

Effective Game Matrix and Inclusive Payoff in Group-Structured Populations

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Abstract We show that a matrix game within groups in a finite-island model is effectively equivalent to a matrix game in a well-mixed population. The effective game matrix is a sum of interaction effects minus competition effects, weighted by identity measures involving up to three individuals. These identity measures are computed in the absence of selection but depend on the selection regime and the dispersal pattern: differential viability or fertility, hard selection or soft selection, uniform dispersal or local extinction followed by uniform recolonization. Hard selection, which allows for group selection, understood as differential contributions of groups, reduces competition within groups compared to soft selection. Moreover, the reduction is more pronounced in the case of uniform dispersal than in the case of local extinction. Fertility differences add competition effects between an individual and itself. A personal inclusive payoff can be defined from the effective game matrix and used to predict the increase or decrease in frequency of a mutant strategy. However, this personal inclusive payoff is generally frequency-dependent and its mean does not necessarily increase over time.

Keywords Evolutionary game · Matrix game · Finite-island model · Group selection · Inclusive fitness · Relatedness

1 Introduction

The replicator equation for a matrix game [36] can be seen as the beginning of evolutionary game dynamics. Since then, a wide variety of dynamical properties have been characterized by the entries of the game matrix, their number and their relationships (see, e.g., [12, 13], and references therein).

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The replicator equation assumes random pairwise interactions in a well-mixed, infinitely-large population. In real populations, however, interactions among close neighbors, relatives or similar individuals are more likely to happen than interactions among distant or dissimilar individuals. In order to take into account local interactions among individuals, group-structured populations have been considered: heterogeneous population [6], island model or stepping-stone model on a lattice [10, 30, 35], graph structure [26, 34], phenotype space [1, 37] or set space [33]. Diffusion approximations and fixation probabilities have also been obtained for family-structured populations [32], island models [17, 31] and under isolation by distance [29]. See, e.g., [24] for a recent review of game dynamics in group-structured populations.

In the vast majority of models dealing with interactions in populations subdivided into group units, the focus is on the evolution of cooperation or altruism, traits that appear to be disadvantageous from an individual point of view. Moreover, it is usually assumed that individuals in interaction have additive effects on the fitness of each other, which is a good approximation if there are small differences in individual strategies. Some authors insist on the role of kin selection, as accounted for by a personal inclusive fitness [9], which is obtained by transferring fitness effects from recipients to donors, weighted by some coefficients of relatedness. Others think that the primary driving force that can explain the spread of cooperation is group selection, involving extinction and recolonization of demes [20, 21], or understood more generally as a variable contribution of groups to the whole population through differential growth or expansion ([39], and references therein), which may prevail over the effects of individual selection within groups.

Group selection and kin selection, which are closely related (see, e.g., [2, 3, 22]) have nourished long debates in population genetics and they remain controversial subjects. Confronted with the intricacies of the effects of interactions among individuals in evolutionary games, some have come to the conclusion that an inclusive fitness approach is useless or unapplicable [25].

In this paper, we will study a matrix game within groups, not necessarily additive, in an infinitely-large, finite-island population with partial uniform dispersal or local extinction followed by uniform recolonization. We will consider that the payoffs are translated into viability or fertility differences under the assumptions of soft selection as well as hard selection, which allows for differential group outputs. The exact dynamical equations for the strategy frequencies will be deduced in the limit of weak selection and compared to the replicator equation for a well-mixed population. The roles of group selection and kin selection will be commented.

This will complement and extend a previous exact study on general matrix games in an infinite family-structured population [19] and diffusion approximation results for additive matrix games in island models for a finite population [17].

2 Matrix Game for Viability Selection

We consider a large, virtually infinite population subdivided into groups of N individuals. This is Wright's [38] island model but with a finite group size. We assume that there exist n possible individual strategies denoted by S_1, \dots, S_n . An ordered group type i is represented by a vector of strategies $\mathbf{S}_i = (S_{i1}, \dots, S_{iN})$ whose entries are the strategies used by the individuals in the group once these are arbitrarily ordered. Moreover, the vector $\mathbf{x}_i = (x_{i1}, \dots, x_{in})$ gives the frequencies of the different strategies in a group of type i .

Namely, we have

$$x_{ik} = \frac{N_{ik}}{N}, \tag{1}$$

where N_{ik} is the number of individuals using strategy S_k among the N individuals in a group of type i . Note that there are n^N different group types, but that several group types can exhibit the same strategy frequency vector. Finally the frequency of group type i at time $t \geq 0$ is denoted by $z_i(t)$. This yields

$$x_k(t) = \sum_i x_{ik} z_i(t) \tag{2}$$

for the frequency of S_k in the whole population at time $t \geq 0$.

Generations are assumed discrete, non-overlapping. From one generation to the next, offspring are produced in large numbers in each group, every member of the group producing the same proportion N^{-1} of offspring. This is followed by viability selection as a result of a matrix game taking place among the offspring in the same groups. More precisely, we assume that every offspring uses the same strategy as its parent in random pairwise interactions among offspring within each group and that the payoff a_{kl} to an offspring using S_k against S_l is such that the viability of the offspring takes the form

$$w_{kl} = 1 + sa_{kl}. \tag{3}$$

Here, 1 represents some reference value and a_{kl} a coefficient of selection with respect to an intensity of selection s . In other words, the payoff translates into an additive effect in units of selection intensity on a relative viability measure initially set equal to 1.

Note that the viability of an offspring I can be written in the form

$$w_I = 1 + sa_I, \tag{4}$$

where

$$a_I = \sum_{k,l=1}^n a_{kl} q_{kI} q_{lI'} \tag{5}$$

represents the payoff to I in interaction with I' , and I' is an offspring chosen at random in the same group as I . In this notation, q_{kI} represents the frequency of S_k in I (1 if I uses strategy S_k , and 0 otherwise), and similarly $q_{lI'}$ the frequency of S_l in an offspring I' .

In a group of type i , the mean payoff to S_k is

$$\bar{a}_{ik} = (A\mathbf{x}_i)_k = \sum_{l=1}^n a_{kl} x_{il}, \tag{6}$$

while the mean payoff in the entire group is

$$\bar{a}_i = \mathbf{x}_i \cdot A\mathbf{x}_i = \sum_{k,l=1}^n a_{kl} x_{ik} x_{il}. \tag{7}$$

Here $A = [a_{kl}]_{k,l=1}^n$ denotes the game matrix and \cdot the usual scalar product. Therefore,

$$\bar{w}_{ik} = \sum_{l=1}^n w_{kl} x_{il} = 1 + s \bar{a}_{ik} \quad (8)$$

is the mean viability of S_k in a group of type i , in which the mean viability is

$$\bar{w}_i = \sum_{k=1}^n \bar{w}_{ik} x_{ik} = 1 + s \bar{a}_i. \quad (9)$$

Consequently, the frequency of S_k in a group of type i after viability selection is given by

$$x_{ik}^* = \frac{x_{ik} \bar{w}_{ik}}{\bar{w}_i} = x_{ik} + s x_{ik} \frac{\bar{a}_{ik} - \bar{a}_i}{1 - s \bar{a}_i}. \quad (10)$$

This leads to the approximation

$$\Delta x_{ik} = x_{ik}^* - x_{ik} = s x_{ik} (\bar{a}_{ik} - \bar{a}_i) + o(s), \quad (11)$$

for the change in the frequency of S_k in a group of type i due to viability differences. Note that this change can be written in the form [27, 28]

$$\Delta x_{ik} = \frac{\text{Cov}_i(q_{kl}, w_l)}{E_i(w_l)} = s \text{Cov}_i(q_{kl}, a_l) + o(s), \quad (12)$$

where E_i and Cov_i denote expectation and covariance, respectively, in a group of type i . As a matter of fact, we have

$$\begin{aligned} E_i(q_{kl}) &= x_{ik}, \\ E_i(a_l) &= \sum_{k,l=1}^n a_{kl} E_i(q_{kl} q_{ll'}) = \sum_{k,l=1}^n a_{kl} x_{ik} x_{il}, \\ E_i(q_{kl} a_l) &= \sum_{l=1}^n a_{kl} E_i(q_{kl} q_{ll'}) = x_{ik} \sum_{l=1}^n a_{kl} x_{il}, \end{aligned} \quad (13)$$

with $E_i(w_l) = 1 + s E_i(a_l)$ and $\text{Cov}_i(q_{kl}, w_l) = s \text{Cov}_i(q_{kl}, a_l)$.

3 Soft Viability Selection with Uniform Dispersal or Local Extinction

In this section, we assume soft viability selection [4] so that the total number of offspring in each group after viability selection is the same as before viability selection. Moreover, we make either of the following assumptions: a fraction m of offspring in each group disperse uniformly among all groups (uniform dispersal); or each group goes extinct with probability m independently of all other groups and then it is recolonized by offspring coming uniformly from all remaining groups (local extinction and uniform recolonization). In both cases, this is followed by random sampling of N individuals within each group to start the next generation.

Under these assumptions and with time scaled so that one generation corresponds to s time units, the frequency of S_k in the whole population at time $t + s$ will be

$$x_k(t + s) = \sum_i x_{ik}^* z_i(t). \tag{14}$$

This yields

$$x_k(t + s) - x_k(t) = sE_{\mathbf{z}(t)}(\text{Cov}_i(q_{kI}, a_I)) + o(s) \tag{15}$$

for the change in the frequency of S_k in the whole population from time t to time $t + s$. Here, we have

$$\begin{aligned} E_{\mathbf{z}(t)}(\text{Cov}_i(q_{kI}, a_I)) &= \sum_i z_i(t) \text{Cov}_i(q_{kI}, a_I) \\ &= \sum_i z_i(t) E_i(q_{kI} a_I) - \sum_i z_i(t) E_i(q_{kJ}) E_i(a_I) \\ &= \sum_i z_i(t) E_i(q_{kI} a_I) - x_k(t) \bar{a}(t) \\ &\quad - \sum_i z_i(t) E_i(q_{kJ}) E_i(a_I) + x_k(t) \bar{a}(t) \\ &= \text{Cov}_{\mathbf{z}(t)}(q_{kI}, a_I) - \text{Cov}_{\mathbf{z}(t)}(q_{kJ}, a_I), \end{aligned} \tag{16}$$

where I and J designate two offspring chosen at random in the same group, and

$$\bar{a}(t) = \sum_i \bar{a}_i z_i(t) \tag{17}$$

is the mean payoff in the whole population at time t .

Finally, we define

$$\dot{x}_k(t) = \lim_{s \rightarrow 0} \frac{x_k(t + s) - x_k(t)}{s}. \tag{18}$$

Then, we obtain

$$\dot{x}_k(t) = \text{Cov}_{\mathbf{z}(t)}(q_{kI}, a_I) - \text{Cov}_{\mathbf{z}(t)}(q_{kJ}, a_I) \tag{19}$$

for the rate of change in the frequency of S_k in the limit of a small intensity of selection.

On the other hand, a group of type i at time t will be transformed into a group of type j at time $t + s$ with some probability $P_{ij}(s, \mathbf{z}(t))$, which depends continuously on the intensity of selection and the frequencies of the different group types at time t . This yields

$$z_j(t + s) = \sum_i z_i(t) P_{ij}(s, \mathbf{z}(t)) \tag{20}$$

for the frequency of type j at time $t + s$, or

$$\mathbf{z}(t + s) = \mathbf{z}(t)^T P(s, \mathbf{z}(t)) \tag{21}$$

in matrix notation.

We assume throughout that $\mathbf{z}(t)$ is continuous as a function of t . Then, taking the limit as s tends to 0 on both sides of the previous equation yields

$$\mathbf{z}(t) = \mathbf{z}(t)^T P(0, \mathbf{z}(t)). \quad (22)$$

This means that $\mathbf{z}(t)$ is an equilibrium of the recurrence equation

$$\mathbf{z}(t + n + 1) = \mathbf{z}(t + n)^T P(0, \mathbf{z}(t + n)) \quad (23)$$

for every integer $n \geq 0$. Note that $P(0, \mathbf{z}(t + n))$ is a transition matrix in the absence of selection.

It can be shown [17] that the entries of

$$\mathbf{z}(t) = \lim_{n \rightarrow \infty} \mathbf{z}(t + n) \quad (24)$$

are given in the form

$$z_j(t) = \sum_{\mathbf{r}} c_j(\mathbf{r}) x_1(t)^{r_1} \cdots x_n(t)^{r_n}. \quad (25)$$

Here, the summation is over all $\mathbf{r} = (r_1, \dots, r_n) \neq (0, \dots, 0)$ satisfying $0 \leq r_k \leq N_{jk}$, for $k = 1, \dots, n$. Note that N_{jk} is the number of individuals of type S_k in a group of type j . Moreover, $c_j(\mathbf{r})$ represents the number of ways for a group of type j to have r_k ancestors of type S_k for $k = 1, \dots, n$, all in different groups. The proof relies on the coalescence approach [14] by tracing the ancestry of a focal group backwards in time under neutrality. Individuals having the same common ancestor are identical-by-descent (ibd) and they are necessarily of the same type. On the other hand, the types of individuals that are not ibd are independent.

Let us summarize our findings in a statement in which the explicit dependence on t has been dropped to simplify the notation.

Result 1 *In the case of soft viability selection with coefficients determined by a matrix game within groups in a finite-island model with uniform dispersal of a fraction m of offspring, or local extinction and uniform recolonization with probability m , the rate of change in the frequency of strategy S_k in the limit of a small selection intensity is given by*

$$\dot{x}_k = \text{Cov}_{\mathbf{z}}(q_{kI}, a_I) - \text{Cov}_{\mathbf{z}}(q_{kJ}, a_I), \quad (26)$$

where a_I and a_J represent the payoffs to two offspring I and J chosen at random in the same group as defined in (5), and q_{kI} the frequency of S_k in I . Moreover, \mathbf{z} is the equilibrium distribution of the group types with respect to the current strategy frequencies in the absence of selection as given in (25).

4 Hard Viability Selection with Local Extinction and Uniform Recolonization

In this section, we suppose that the total number of offspring in each group after viability selection is proportional to the mean viability in the group. This is a case of hard selection [4]. Moreover, we suppose that each group goes extinct with probability m independently of all other groups. In this case, it is recolonized by offspring coming from all remaining

groups weighted by their mean viabilities. In other words, there is local extinction followed by uniform recolonization

Under the above assumptions, the frequency of S_k in the whole population at time $t + s$ is given by

$$x_k(t + s) = (1 - m) \sum_i x_{ik}^* z_i(t) + m \frac{\sum_i \bar{w}_i x_{ik}^* z_i(t)}{\bar{w}(t)}, \tag{27}$$

where

$$\bar{w}(t) = \sum_i \bar{w}_i z_i(t) = 1 + s\bar{a}(t) \tag{28}$$

is the mean viability in the whole population at time t . This leads to the approximation

$$\begin{aligned} x_k(t + s) - x_k(t) &= s \{ (1 - m) E_{z(t)}(\text{Cov}_i(q_{kI}, a_I)) + m \text{Cov}_{z(t)}(q_{kJ}, a_I) \} + o(s), \end{aligned} \tag{29}$$

from which the following conclusion can be drawn *mutatis mutandis*.

Result 2 *In the case of hard viability selection with local extinction and uniform recolonization with probability m , Result 1 for the rate of change in the frequency of S_k becomes*

$$\dot{x}_k = \text{Cov}_z(q_{kI}, a_I) - (1 - m) \text{Cov}_z(q_{kJ}, a_I), \tag{30}$$

where I and J are two offspring chosen at random in the same group.

5 Hard Viability Selection with Uniform Dispersal

Now suppose hard selection as in the previous model but with uniform dispersal so that each group receives the same number of migrants. Then, the relative size of a group of type i after dispersal of a proportion m of offspring will be $(1 - m)\bar{w}_i + m\bar{w}$, where \bar{w}_i is its relative size before dispersal and \bar{w} the average relative group size in the whole population.

Moreover, the frequency of S_k in a group of type i at time t after selection and migration will be

$$\begin{aligned} \tilde{x}_{ik}^*(t) &= \frac{(1 - m)\bar{w}_i x_{ik}^* + m \sum_j \bar{w}_j x_{jk}^* z_j(t)}{(1 - m)\bar{w}_i + m\bar{w}(t)} \\ &= (1 - m)x_{ik} + mx_k(t) + s(1 - m)\bar{a}_{ik}x_{ik} + sm \sum_j \bar{a}_{jk}x_{jk}z_j(t) \\ &\quad - s \{ (1 - m)\bar{a}_i + m\bar{a}(t) \} \{ (1 - m)x_{ik} + mx_k(t) \} + o(s). \end{aligned} \tag{31}$$

Then, the frequency of S_k in the whole population at time $t + s$ is given by

$$x_k(t + s) = \sum_i \tilde{x}_{ik}^*(t) z_i(t), \tag{32}$$

and we have the approximation

$$x_k(t+s) = x_k(t) + s \left(\sum_i \bar{a}_{ik} x_{ik} z_i(t) - \bar{a}(t) x_k(t) \right) - s(1-m)^2 \left(\sum_i \bar{a}_{ik} x_{ik} z_i(t) - \bar{a}(t) x_k(t) \right) + o(s). \quad (33)$$

This yields the following result.

Result 3 *In the case of hard viability selection with uniform dispersal of a fraction m of offspring, Result 1 for the rate of change in the frequency of S_k becomes*

$$\dot{x}_k = \text{Cov}_z(q_{kI}, a_I) - (1-m)^2 \text{Cov}_z(q_{kJ}, a_J), \quad (34)$$

where I and J are two offspring chosen at random in the same group.

6 Matrix Game for Fertility Selection

In this section, we assume that the matrix game takes place among parents within groups so that the mean payoff to a parent using S_k in a group of type i is given by

$$\bar{a}_{ik} = (\mathbf{A}\mathbf{x}_i)_k, \quad (35)$$

where

$$\mathbf{x}_i(k) = \frac{N\mathbf{x}_i - \mathbf{e}_k}{N-1} \quad (36)$$

is the mean strategy used against S_k in a group of type i . This assumes random pairwise interactions among the N parents of a group and excludes self-interactions. Here, \mathbf{e}_k denotes the standard k th n -dimensional coordinate vector, so that $\mathbf{x}_i(k) = (x_{i1}(k), \dots, x_{in}(k))$ with

$$x_{ik}(k) = \frac{N_{ik} - 1}{N - 1} \quad (37)$$

and

$$x_{il}(k) = \frac{N_{il}}{N - 1}, \quad (38)$$

for $l \neq k$. Moreover, it is assumed that the payoff has an effect on fertility in such a way that the mean fertility of a parent using S_k in a group of type i is given by

$$\bar{w}_{ik} = 1 + s\bar{a}_{ik} = 1 + \frac{sN}{N-1} \left((\mathbf{A}\mathbf{x}_i)_k - \frac{a_{kk}}{N} \right). \quad (39)$$

This fertility model corresponds to a situation in which the viability of an offspring whose parent uses S_k against another parent in the same group using S_l is $w_{kl} = 1 + sa_{kl}$. In other words, the viability of an offspring I is given by $w_I = 1 + sa_I$ as previously with a payoff in the form

$$a_I = \sum_{k,l=1}^n a_{kl} q_{kI} q_{lI'}, \quad (40)$$

where I' designates an offspring chosen at random in the same group as I , but produced by a different parent.

Therefore, all previous results apply modulo this modification in the expression of an offspring's payoff.

Result 4 *In the case of fertility selection instead of viability selection, Results 1, 2 and 3 for the rate of change in the frequency of S_k apply with the restriction that only interactions among non-sib offspring are considered in the payoff a_I for an offspring I .*

7 Effective Game Matrix

In all the models of the previous sections, the rate of change in the frequency of S_k has been expressed in terms of the covariances

$$\text{Cov}_z(q_{kI}, a_I) = \sum_{l,m=1}^n a_{lm} \text{Cov}_z(q_{kI}, q_{lI}q_{mI'}) \tag{41}$$

and

$$\text{Cov}_z(q_{kJ}, a_I) = \sum_{l,m=1}^n a_{lm} \text{Cov}_z(q_{kJ}, q_{lI}q_{mI'}), \tag{42}$$

where I, I' and J represent offspring in the same group. In the viability models, these offspring are chosen at random among all offspring within the group. In the fertility models, I and J are chosen at random among all offspring, while I' is chosen at random among all non-sibs of I . In all cases, the covariances are calculated with respect to the equilibrium distribution of the group types in a neutral population, given the current strategy frequencies as expressed in (25).

In order to compute the covariances, we introduce the following identity measures for offspring I, J and K in the same group in a neutral population:

$$\begin{aligned} \phi_{IJ} &= \text{Pr}(I \equiv J), \\ \phi_{IJ/K} &= \text{Pr}(I \equiv J \not\equiv K), \\ \phi_{IJK} &= \text{Pr}(I \equiv J \equiv K). \end{aligned} \tag{43}$$

Here, the symbol \equiv means identical-by-descent (ibd) and $\not\equiv$ non-identical-by-descent (non-ibd). Note that

$$\begin{aligned} \phi_{IJ} &= \phi_{IJ/K} + \phi_{IJK}, \\ \phi_{I/J} &= \text{Pr}(I \not\equiv J) = 1 - \phi_{IJ}, \\ \phi_{I/J/K} &= \text{Pr}(I \not\equiv J, I \not\equiv K, J \not\equiv K) = 1 - \phi_{IJ} - \phi_{IK/J} - \phi_{JK/I}. \end{aligned} \tag{44}$$

These measures will be used to develop the formulas (41) and (42).

Conditioning on the ibd status of two offspring I and I' in the same group, we find that

$$\begin{aligned} \text{Cov}_z(q_{kI}, q_{lI}q_{mI'}) &= \phi_{II'}(x_k \delta_{klm} - x_k x_l \delta_{lm}) \\ &\quad + \phi_{I/I'}(x_k x_m \delta_{kl} - x_k x_l x_m). \end{aligned} \tag{45}$$

Here, $\delta_{kl} = 1$ if $k = l$, and 0 otherwise, and similarly $\delta_{klm} = 1$ if $k = l = m$, and 0 otherwise.

Analogously, for three offspring I , I' and J in the same group, we have

$$\begin{aligned} \text{Cov}_{\mathbf{z}}(q_{kJ}, q_{II}q_{mI'}) &= \phi_{JII'}(x_k\delta_{klm} - x_kx_l\delta_{lm}) \\ &\quad + \phi_{JII'/I'}(x_kx_m\delta_{kl} - x_kx_lx_m) \\ &\quad + \phi_{JII'/I}(x_kx_l\delta_{km} - x_kx_lx_m). \end{aligned} \quad (46)$$

Note that this covariance given that J is not ibd to I and I' is equal to 0.

Finally, we find that

$$\text{Cov}_{\mathbf{z}}(q_{kI}, a_I) = x_k \left(\sum_{l=1}^n a_{kl}^I x_l - \sum_{l,m=1}^n a_{lm}^I x_l x_m \right) \quad (47)$$

and

$$\text{Cov}_{\mathbf{z}}(q_{kJ}, a_I) = x_k \left(\sum_{l=1}^n a_{kl}^{JI} x_l - \sum_{l,m=1}^n a_{lm}^{JI} x_l x_m \right), \quad (48)$$

where

$$a_{kl}^I = \phi_{II'}a_{kk} + \phi_{II'/I}a_{kl} \quad (49)$$

and

$$a_{kl}^{JI} = \phi_{JII'}a_{kk} + \phi_{JII'/I}a_{kl} + \phi_{JII'/I}a_{lk}. \quad (50)$$

Note that $a_{kl}^{JI} = a_{kl}^I$ when J is replaced by I .

For the viability or fertility models of the previous sections, this leads to a rate of change in the frequency of S_k in the form of the replicator equation [36]

$$\dot{x}_k = x_k \left((A^\circ \mathbf{x})_k - \mathbf{x} \cdot A^\circ \mathbf{x} \right), \quad (51)$$

for some *effective game matrix* $A^\circ = [a_{kl}^\circ]$.

Result 5 *With viability or fertility selection within groups in a finite-island model with coefficients of selection given by a game matrix $A = [a_{kl}]$, the rate of change in the frequency of S_k is given by the replicator equation as in a well-mixed population with an effective game matrix $A^\circ = [a_{kl}^\circ]$, where*

$$a_{kl}^\circ = a_{kl}^I - a_{kl}^{JI} \quad (52)$$

in the case of soft selection with uniform dispersal of a fraction m of offspring, or local extinction and uniform recolonization with probability m ,

$$a_{kl}^\circ = a_{kl}^I - (1 - m)a_{kl}^{JI} \quad (53)$$

in the case of hard selection with local extinction and uniform recolonization with probability m , and

$$a_{kl}^\circ = a_{kl}^I - (1 - m)^2 a_{kl}^{JI} \quad (54)$$

in the case of hard selection with uniform dispersal of a fraction m of offspring. In all cases, the entries a_{kl}^I and a_{kl}^{JI} are given by (49) and (50), respectively.

8 Computation of the Identity Measures

8.1 Case of Uniform Dispersal

The identity measures for three offspring I, J and K chosen at random among all offspring in the same group in a neutral population before uniform dispersal of a fraction m of offspring satisfy the equilibrium equations

$$\begin{aligned} \phi_{IJ} &= \frac{1}{N} + \left(1 - \frac{1}{N}\right)(1 - m)^2 \phi_{IJ}, \\ \phi_{IJK} &= \frac{1}{N^2} + \frac{3}{N} \left(1 - \frac{1}{N}\right)(1 - m)^2 \phi_{IJ} \\ &\quad + \left(1 - \frac{1}{N}\right) \left(1 - \frac{2}{N}\right)(1 - m)^3 \phi_{IJK}. \end{aligned} \tag{55}$$

The solution is given by

$$\begin{aligned} \phi_{IJ} &= \frac{1}{Nm(2 - m) + (1 - m)^2}, \\ \phi_{IJK} &= \left[\frac{N + 2(N - 1)(1 - m)^2}{N^2m(3 - 3m + m^2) + (3N - 2)(1 - m)^3} \right] \phi_{IJ}. \end{aligned} \tag{56}$$

Moreover, we have the equality

$$\phi_{IJ/K} = \phi_{IJ} - \phi_{IJK}. \tag{57}$$

In the limit of a large group size ($N \rightarrow \infty$) and a small dispersal rate ($m \rightarrow 0$) so that the product tends to a constant ($Nm \rightarrow M$), the above identity measures converge to

$$\begin{aligned} \phi_{IJ}^{(\infty)} &= \frac{1}{2M + 1}, \\ \phi_{IJK}^{(\infty)} &= \frac{1}{(2M + 1)(M + 1)}, \\ \phi_{IJ/K}^{(\infty)} &= \frac{M}{(2M + 1)(M + 1)}, \end{aligned} \tag{58}$$

respectively. Note that

$$\frac{\phi_{IJK}^{(\infty)}}{\phi_{JK}^{(\infty)}} = \frac{\phi_{IJ/K}^{(\infty)} + \phi_{IK/J}^{(\infty)}}{\phi_{JK}^{(\infty)}} = \frac{2\phi_{IJ}^{(\infty)}}{1 + \phi_{IJ}^{(\infty)}} = \frac{1}{M + 1}. \tag{59}$$

The above equation states that the probability for a third individual to be ibd to at least one of two previous individuals chosen at random in the same group does not depend on the event that the two previous individuals are ibd or not. Moreover, this probability is given by the scaled rate of coalescence 1 over this scaled rate plus the scaled rate of migration M . This is in agreement with the Ewens sampling formula [5] with migration playing the role of mutation and identity-by-descent that of identity-by-state under the infinitely-many-alleles assumption.

Note that we have

$$\begin{aligned}\phi_{IJ} &= \frac{1}{N} + \left(1 - \frac{1}{N}\right)\phi_{I'I'}, \\ \phi_{IJK} &= \frac{1}{N}\phi_{IJ} + \left(1 - \frac{1}{N}\right)\phi_{J'I'}, \\ \phi_{IJK} &= \left(1 - \frac{1}{N}\right)\phi_{J'I'},\end{aligned}\tag{60}$$

if I' is an offspring chosen at random among all non-sibs of I in the same group. This leads to the relationships

$$\begin{aligned}\phi_{I'I'} &= \frac{N\phi_{IJ} - 1}{N - 1}, \\ \phi_{J'I'} &= \frac{N\phi_{IJK} - \phi_{IJ}}{N - 1}, \\ \phi_{J'I'I'} &= \frac{N\phi_{IJK}}{N - 1},\end{aligned}\tag{61}$$

between identity measures for offspring I , J and K chosen at random among all offspring in the same group and identity measures for offspring I , I' and J chosen at random in the same group under the restriction that I and I' are not sibs. Note that there is no difference in the limit of a large group size. Moreover, we have always $\phi_{J'I'/I} = \phi_{J'I'I'}$ by symmetry.

8.2 Case of Local Extension and Uniform Recolonization

In the case of local extinction and uniform recolonization with probability m , the equilibrium equations become

$$\begin{aligned}\phi_{IJ} &= \frac{1}{N} + \left(1 - \frac{1}{N}\right)(1 - m)\phi_{IJ}, \\ \phi_{IJK} &= \frac{1}{N^2} + \frac{3}{N}\left(1 - \frac{1}{N}\right)(1 - m)\phi_{IJ} + \left(1 - \frac{1}{N}\right)\left(1 - \frac{2}{N}\right)(1 - m)\phi_{IJK},\end{aligned}\tag{62}$$

from which

$$\begin{aligned}\phi_{IJ} &= \frac{1}{Nm + 1 - m}, \\ \phi_{IJK} &= \left[\frac{N + 2(N - 1)(1 - m)}{N^2m + (3N - 2)(1 - m)} \right] \phi_{IJ},\end{aligned}\tag{63}$$

whose limiting values, as $N \rightarrow \infty$ and $m \rightarrow 0$ so that $Nm \rightarrow M$, are

$$\begin{aligned}\phi_{IJ}^{(\infty)} &= \frac{1}{M + 1}, \\ \phi_{IJK}^{(\infty)} &= \frac{M}{(M + 1)(M + 3)}.\end{aligned}\tag{64}$$

Note that the relationships in (59) do not hold in this case.

On the other hand, the relationships in (61) between identity measures for offspring chosen at random without restriction and offspring chosen at random under the restriction that two given offspring are not sibs are still valid.

9 Discussion

9.1 Effective Game Matrix

We have shown that a matrix game within groups in a finite-island model with partial dispersal or local extinction is equivalent to a matrix game in a well-mixed population defined with respect to some *effective game matrix*. Then, everything that is known about such matrix games (see, e.g., [12, 13]) can be applied *mutatis mutandis*.

The equivalence holds in the limit of weak viability or fertility selection with coefficients given by the entries of a game matrix $A = [a_{kl}]$ as a result of pairwise interactions within groups. The corresponding effective game matrix $A^\circ = [a_{kl}^\circ]$ is a linear combination of two matrices, $A^I = [a_{kl}^I]$ for the effects of I in interaction with an offspring I' that may be ibd or not to I , and $A^{J'I} = [a_{kl}^{J'I}]$ for the effects of I in competition with another offspring J that may be ibd to either I or I' , or both.

In the case of soft selection followed by uniform dispersal or local extinction, competition occurs effectively among all offspring within groups before dispersal whatever the dispersal rate is. In the case of hard selection followed by uniform dispersal, competition occurs after dispersal and is effective only in a proportion $(1 - m)^2$ of the group, which is the probability for two competitors to come from the same group. If hard selection is followed by local extinction and uniform recolonization, then this proportion becomes $1 - m$, which corresponds to the probability for the whole group not to have been recolonized.

Note that local extinction and uniform recolonization following hard selection has the same effect on the strategy frequencies in the whole population as proportional dispersal, that is, dispersal of a fraction m of offspring in each group and replacement by as many migrant offspring chosen at random among all migrants so that dispersal does not change the number of offspring in each group.

More important is the fact that hard selection, which allows for group selection understood as differential contributions of groups, reduces competition within groups compared to soft selection. Moreover, the effect becomes more pronounced as the dispersal rate or extinction probability increases.

In all cases, the entries of the effective game matrix are sums of interaction effects minus competition effects. They take the form

$$a_{kl}^\circ = \phi_{I'I'}a_{kk} + \phi_{I/I'}a_{kl} - \phi_{I_c I'I'}a_{kk} - \phi_{I_c I/I'}a_{kl} - \phi_{I_c I'/I'}a_{lk}. \tag{65}$$

Here, I' designates an offspring chosen at random in the same group as I *before dispersal*, with the restriction of not being a sib of I in fertility models, and in interaction with it. On the other hand, I_c is an offspring chosen at random in the same group as I , *before dispersal* in the case of soft selection, but *after dispersal* in the case of hard selection, and in competition with it. Therefore, the above identity measures involving I_c in the case of hard selection are those in the case of soft selection as computed in the previous section, but multiplied by $1 - m$ or $(1 - m)^2$ in models with local extinction or uniform dispersal, respectively. Moreover, I and I' can be permuted in the last term of (65) so that

$$a_{kl}^\circ = \phi_{I'I'}a_{kk} + \phi_{I/I'}a_{kl} - \phi_{I_c I'I'}a_{kk} - \phi_{I_c I/I'}a_{kl} - \phi_{I_c I'/I'}a_{lk}, \tag{66}$$

where I'_c designates an offspring in competition with I' .

9.2 Personal Inclusive Payoff

The effective game matrix corresponds to a mean payoff to S_k given by

$$a_{k\bullet}^\circ = \phi_{I'I'} a_{kk} + \phi_{I/I'} a_{k\bullet} - \phi_{I_c I'I'} a_{kk} - \phi_{I_c I/I'} a_{k\bullet} - \phi_{I'_c I/I'} a_{\bullet k}, \quad (67)$$

where

$$a_{k\bullet} = (A\mathbf{x})_k = \sum_{l=1}^n a_{kl} x_l \quad (68)$$

and

$$a_{\bullet k} = (A^T \mathbf{x})_k = \sum_{l=1}^n a_{lk} x_l. \quad (69)$$

This can be interpreted as a *personal inclusive payoff*. As a matter of fact, the overall expected payoff to S_k played by an offspring I is a_{kk} if I is ibd to the interacting offspring I' but not ibd to a competitor I_c , while it is $a_{k\bullet}$ if I is not ibd to I' and not ibd to I_c . Moreover, we must subtract $a_{\bullet k}$, the expected payoff to I' not ibd to I , if its competitor I'_c is ibd to I .

Consider the special case of a game matrix $A = [a_{kl}]$ with entries in the additive form

$$a_{kl} = -c_k + b_l, \quad (70)$$

where c_k represents some cost associated to playing S_k and b_l some benefit associated to interacting with S_l . Then, the inclusive payoff to S_k is

$$\begin{aligned} a_{k\bullet}^\circ &= -(1 - \phi_{I_c I})c_k + (\phi_{I'I'} - \phi_{I_c I'I'} - \phi_{I'_c I/I'})b_k \\ &\quad + (\phi_{I/I'} - \phi_{I_c I/I'})b_{\bullet} + \phi_{I'_c I/I'} c_{\bullet}, \end{aligned} \quad (71)$$

where

$$c_{\bullet} = \sum_{l=1}^n c_l x_l \quad (72)$$

and

$$b_{\bullet} = \sum_{l=1}^n b_l x_l. \quad (73)$$

Actually, this is equivalent to a frequency-independent inclusive payoff to S_k given by

$$a_{k\bullet}^{\circ\circ} = -(1 - \phi_{I_c I})c_k + (\phi_{I'I'} - \phi_{I_c I'I'} - \phi_{I'_c I/I'})b_k. \quad (74)$$

This is the case since the replicator equation

$$\dot{x}_k = x_k (a_{k\bullet}^\circ - a_{\bullet\bullet}^\circ), \quad (75)$$

where $a_{\bullet\bullet}^\circ = \sum_{k=1}^n a_{k\bullet}^\circ$, is the same if $a_{k\bullet}^\circ$ is replaced by $a_{k\bullet}^{\circ\circ}$.

In general, however, the inclusive payoff to S_k will be frequency-dependent. One of the original objectives of the inclusive fitness approach [9] was to find a quantity that is maximized under the effects of natural selection in the case of interactions among related individuals. The main idea was to transfer fitness effects from recipients to donors weighted by coefficients of relatedness and then to apply Fisher’s [7] Fundamental Theorem of Natural Selection to this inclusive fitness to predict an increase of its mean. However, this requires that the inclusive fitness is frequency-independent.

Although a frequency-dependent inclusive fitness can account for the selection effects in a population, its usefulness may be questioned. This can explain recent criticisms about the inclusive fitness approach [25]. The sign of $a_{k\bullet}^\circ - a_{\bullet\bullet}^\circ$, however, informs us about the initial fate of a mutant strategy S_k introduced in small frequency into a population that was previously fixed or at equilibrium. In the additive case with $c_l = b_l = 0$ for all $l \neq k$, the condition for the initial increase in frequency of S_k , $a_{k\bullet}^\circ - a_{\bullet\bullet}^\circ > 0$, is the same as the condition for its increase to fixation. Moreover, it reduces to

$$\frac{b_k}{c_k} > \frac{1 - \phi_{IcI}}{\phi_{II'} - \phi_{IcII'} - \phi_{I'cI/I'}}. \tag{76}$$

This is an extension of Hamilton’s [9] rule for the evolution of altruism, which corresponds to the case $\phi_{II'} = R$ and $\phi_{IcI} = \phi_{IcII'} = \phi_{I'cI/I'} = 0$.

In the general framework of matrix games in group-structured populations, the notion of effective game matrix appears to be more useful since a linear game in a well-mixed population is entirely characterized by its game matrix. The terminology is akin to the notion of effective size in population genetics, defined as “the number of breeding individuals in an idealized population that would show the same amount of dispersion of allele frequencies under random genetic drift or the same amount of inbreeding as the population under consideration” [38]. In the case of a matrix game, the effective game matrix mimics in a single population all interactions that may occur locally in a subdivided population.

9.3 Coefficients of Relatedness

The identity measures in the expressions of the inclusive payoff to S_k are coefficients of relatedness between donors and recipients that involve up to three individuals. In all cases, they represent the probability for the recipient to be ibd (identical-by-descent) to the donor and ibd or not ibd to the individual in interaction with the donor. Similar identity measures have already been considered for kin selection in Mendelian populations with inbreeding (see, e.g., [8, 15, 19, 23]).

Note that the recipient can be the donor itself, I , or the individual in interaction with it, I' , and then the coefficient of relatedness to consider is

$$\phi_{II/I'} = \phi_{I/I'} \tag{77}$$

or

$$\phi_{I'I/I'} = \phi_{I'/I}, \tag{78}$$

respectively. When the donor, I , and the individual in interaction with it, I' , are not ibd, the recipient can be a competitor of I or I' , but the coefficient of relatedness to consider is the same since

$$\phi_{I'I/I'} = \phi_{IcI/I'} \tag{79}$$

by symmetry.

All coefficients of relatedness are computed in the absence of selection. Exact expressions are given by the identity measures calculated in Section 8 for three offspring chosen at random in the same group, excluding the possibility that two sibs may be in interaction in the case of fertility models. These expressions generally depend on the assumptions made: soft selection or hard selection, differential viabilities or differential fertilities, uniform dispersal or local extinction and uniform recolonization. Approximations in the case of a large group size are the same for fertility models and viability models. In the case of uniform dispersal, these approximations are related to the Ewens sampling formula, which predict that the probability for a third offspring to be ibd to at least one of two previous offspring is the same or given that they are not ibd.

9.4 Complete Uniform Dispersal

In the case of uniform dispersal with $m = 1$, offspring in the same group are ibd only if they have the same parent. For I, I', I_c and I'_c chosen at random in the same group before dispersal, we have

$$\begin{aligned}\phi_{II'} &= \frac{1}{N}, \\ \phi_{I_c I'} &= \frac{1}{N^2}, \\ \phi_{I'_c I'} &= \phi_{I_c I'} = \frac{N-1}{N^2},\end{aligned}\tag{80}$$

in the absence of constraint, but

$$\begin{aligned}\phi_{II'} &= \phi_{I_c I'} = 0, \\ \phi_{I'_c I'} &= \phi_{I_c I'} = \frac{1}{N},\end{aligned}\tag{81}$$

under the constraint that I and I' are not sibs. This leads to entries of the effective game matrix in the case of soft selection in the form

$$a_{kl}^\circ = \left(1 - \frac{2}{N} + \frac{1}{N^2}\right)a_{kl} + \frac{1}{N} \left(1 - \frac{1}{N}\right)(a_{kk} - a_{lk})\tag{82}$$

for the viability model, but in the form

$$a_{kl}^\circ = \left(1 - \frac{1}{N}\right)a_{kl} - \frac{1}{N}a_{lk}\tag{83}$$

for the fertility model. This means that the effective game matrix for the soft fertility model with complete dispersal is

$$A^\circ = A - \frac{A + A^T}{N}.\tag{84}$$

This is in agreement with Hilbe [11]. The same effective game matrix had been obtained previously for fertility models in well-mixed finite populations [16, 18]. In the light of our

present analysis, this particular form of the effective game matrix can be explained by negative effects of competition between two sibs, or since interactions occur among parents in the fertility model, negative effects of *competition between a parent and itself*.

Note that these competition effects disappear in the case of hard selection since

$$\phi_{I_c I I'} = \phi_{I'_c I I'} = \phi_{I_c I I'} = 0, \quad (85)$$

if I_c , I'_c and I are chosen at random in the same group after dispersal. This leads to an effective game matrix

$$A^\circ = [a_{kl} - N^{-1}(a_{kl} - a_{kk})] \quad (86)$$

for the hard viability model, but $A^\circ = A$ for the hard fertility model, both in the case of complete dispersal.

9.5 Finite Number of Groups

With a finite number of groups, D , and an intensity of selection given by the inverse of the total population size, $s = (ND)^{-1}$, the limit as $D \rightarrow \infty$ leads to a diffusion whose drift functions are given by the time derivatives of the expected changes in the strategy frequencies [17]. Then, the effective game matrices in Result 5 come into play in diffusion approximations. In particular, they can be used to compute probabilities of fixation to find conditions for weak selection to favor one strategy to replace another one [16].

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