

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 breeding true population is deduced. It is shown that the condition is more stringent when the reproductive success of an individual is a random variable having a highly skewed probability distribution. On the other hand the condition becomes less stringent in a group-structured population with uniform dispersal of offspring followed by interactions within groups.

1. INTRODUCTION

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 described 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, which is known as 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 using the previous strategy of the opponent in the next rounds. Note that two players using Tit-for-Tat will always cooperate. See, e.g., Hofbauer and Sigmund (1998, Chap. 9) and references therein for more details and historical perspectives.

Let us assume that the payoffs in the different rounds 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 rounds is large

2000 *Mathematics Subject Classification.* Primary 60C05; Secondary 92D15 .
Research supported in part by NSERC Grant 8833.

| | | |
|-----------|------------------|----------------------|
| 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.

enough, that is,

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

Actually this is the 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

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

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 $\frac{T-P}{R-P}$ to ∞ , 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

Suppose an infinite haploid population undergoing discrete nonoverlapping generations and random pairwise interactions among the offspring of the same generation that have an additive effect on viability. More precisely the probability for an individual to survive

| | | |
|----------------------------|--------------------------|--------------------------|
| 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.

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 $s > 0$ represents the intensity of viability selection with the payoff to the individual as coefficient. The intensity of selection will be assumed small throughout the paper.

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 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

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

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. This 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 as a result of sampling effects can 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 which produce virtually infinite numbers of offspring identical to themselves in the relative proportions v_1, \dots, v_N , respectively. The population size N is assumed to be finite and constant. The proportions v_1, \dots, v_N are exchangeable random variables. This means that the joint distribution is invariant under any permutation. Furthermore, they satisfy $0 \leq v_i \leq 1$ for $i = 1, \dots, N$ and $\sum_{i=1}^N v_i = 1$. In particular this implies that the expected proportion of offspring produced by each parent is the same, and then given by

$$(3.1) \quad E(v_1) = N^{-1} \sum_{i=1}^N E(v_i) = N^{-1} E \left(\sum_{i=1}^N v_i \right) = N^{-1}.$$

Moreover, it is assumed that

$$(3.2) \quad NE(v_1^2) = \sum_{i=1}^N E(v_i^2) \rightarrow 0$$

as $N \rightarrow \infty$. This means 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 case where $v_i = N^{-1}$ for $i = 1, \dots, N$. In another hand a model with a skewed distribution of progeny size can be obtained by taking $v_i = \psi$ for some i and $v_j = (1 - \psi)(N - 1)^{-1}$ for every $j \neq i$ for some $0 < \psi < 1$. A combination of the former model with probability $1 - N^{-\alpha}$ for each generation and the latter with the complementary probability $N^{-\alpha}$ can also be considered (Eldon and Wakeley 2006). The general situation corresponds to the Cannings model (Cannings 1974).

The frequency of A in the parents of generation t is represented by a random variable $z(t)$ which 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 $z(t + 1)$ which is conditionally distributed given $x(t)$ as 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 $0/N, 1/N, \dots, N/N$ 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

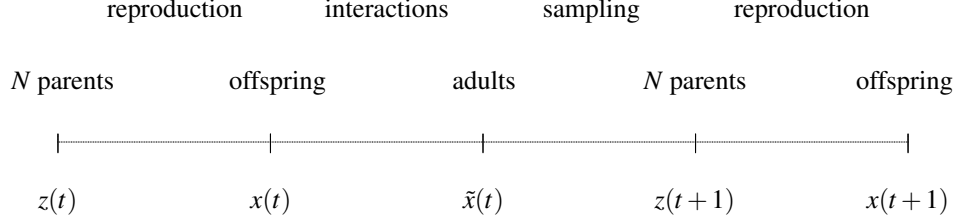


FIGURE 3. Life cycle from generation t to generation $t + 1$ with notation for the frequency of A .

to hit 1 before 0, and the value 0 with the complementary probability $1 - u(s)$. Here $u(s)$ represents the probability of fixation of A as a function of the intensity of selection.

Note that

$$(3.3) \quad u(s) = E_s[z(\infty)],$$

where E_s denotes the 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

$$(3.4) \quad \begin{aligned} E_s[z(\infty)] &= \lim_{T \rightarrow \infty} E_s[z(T)] \\ &= \lim_{T \rightarrow \infty} E_s[z(0) + \sum_{t=0}^{T-1} [z(t+1) - z(t)]] \\ &= z(0) + \lim_{T \rightarrow \infty} \sum_{t=0}^{T-1} E_s[z(t+1) - z(t)] \\ &= z(0) + \sum_{t=0}^{\infty} E_s[z(t+1) - z(t)]. \end{aligned}$$

On the other hand

$$(3.5) \quad \begin{aligned} E_s[z(t+1) - z(t)] &= E_s[x(t+1) - x(t)] \\ &= E_s[E_s[x(t+1) - x(t) | x(t)]] \\ &= s(a - b - c + d) E_s \left[\frac{x(t)(1 - x(t))(x(t) - x^*)}{1 + sw(x(t))} \right] \\ &= s(a - b - c + d) E[x(t)(1 - x(t))(x(t) - x^*)] + o(s), \end{aligned}$$

where E denotes the expectation under neutrality, that is, E_s when $s = 0$, while $o(s)/s \rightarrow 0$ as $s \rightarrow 0$. This leads to

$$(3.6) \quad u(s) = u(0) + s(a - b - c + d) \sum_{t=0}^{\infty} E[x(t)(1 - x(t))(x(t) - x^*)] + o(s).$$

This 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 inequality $u(s) > u(0)$ for $s > 0$ small enough guarantees that weak selection favors A replacing B . Since $a - b - c + d > 0$, this condition can be written in the form

$$(3.7) \quad x^* < \frac{\sum_{t \geq 0} E[x(t)^2(1-x(t))]}{\sum_{t \geq 0} E[x(t)(1-x(t))]} = \hat{x}.$$

Note that the condition for cooperation to be favored is more stringent if the upper bound \hat{x} which satisfies $0 < \hat{x} < 1$ is closer to 0.

4. GENERALIZED ONE-THIRD LAW OF EVOLUTION

In this section we will calculate the upper bound \hat{x} . This will be done under the assumption that A is initially a single mutant, that is, $u(0) = z(0) = N^{-1}$. Moreover all calculations will be 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. As a matter of fact, using the indicator 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 . Here $p_{22} = 1 - NE(v_1^2)$ represents 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. 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

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

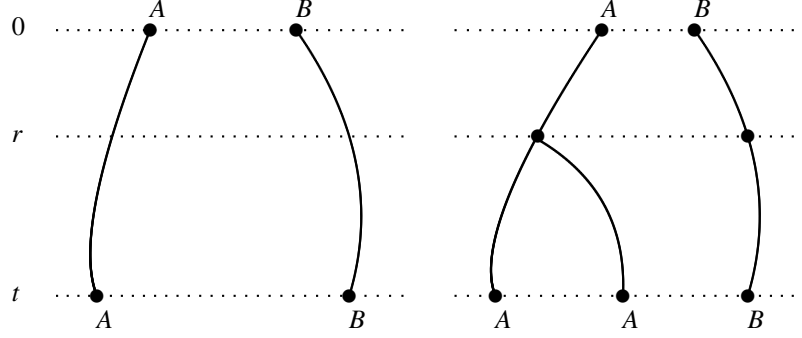


FIGURE 4. Lineages of two offspring of types A, B and three offspring of types A, A, B from generation t to generation 0 .

represents the probability that i offspring chosen at random without replacement in the same generation have j distinct parents. (See Fig 4.) 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

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

We conclude that

$$(4.9) \quad \lim_{N \rightarrow \infty} \hat{x} = \lim_{N \rightarrow \infty} \frac{p_{32}}{3(1 - p_{33})} \leq \frac{1}{3}$$

with an equality on the right-hand side if and only if at most 2 lineages out of 3 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 limit backward process of the neutral Cannings model to be the Kingman (1982) coalescent (Möhle 2000).

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 wider 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 2007).

In the case of the Eldon-Wakeley model, we find

$$(4.10) \quad p_{31} = \frac{1}{N^2} \left(1 - \frac{1}{N^\alpha}\right) + \frac{1}{N^\alpha} \left(\psi^3 + \frac{(1 - \psi)^3}{(N - 1)^2}\right)$$

and

$$(4.11) \quad p_{32} = \frac{3}{N} \left(1 - \frac{1}{N}\right) \left(1 - \frac{1}{N^\alpha}\right) + \frac{3(1 - \psi)}{N^\alpha} \left(\psi^2 + \frac{1 - \psi}{N - 1} - \frac{(1 - \psi)^2}{(N - 1)^2}\right).$$

Then

$$(4.12) \quad \lim_{N \rightarrow \infty} \frac{p_{32}}{3(1-p_{33})} = \begin{cases} \frac{1}{3} & \text{if } \alpha > 1, \\ \frac{1-\psi}{3-2\psi} & \text{if } \alpha < 1, \\ \frac{1+\psi^2(1-\psi)}{3+\psi^3(3-2\psi)} & \text{if } \alpha = 1. \end{cases}$$

This limit is strictly less than $1/3$ if and only if $\alpha \leq 1$. This means a more stringent condition for cooperation to be favored 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 to be a Λ -coalescent allowing for multiple mergers involving more than two lineages (Pitman 1999, Sagitov 1999).

5. EFFECT OF POPULATION SUBDIVISION

In this section we examine the effect of a group structure on the condition for cooperation to be favored. Actually we consider the finite Wright (1931) island model in the limit of a large number of small groups.

We assume 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.

Let $x_k(t)$ be the frequency of A in the offspring in group k in generation t after dispersal but before selection for $k = 1, \dots, D$ and $t \geq 0$. This frequency becomes

$$(5.1) \quad \tilde{x}_k(t) = \frac{x_k(t)(1 + w_A(x_k(t)))}{1 + sw(x_k(t))}$$

after selection. Note that

$$(5.2) \quad \overline{x(t)} = D^{-1} \sum_{k=1}^D x_k(t)$$

is equal to the frequency of A in the parents of generation t given by

$$(5.3) \quad \overline{z(t)} = D^{-1} \sum_{k=1}^D z_k(t),$$

where $z_k(t)$ represents this frequency in group k .

Proceeding as previously, we find that the condition for weak selection to favor A replacing B is $x^* < \hat{x}$ where

$$(5.4) \quad \hat{x} = \frac{\sum_{t \geq 0} E[\overline{x(t)^2(1-x(t))}]}{\sum_{t \geq 0} E[\overline{x(t)(1-x(t))}]}$$

Here

$$(5.5) \quad \overline{x(t)^2(1-x(t))} = D^{-1} \sum_{k=1}^D x_k(t)^2(1-x_k(t))$$

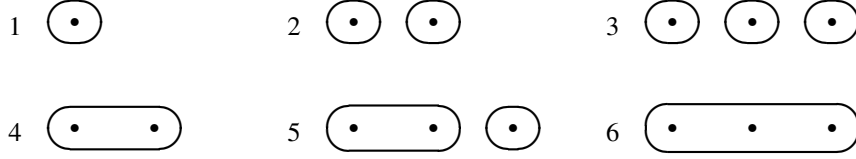


FIGURE 5. States for the ancestors of three offspring.

and

$$(5.6) \quad \overline{x(t)(1-x(t))} = D^{-1} \sum_{k=1}^D x_k(t)(1-x_k(t)).$$

We conclude that

$$(5.7) \quad \hat{x} = \frac{\sum_{t \geq 0} E[\xi_1(t)\xi_2(t)(1-\xi_3(t))]}{\sum_{t \geq 0} E[\xi_1(t)(1-\xi_2(t))]},$$

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

We want to calculate \hat{x} in the case where A is initially a single mutant, which means without loss of generality that $z_1(0) = N^{-1}$ and $z_k(0) = 0$ for $k = 2, \dots, D$. We will have to trace backwards in time the ancestors of two or three offspring. 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. 5). 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 time scales with expected sojourn times in state 4, 5 or 6 becoming negligible compared to expected sojourn times in state 2 or 3. More precisely, in the limit $D \rightarrow \infty$ with ND generations as unit of time, lineages within the same group either coalesce or migrate to different groups instantaneously, while each pair of lineages in different groups coalesces at rate f_{22} , which is the probability for two offspring chosen at random in the same group after dispersal to have 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 with rate f_{22} . (See Appendix.)

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

$$(5.8) \quad v_{ij} = \sum_{t \geq 1} v_{ij}(t)$$

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

$$(5.9) \quad E(T_i) = (ND)^{-1} \sum_{t \geq 0} p_{ii}(t)$$

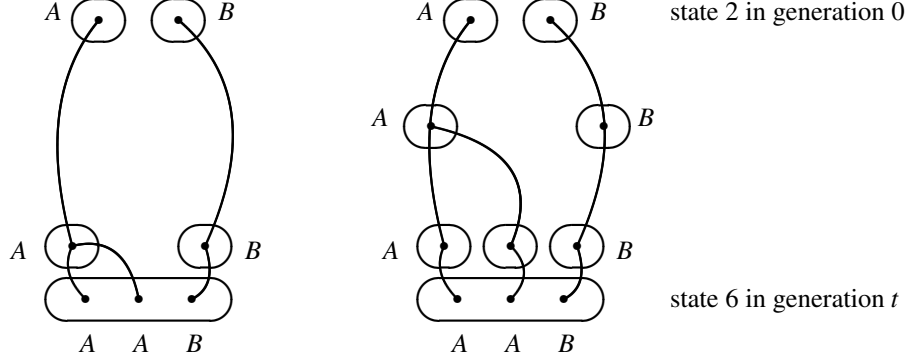


FIGURE 6. Lineages of three offspring of types A, A, B in the same group from generation t to generation 0.

is the expected time 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)

$$(5.10) \quad \lim_{D \rightarrow \infty} E(T_2) = f_{22}^{-1} \text{ and } \lim_{D \rightarrow \infty} E(T_4) = 0,$$

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,

$$(5.11) \quad \lim_{D \rightarrow \infty} v_{42} = f_{22} = 1 - f_{21} \text{ and } \lim_{D \rightarrow \infty} v_{62} = f_{32} + f_{33} = 1 - f_{31},$$

where f_{nk} represents the probability for n offspring chosen at random in the same group after dispersal to have 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 respectively, we obtain

$$(5.12) \quad \begin{aligned} \sum_{t \geq 0} E[\xi_1(t)(1 - \xi_2(t))] &= (ND)^{-1} \sum_{t \geq 1} p_{42}(t) + (ND)^{-1} \sum_{t \geq 1} p_{44}(t) \\ &= v_{42}E(T_2) + E(T_4) - (ND)^{-1}, \end{aligned}$$

since

$$(5.13) \quad \sum_{t \geq 1} p_{42}(t) = \sum_{t \geq 1} \sum_{r=1}^t v_{42}(r) p_{22}(t-r) = \sum_{r \geq 1} \sum_{t \geq 0} v_{42}(r) p_{22}(t).$$

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

$$(5.14) \quad \begin{aligned} \sum_{t \geq 0} E[\xi_1(t)\xi_2(t)(1 - \xi_3(t))] &= (3ND)^{-1} \sum_{t \geq 1} p_{62}(t) + (3ND)^{-1} \sum_{t \geq 1} p_{64}(t) \\ &= \frac{v_{62}}{3} E(T_2) + \frac{v_{64}}{3} E(T_4). \end{aligned}$$

Here $1/3$ is the probability that the two lineages in particular coalesce given that 2 out of 3 coalesce (see Fig. 6).

Finally we find that

$$(5.15) \quad \lim_{D \rightarrow \infty} \hat{x} = \frac{1 - f_{31}}{3(1 - f_{21})} > \frac{1}{3}.$$

This means a less stringent condition for cooperation to be favored when the population is subdivided into a large number of small groups. (See Appendix for expressions of f_{21} and f_{31} in terms of m and N .)

6. VARIANTS AND INTERPRETATIONS

In this section we will consider different timings for dispersal and selection and we will interpret the results in terms of effective payoffs in the presence of kin selection.

APPENDIX

As in Lessard and Wakeley (2004), the transition matrix on S from one generation to the previous one whose entries are $p_{ij}(1)$ for $i, j = 1, \dots, 6$ takes the form

$$(6.1) \quad \mathbf{P} = \mathbf{R} + (ND)^{-1}\mathbf{M}(D),$$

where \mathbf{Q} is the transition matrix in the case of an infinite number of groups. Since all states in S_1 are absorbing and all states in S_2 transient in the case $D = \infty$, the ergodic theorem guarantees that

$$(6.2) \quad \mathbf{R}^t \rightarrow \mathbf{H} = \begin{pmatrix} \mathbf{I} & \mathbf{0} \\ \mathbf{F} & \mathbf{0} \end{pmatrix}$$

as $t \rightarrow \infty$, where \mathbf{I} designates the 3×3 identity matrix and $\mathbf{0}$ the 3×3 zero matrix. Moreover

$$(6.3) \quad \mathbf{F} = \begin{pmatrix} f_{21} & f_{22} & 0 \\ 0 & f_{21} & f_{22} \\ f_{31} & f_{32} & f_{33} \end{pmatrix}$$

with f_{nk} denoting the probability for n offspring chosen at random in the same group after dispersal to have k ancestors in different groups in the case of an infinite number of groups. On the other hand

$$(6.4) \quad \mathbf{M}(D) \rightarrow \mathbf{M} = \begin{pmatrix} \mathbf{M}_{11} & \mathbf{M}_{12} \\ \mathbf{M}_{21} & \mathbf{M}_{22} \end{pmatrix}$$

as $D \rightarrow \infty$, where

$$(6.5) \quad \mathbf{M}_{11} = \begin{pmatrix} 0 & 0 & 0 \\ m(2-m) & -Nm(2-m) & 0 \\ 0 & 3m(2-m) & -3Nm(2-m) \end{pmatrix}$$

and

$$(6.6) \quad \mathbf{M}_{12} = \begin{pmatrix} 0 & 0 & 0 \\ (N-1)m(2-m) & 0 & 0 \\ 0 & 3(N-1)m(2-m) & 0 \end{pmatrix}.$$

Applying a lemma due to Möhle (1998) to the transition matrix from time 0 to time τ in the past with NDf_{22}^{-1} generations as unit of time, we obtain

$$(6.7) \quad \mathbf{P}^{[ND\tau]} \rightarrow \mathbf{H}e^{\tau\mathbf{H}\mathbf{M}\mathbf{H}} = \begin{pmatrix} e^{\tau\mathbf{G}} & \mathbf{0} \\ \mathbf{F}e^{\tau\mathbf{G}} & \mathbf{0} \end{pmatrix} = \mathbf{Q}(\tau)$$

as $D \rightarrow \infty$, where $\lfloor \cdot \rfloor$ denotes the integer value and

$$(6.8) \quad \mathbf{G} = \mathbf{M}_{11} + \mathbf{M}_{12}\mathbf{F} = f_{22} \begin{pmatrix} 0 & 0 & 0 \\ 1 & -1 & 0 \\ 0 & 3 & -3 \end{pmatrix}.$$

This is the generator of the death process of the Kingman (1982) coalescent with rate f_{22} instead of 1. The matrix $Q(\tau)$ whose entries are denoted by $q_{ij}(\tau)$ for $i, j = 1, \dots, 6$ is a transition matrix from time 0 to time τ 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 .

Note that

$$(6.9) \quad E(T_2) = (ND)^{-1} \sum_{t=0}^{\infty} p_{22}(t) = \int_0^{\infty} p_{22}(\lfloor ND\tau \rfloor) d\tau \rightarrow \int_0^{\infty} q_{22}(\tau) d\tau = f_{22}^{-1}$$

as $D \rightarrow \infty$. This is the case because the integral on the right side is the expected time with two lineages that coalesce at the rate f_{22} and

$$(6.10) \quad p_{22}(\lfloor ND\tau \rfloor) \leq \left(1 - \frac{m(2-m)}{ND}\right)^{\lfloor ND\tau \rfloor} \leq e^{-m(2-m)\tau}.$$

Therefore, the dominated convergence theorem can be applied. Similarly

$$(6.11) \quad E(T_4) = (ND)^{-1} \sum_{t=0}^{\infty} p_{44}(t) \rightarrow \int_0^{\infty} q_{44}(\tau) d\tau = 0,$$

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

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

$$(6.12) \quad \mathbf{v} = \tilde{\mathbf{P}}^{ND} \mathbf{v},$$

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

$$(6.13) \quad \lim_{D \rightarrow \infty} \tilde{\mathbf{P}}^{ND} = \tilde{\mathbf{Q}} = \begin{pmatrix} e^{\tilde{\mathbf{G}}} & \mathbf{0} \\ \mathbf{F}e^{\tilde{\mathbf{G}}} & \mathbf{0} \end{pmatrix},$$

where

$$(6.14) \quad \tilde{\mathbf{G}} = f_{22} \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 3 & -3 \end{pmatrix}.$$

Therefore

$$(6.15) \quad \lim_{D \rightarrow \infty} \mathbf{v} = \tilde{\mathbf{Q}} \lim_{D \rightarrow \infty} \mathbf{v}.$$

It can be checked directly that the unique solution is

$$(6.16) \quad \lim_{D \rightarrow \infty} \mathbf{v} = (0, 1, 1, f_{22}, 1, f_{32} + f_{33}).$$

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

$$(6.17) \quad \begin{aligned} f_{21} &= (1-m)^2 \left(\frac{1}{N} + \left(1 - \frac{1}{N}\right) f_{21} \right), \\ f_{31} &= (1-m)^3 \left(\frac{1}{N^2} + \frac{3}{N} \left(1 - \frac{1}{N}\right) f_{21} + \left(1 - \frac{1}{N}\right) \left(1 - \frac{2}{N}\right) f_{31} \right), \end{aligned}$$

from which

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

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

REFERENCES

- [1] AXELROD, R. AND HAMILTON, W. D. (1981) The evolution of cooperation. *Science* **211**, 1390–1396.
- [2] AXELROD, R. (1984) *The Evolution of Cooperation*. New York: Basic Books.
- [3] CANNINGS, C. (1974) The latent roots of certain Markov chains arising in genetics: a new approach. I. Haploid models. *Adv. Appl. Prob.* **6**, 260–290.
- [4] ELDON, B. AND WAKELEY, J. (2006) Coalescent processes when the distribution of offspring number among individuals is highly skewed. *Genetics* **172**, 2621–2633.
- [5] FISHER, R. A. (1930) *The Genetical Theory of Natural Selection*. Oxford: Clarendon.
- [6] HOFBAUER, J. AND SIGMUND, K. (1998) *Evolutionary Games and Population Dynamics*. Cambridge: Cambridge University Press.
- [7] IMHOF, L. A. AND NOWAK, M. A. (2006) Evolutionary game dynamics in a Wright-Fisher process. *J. Math. Biol.* **52**, 667–681.
- [8] KINGMAN, J. F. C. (1982) The coalescent. *Stoch. Proc. Appl.* **13**, 235–248.
- [9] LESSARD, S. (1990) Evolutionary stability: One concept, several meanings. *Theor. Pop. Biol.* **37**, 159–170.
- [10] LESSARD, S. (2005) Long-term stability from fixation probabilities in finite populations: New perspectives for ESS theory. *Theor. Pop. Biol.* **68**, 19–27.
- [11] LESSARD, S. (2007) Cooperation is less likely to evolve in a finite population with a highly skewed distribution of family size. *Proc. Roy. Soc. B* **274**, 1861–1865.
- [12] LESSARD, S. (2009) Diffusion approximations for one-locus multi-allele kin selection, mutation and random drift in group-structured populations: a unifying approach to selection models in population genetics. *J. Math. Biol.* **59**, 659–696.
- [13] LESSARD, S. AND LADRET, V. (2007) The probability of fixation of a single mutant in an exchangeable selection model. *J. Math. Biol.* **54**, 721–744.
- [14] LESSARD, S. AND WAKELEY, J. (2004) The two-locus ancestral graph in a subdivided population: convergence as the number of demes grows in the island model. *J. Math. Biol.* **48**, 275–292.
- [15] MÖHLE, M. (1998) A convergence theorem for Markov chains arising in population genetics and the coalescent with selfing. *Adv. Appl. Prob.* **30**, 493–512.
- [16] MÖHLE, M. (2000) Total variation distances and rates of convergence for ancestral coalescent processes in exchangeable population models. *Adv. Appl. Prob.* **32**, 983–993.
- [17] MORAN, P. A. P. (1958) Random processes in genetics. *Proc. Camb. Phil. Soc.* **54**, 60–71.
- [18] NOWAK, M. A., SASAKI, A., TAYLOR, C. AND FUDENBERG, D. (2004) Emergence of cooperation and evolutionary stability in finite populations. *Nature* **428**, 646–650.
- [19] PITMAN, J. (1999). Coalescents with multiple collisions. *Annals of Probability* **27**, 1870–1902.
- [20] SAGITOV, S. (1999). The general coalescent with asynchronous mergers of ancestral lines. *Journal of Applied Probability* **36**, 1116–1125.
- [21] ROUSSET, F. (2003) A minimal derivation of convergence stability measures. *J. Theor. Biol.* **221**, 665–668.
- [22] WRIGHT, S. (1931) Evolution in Mendelian populations. *Genetics* **16**, 97–159.

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