_0^{\infty} q_{22}(\tau) d\tau = f_{22}^{-1}.$$

This is the case because two lineages coalesce at the rate  $f_{22}$  in the limit of a large number of groups. Moreover,

$$(10.12) \quad p_{22}(\lfloor ND\tau \rfloor) \leq \left(1 - \frac{m(2-m)}{ND}\right)^{\lfloor ND\tau \rfloor} \leq (1 - N^{-1})^{-1} e^{-m(2-m)\tau}.$$

Therefore, the dominated convergence theorem can be applied. Similarly the expected time in state 4 in number of  $ND$  generations is

$$(10.13) \quad E(T_4) = (ND)^{-1} \sum_{t=0}^{\infty} p_{44}(t)$$

and

$$(10.14) \quad \lim_{D \rightarrow \infty} E(T_4) = \int_0^{\infty} q_{44}(\tau) d\tau = 0,$$

since  $q_{44}(\tau) = 0$  for all  $\tau > 0$ .

On the other hand, the vector  $\mathbf{v}_{\bullet 2}^T = (0, 1, v_{32}, v_{42}, v_{52}, v_{62})$ , where  $v_{i2}$  is the probability of reaching state 2 from state  $i$  for  $i = 3, \dots, 6$ , satisfies the linear system of equations

$$(10.15) \quad \mathbf{v}_{\bullet 2} = \tilde{\mathbf{P}}^{ND} \mathbf{v}_{\bullet 2},$$

where  $\tilde{\mathbf{P}}$  is the transition matrix on  $S$  with state 2 assumed to be absorbing. In this case, Möhle's (1998) lemma yields

$$(10.16) \quad \lim_{D \rightarrow \infty} \tilde{\mathbf{P}}^{ND} = \tilde{\mathbf{Q}} = \begin{pmatrix} e^{\tilde{\mathbf{G}}} & \mathbf{0} \\ \mathbf{F}e^{\tilde{\mathbf{G}}} & \mathbf{0} \end{pmatrix},$$

where

$$(10.17) \quad \tilde{\mathbf{G}} = f_{22} \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 3 & -3 \end{pmatrix}.$$

Therefore,

$$(10.18) \quad \lim_{D \rightarrow \infty} \mathbf{v}_{\bullet 2} = \tilde{\mathbf{Q}} \lim_{D \rightarrow \infty} \mathbf{v}_{\bullet 2}.$$

It can be checked directly that the unique solution is

$$(10.19) \quad \lim_{D \rightarrow \infty} \mathbf{v}_{\bullet 2}^T = (0, 1, 1, f_{22}, 1, f_{32} + f_{33}).$$



Finally,  $f_{22} = 1 - f_{21}$  and  $f_{32} + f_{33} = 1 - f_{31}$ , where

$$(10.20) \quad f_{21} = (1-m)^2 \left[ \frac{1}{N} + \left(1 - \frac{1}{N}\right) f_{21} \right],$$

$$(10.21) \quad f_{31} = (1-m)^3 \left[ \frac{1}{N^2} + \frac{3}{N} \left(1 - \frac{1}{N}\right) f_{21} + \left(1 - \frac{1}{N}\right) \left(1 - \frac{2}{N}\right) f_{31} \right].$$

This system of linear equations is obtained from a first-step analysis. Its solution is given by

$$(10.22) \quad f_{21} = \frac{(1-m)^2}{Nm(2-m) + (1-m)^2},$$

$$(10.23) \quad f_{31} = f_{21} \left[ \frac{N(1-m) + 2(N-1)(1-m)^3}{N^2m(3-3m+m^2) + (3N-2)(1-m)^3} \right].$$

Note that

$$(10.24) \quad f_{32} = 3(f_{21} - f_{31}).$$

This is the case because there are 3 possibilities for two offspring out of three to have a common ancestor.

Similarly the vector  $\mathbf{v}_{\bullet 3} = (0, 0, 1, v_{43}, v_{53}, v_{63})$ , where  $v_{i3}$  is the probability of reaching state 3 from state  $i$  for  $i = 3, \dots, 6$ , must satisfy

$$(10.25) \quad \lim_{D \rightarrow \infty} \mathbf{v}_{\bullet 3} = \tilde{\mathbf{Q}} \lim_{D \rightarrow \infty} \mathbf{v}_{\bullet 3},$$

where

$$(10.26) \quad \tilde{\mathbf{Q}} = \begin{pmatrix} \mathbf{I} & \mathbf{0} \\ \mathbf{F} & \mathbf{0} \end{pmatrix}.$$

The unique solution is

$$(10.27) \quad \lim_{D \rightarrow \infty} \mathbf{v}_{\bullet 3}^T = (0, 0, 1, 0, f_{22}, f_{33}).$$

## APPENDIX A2. TWO TIMESCALES FOR THE MODIFIED WRIGHT ISLAND MODEL

Consider the neutral Wright island model for  $D$  groups of size  $N$  but suppose that, in each generation and with probability  $D^{-\beta}$  for  $\beta < 1$ , the proportion of offspring produced equally by all members of a group chosen at random is  $\chi$  compared to  $(1-\chi)(D-1)^{-1}$  in every other group. With the complementary probability, the proportion is uniformly the same. In all cases, a proportion  $m$  of offspring in each group disperse and they are replaced by as many migrants chosen at random among all migrants before random sampling of  $N$  offspring to start the next generation.

The transition matrix on the state space for the ancestors of three offspring chosen after dispersal takes the form

$$(10.28) \quad \mathbf{P} = \mathbf{R} + (ND^\beta)^{-1} \mathbf{M}(D),$$

where  $\mathbf{R}$  is the same as in Appendix A1. The entries of the matrix  $\mathbf{M}(D)$  can be found explicitly (Lasalle Ialongo 2008). The important point is that

$$(10.29) \quad \lim_{D \rightarrow \infty} \mathbf{M}(D) = \mathbf{M} = \begin{pmatrix} \mathbf{M}_{11} & \mathbf{M}_{12} \\ \mathbf{M}_{21} & \mathbf{M}_{22} \end{pmatrix},$$

where

$$\mathbf{M}_{11} = \begin{pmatrix} 0 & 0 & 0 \\ (\chi m)^2 & -N(\chi m)^2 & 0 \\ N^{-1}(\chi m)^3 & 3(\chi m)^2(1-\chi m) & -3N(\chi m)^2 + 2N(\chi m)^3 \end{pmatrix}$$

and

$$\mathbf{M}_{12} = \begin{pmatrix} 0 & 0 & 0 \\ (N-1)(\chi m)^2 & 0 & 0 \\ 3(1-N^{-1})(\chi m)^3 & 3(N-1)(\chi m)^2(1-\chi m) & (1-N^{-1})(N-2)(\chi m)^3 \end{pmatrix}.$$

In this case, Möhle's (1998) lemma guarantees that

$$(10.30) \quad \lim_{D \rightarrow \infty} \mathbf{P}^{\lfloor ND^\beta \tau \rfloor} = \begin{pmatrix} e^{\tau \mathbf{G}} & \mathbf{0} \\ \mathbf{F} e^{\tau \mathbf{G}} & \mathbf{0} \end{pmatrix} = \mathbf{Q}(\tau),$$

where

$$(10.31) \quad \mathbf{G} = \mathbf{M}_{11} + \mathbf{M}_{12} \mathbf{F} = \begin{pmatrix} 0 & 0 & 0 \\ \lambda_{21} & -\lambda_{21} & 0 \\ \lambda_{31} & \lambda_{32} & -\lambda_{31} - \lambda_{32} \end{pmatrix}.$$

The parameters  $\lambda_{lk}$  for  $l > k \geq 1$  are the rates of transition from  $l$  to  $k$  lineages in different groups backwards in time with  $ND^\beta$  generations as unit of time as  $D \rightarrow \infty$ . We find that

$$(10.32) \quad \lambda_{21} = N(\chi m)^2 \left[ \frac{1}{N} + \left(1 - \frac{1}{N}\right) f_{21} \right],$$

$$(10.33) \quad \lambda_{31} = N(\chi m)^3 \left[ \frac{1}{N^2} + \frac{3}{N} \left(1 - \frac{1}{N}\right) f_{21} + \left(1 - \frac{1}{N}\right) \left(1 - \frac{2}{N}\right) f_{31} \right],$$

$$(10.34) \quad \lambda_{32} = N(\chi m)^3 \left[ \frac{3}{N} \left(1 - \frac{1}{N}\right) f_{22} + \left(1 - \frac{1}{N}\right) \left(1 - \frac{2}{N}\right) f_{32} \right] \\ + 3N(\chi m)^2(1-\chi m) \left[ \frac{1}{N} + \left(1 - \frac{1}{N}\right) f_{21} \right].$$

Note that

$$(10.35) \quad \lambda_{lk} = N \sum_{l \geq j \geq n \geq k-l+j \geq 1} \binom{l}{j} (\chi m)^j (1-\chi m)^{l-j} p_{jn} f_{n,k-l+j},$$

where  $p_{jn}$  is the probability that  $j$  offspring chosen at random without replacement in the same group before dispersal have  $n$  parents, and  $f_{nk}$  is the probability that  $n$  parents chosen at random without replacement in the same group have ultimately  $k$  ancestors in different groups in the case  $D = \infty$ . The relationships between the parameters  $f_{nk}$  for  $3 \geq n \geq k \geq 1$  exhibited in Appendix A1 lead to the expressions

$$(10.36) \quad \lambda_{21} = N \left( \frac{\chi m}{1-m} \right)^2 f_{21},$$

$$(10.37) \quad \lambda_{31} = N \left( \frac{\chi m}{1-m} \right)^3 f_{31},$$

$$(10.38) \quad \lambda_{32} = 3N \left( \frac{\chi m}{1-m} \right)^2 f_{21} - 3N \left( \frac{\chi m}{1-m} \right)^3 f_{31}.$$

Note that

$$(10.39) \quad \lambda_{lk} = N \sum_{l \geq j \geq k-l+j \geq 1} \binom{l}{j} (\chi m)^j (1-\chi m)^{l-j} \tilde{f}_{n,k-l+j},$$

where  $\tilde{f}_{nk}$  is the probability that  $n$  offspring chosen at random without replacement in the same group *before dispersal* have ultimately  $k$  ancestors in different groups in the case  $D = \infty$ .

Proceeding as previously, the expected time with two lineages in different groups in number of  $ND^\beta$  generations before coalescence satisfies

$$(10.40) \quad E(T_2) = (ND^\beta)^{-1} \sum_{t=0}^{\infty} p_{22}(t) \rightarrow \lambda_{21}^{-1}$$

as  $D \rightarrow \infty$ , while the corresponding expected time with two lineages in the same group,  $E(T_4)$ , tends to 0.

Finally the vector  $\mathbf{v}_{\bullet 2}^T = (0, 1, v_{32}, v_{42}, v_{52}, v_{62})$ , where  $v_{i2}$  is the probability of reaching state 2 from state  $i$  for  $i = 3, \dots, 6$ , satisfies

$$(10.41) \quad \lim_{D \rightarrow \infty} \mathbf{v}_{\bullet 2} = \begin{pmatrix} e^{\tilde{\mathbf{G}}} & \mathbf{0} \\ \mathbf{F}e^{\tilde{\mathbf{G}}} & \mathbf{0} \end{pmatrix} \lim_{D \rightarrow \infty} \mathbf{v}_{\bullet 2},$$

where

$$(10.42) \quad \tilde{\mathbf{G}} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ \lambda_{31} & \lambda_{32} & -\lambda_{31} - \lambda_{32} \end{pmatrix}.$$

The solution is found to be

$$(10.43) \quad \lim_{D \rightarrow \infty} \mathbf{v}_{\bullet 2}^T = \left( 0, 1, \frac{\lambda_{32}}{\lambda_{32} + \lambda_{31}}, f_{22}, f_{21} + \frac{f_{22}\lambda_{32}}{\lambda_{32} + \lambda_{31}}, f_{32} + \frac{f_{33}\lambda_{32}}{\lambda_{32} + \lambda_{31}} \right).$$

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