Stochastic group selection model for the evolution of altruism

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Abstract

We study numerically and analytically a stochastic group selection model in which a population of asexually reproducing individuals, each of which can be either altruist or non-altruist, is subdivided into $M$ reproductively isolated groups (demes) of size $N$. The cost associated with being altruistic is modelled by assigning the fitness $1 - \tau$, with $\tau \in [0, 1]$, to the altruists and the fitness 1 to the non-altruists. In the case that the altruistic disadvantage $\tau$ is not too large, we show that the finite $M$ fluctuations are small and practically do not alter the deterministic results obtained for $M \to \infty$. However, for large $\tau$ these fluctuations greatly increase the instability of the altruistic demes to mutations. These results may be relevant to the dynamics of parasite-host systems and, in particular, to explain the importance of mutation in the evolution of parasite virulence.

Key words: stochastic processes, group selection, altruism, parasite-host

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1 Introduction

Despite the scarcity of empirical facts supporting group selection as a relevant evolutive force in nature, the mathematical problems involved in its modeling have kept a recurrent theoretical interest on this controversial theory [1,2]. Group selection is based on an analogy between individuals (or genes) and reproductively isolated subpopulations, termed demes. If the extinction of demes occurs at a rate depending on their composition, then such extinctions will favor the existence of individuals that increase the probability of survival of the deme they belong to. In the case that these individuals are disfavored by the
usual selection at the individual level, group selection will oppose individual selection, and so it has been advanced as an explanation for the existence of altruistic traits in nature. Such a trait is defined as one that is detrimental to the fitness of the individual who expresses it, but that confers an advantage on the group of which that individual is a member.

The standard mathematical framework to study group selection was proposed by Levins more than 20 years ago [1,2]. The key ingredients are the differential survival probability favoring demes with a large number of altruists, and the subsequent recolonization of the extinguished demes by the surviving ones. In fact, this is practically the only generally accepted mechanism to produce group selection in nature (see [3,4] for an alternative proposal). However, the mathematical complexity of Levins’ formulation, based on a nonlinear integral partial differential equation, as well as the need for too restrictive assumptions, have motivated the proposal and study of a variety of discrete time versions of Levins’ model [5–8]. These analyses have concentrated mainly on the deterministic regime, in which the number of demes $M$ is infinite, though the deme size $N$ (i.e., the number of individuals in each deme) is finite. In the absence of mutation, the finitude of $N$ is crucial to guarantee the fixation through random drift of the altruistic trait within some demes. The undesirable feature of considering $M$ finite as well, besides obliterating the possibility of an analytical solution to the problem, is that the fluctuations occurring during the extinction process will ultimately lead to the complete extinction of the population. This is a consequence of the sequential procedure that considers first the extinction of demes and then the recolonization of the extinct demes by the surviving ones. In this paper we modify the sequential extinction-recolonization procedure so as to avoid global extinction, allowing thus the numerical and analytical study of the effects of a finite population on the steady-state of the metapopulation (i.e., the population of demes). More pointedly, once a deme is extinct we immediately assign one of the $M-1$ surviving demes to replace it, although the effective replacement of the extinct demes will take place only after all demes have passed the extinction stage. This replacement or recolonization occurs simultaneously for all demes.

Our goal is to study the effects of the fluctuations due to the finitude of the population on the stability of the altruistic state predicted by Eshel in the deterministic regime [6]. The remainder of this paper is organized as follows. In section 2 we describe the events that comprise the life cycles of the individuals in the metapopulation and present the stochastic dynamics governing the time evolution of the metapopulation. A mean-field recursion equation is derived and its validity discussed in section 3. The results of the simulations as well as those of the mean-field approximation are presented and analyzed in section 4. Finally, in section 5 we present some concluding remarks and, in particular, point out the relevance of our results to the dynamics of parasite-host systems.
2 Model

The metapopulation is composed of \( M \) demes, each of which being composed of \( N \) haploid, asexually reproducing individuals. An individual can be either altruist or non-altruist. The cost associated with being altruistic is modelled by assigning the reproductive rate \( 1 - \tau \), with \( \tau \in [0, 1] \), to the altruists and the reproductive rate 1 to the non-altruists. The demes are classified according to the number of altruistic individuals they have, so that there are \( N + 1 \) different types of demes, labeled by the integers \( i = 0, 1, \ldots, N \). In each generation the metapopulation is described by the vector \( \mathbf{n} = (n_0, n_1, \ldots, n_N) \), where \( n_i \) is the number of demes of type \( i \), so that \( \sum_i n_i = M \). The life cycle (i.e., one generation) consists of the following events, which will be discussed in detail in the sequel: extinction, recolonization, reproduction, and mutation.

2.1 Extinction and Recolonization

Within the differential extinction framework, we define the probability that a deme of type \( i \) survives extinction, \( \alpha_i \), by

\[
\alpha_i = \begin{cases} 
\frac{1}{2} \left( 1 + \frac{i}{i_c} \right) & \text{if } i < i_c \\
1 & \text{otherwise},
\end{cases}
\]

where \( i_c = 0, 1, \ldots, N \) is a parameter measuring the intensity of the group selection pressure. The larger the number of altruists in a deme, the larger its chance of surviving extinction. Once a deme is extinct, a randomly chosen deme among the \( M - 1 \) surviving ones will immediately be assigned to replaced it. This contrasts with the standard modelling in which recolonization takes places only after all demes have passed the extinction procedure. Hence, given \( \mathbf{n} \), the probability that a deme of type \( j \) changes to a deme of type \( i \), denoted by \( E_{ij} \), is simply

\[
E_{ij} = \begin{cases} 
\alpha_i + (1 - \alpha_i) \frac{(n_i - 1)}{(M - 1)} & \text{if } i = j \\
(1 - \alpha_j) \frac{n_i}{(M - 1)} & \text{if } i \neq j.
\end{cases}
\]

As expected, \( \sum_i E_{ij} = 1 \) \( \forall j \). We note that the transition matrix \( \mathbf{E} \) depends on \( \mathbf{n} \) and so it changes as the population evolves. The conjunction of the extinction and recolonization procedures is termed interdemic selection since the correlation between the elements belonging to a same column of \( \mathbf{E} \) yields an effective, indirect interaction between the demes.
2.2 Reproduction

The reproduction process occurs inside the demes and hence is termed intra-demic selection. Since the size of the demes is fixed and finite \((N)\), random drift occurs. Following Wright’s classical model \([9]\) we assume that the number of offspring that an individual contributes to the new generation is proportional to its relative reproductive rate. Thus, the probability that a deme of type \(j\) changes to a deme of type \(i\) is written as

\[
R_{ij} = \binom{N}{i} w^j_j (1 - w^j_j)^{N-i}, \tag{3}
\]

where

\[
w^j_j = \frac{j (1 - \tau)}{N - j \tau} \tag{4}
\]

is the relative reproductive rate of the subpopulation of altruists in a deme of type \(j\). We note that \(\sum_i R_{ij} = 1 \forall j\) and \(\sum_j i R_{ij} = N w_j\). In the absence of mutations, the random drift inherent to the reproduction process will prevent the existence of mixed demes, i.e., a deme will be either of type \(N\) (only altruists) or of type \(0\) (only non-altruists). As a result, a choice of the parameter \(i_c\) different from 0 or \(N\) in the definition of the survival probability \(\alpha_i\) will have practically no effect on the metapopulation evolution.

2.3 Mutation

To include mutation into the model, we must descend to the level of the genes that determine the characteristics of the individuals. In particular, we assume that two alleles, say \(A\) or \(B\), at a single locus determine whether a given individual is altruist or non-altruist, respectively. Since the replication of a gene may not be perfect, we introduce the mutation rate \(u \in [0, 1/2]\), which gives the probability that the allele \(A\) mutates to \(B\) and vice-versa. Hence the probability that a deme of type \(j\) changes to a deme of type \(i\) due to mutations of its members is given by

\[
U_{ij} = \sum_{l=l_i}^{l_u} \binom{j}{l} \binom{N-j}{i-l} u^{i+j-2l} (1 - u)^{N-i-j+2l}, \tag{5}
\]
where \( l_l = \max (0, i + j - N) \) and \( l_u = \min (i, j) \). Clearly, \( \sum_i U_{ij} = 1 \ \forall j \) and \( \sum_i iU_{ij} = Nu + j (1 - 2u) \).

### 2.4 Stochastic dynamics

Given a population characterized by the vector \( \mathbf{n} \) which will change into a new population characterized by \( \mathbf{n}' \) due to a generic transition matrix \( \mathbf{T} \) \((\sum_i T_{ij} = 1 \ \forall j)\), the stochastic dynamics is defined by the conditional probability distribution \( P_T (\mathbf{n}'|\mathbf{n}) \). To evaluate this quantity, it is more convenient to introduce the set of integers \( \{b_{ij}\} \), where \( b_{ij} \) stands for the number of demes of type \( j \) that have changed to a deme of type \( i \). Hence \( n_j = \sum_i b_{ij} \) and \( n'_j = \sum_j b_{ij} \), so that given the set \( \{b_{ij}\} \), the vector \( \mathbf{n}' \) can be readily determined. In fact, given \( n_j \) the conditional probability distribution of \( b_j = (b_{0j}, b_{1j}, \ldots, b_{Nj}) \) is a multinomial

\[
P_T (b_j|n_j) = \frac{n_j!}{b_{0j}! b_{1j}! \ldots b_{Nj}!} T_{0j}^{b_{0j}} T_{1j}^{b_{1j}} \ldots T_{Nj}^{b_{Nj}}
\]

for \( j = 0, \ldots, N \). Clearly, the random variables \( b_{kj} \) and \( b_{li} \) are statistically independent for \( i \neq j \), regardless of the values assumed by the indices \( k \) and \( l \). We must emphasize that since the transition matrix \( \mathbf{E} \), which governs the extinction and recolonization procedures, depends explicitly on \( \mathbf{n} \), this dynamics must be applied in parallel (simultaneously) to all demes.

The dynamics proceeds as follows. Given the population vector in generation \( t \), denoted by \( \mathbf{n}^t \), first we consider the extinction-recolonization event and generate the conditional probability distributions \( P_E (b_j|n^t_j) \ \forall j \). The choice of \((N + 1)^2\) uniformly distributed random numbers allows the determination of the set \( \{b_{ij}\} \) and, consequently, of the new population vector \( \mathbf{n}' \). Next, given \( \mathbf{n}' \) we repeat this procedure for the reproduction event, then generating the population vector \( \mathbf{n}'' \). Finally, the same procedure is repeated again for the mutation event, leading from \( \mathbf{n}'' \) to \( \mathbf{n}^{t+1} \), which thus completes the life cycle.

### 3 Expectations

The (conditional) expected value of the number of demes of type \( i \) after a life cycle given the population vector \( \mathbf{n}' \) in generation \( t \) is defined by

\[
\langle n_i^{t+1} \rangle = \sum_{k,l,m} k_i P_U (k|l) P_R (l|m) P_E (m|n^t)
\]
where the conditional probabilities are given by Eq. (6) with the generic transition matrix replaced by the specific matrices $U$, $R$ and $E$ as indicated. Here we have used the notation

$$P_T (k|l) = \prod_{j=0}^{N} P_T (b_j|l_j)$$  \hspace{1cm} (8)$$

with $k_i = \sum_j b_{ij} \forall i$. Moreover, using

$$\sum_k k_i P_T (k|l) = \sum_j T_{ij} l_j,$$  \hspace{1cm} (9)$$

we find

$$\langle n_{t+1}^i \rangle = \sum_{jkl} U_{ij} R_{jk} E_{kl} n_t^l,$$  \hspace{1cm} (10)$$

which, by making explicit the dependence of $E$ on $n_t$, can be rewritten as

$$\langle n_{t+1}^i \rangle = \sum_{jk} U_{ij} R_{jk} \left\{ n_k^i \alpha_k + \frac{n_k^i}{M-1} \left[ \sum_l (1-\alpha_l) n_l^i - (1-\alpha_k) \right] \right\}.$$  \hspace{1cm} (11)$$

At this stage we can readily derive a mean-field recursion equation for the average number of demes of type $i$. In fact, assuming that the covariance

$$\text{Cov} (n_t^i, n_t^j) = \langle n_t^i n_t^j \rangle - \langle n_t^i \rangle \langle n_t^j \rangle$$  \hspace{1cm} (12)$$

vanishes at any $t$ for all pairs $(i, j)$, and setting $\langle n_t^i \rangle = \nu_t^i$ yield

$$\nu_{t+1}^i = \sum_{jk} U_{ij} R_{jk} \left\{ \nu_k^i \alpha_k + \frac{\nu_k^i}{M-1} \left[ \sum_l (1-\alpha_l) \nu_l^i - (1-\alpha_k) \right] \right\}.$$  \hspace{1cm} (13)$$

Thus, rather than studying the evolution of a specific population, in this approximation scheme we focus on the evolution of an average population whose deme frequencies at each generation are regarded as the average of the deme frequencies of an infinite number of populations at that generation. Of course, for finite $M$ the covariance can never vanish for all pairs $(i, j)$ since the random variables $n_t^i$ are not statistically independent (for instance, they obey the normalization condition $\sum_i n_t^i = M$). However, depending on the values of the control parameters $\tau$, $u$ and $M$, either the covariance $\text{Cov}(n_k, n_i)$ or its coefficient $\sum_j U_{ij} R_{jk} (1-\alpha_l)$ may be sufficiently small so as to validate the mean-field equation as a good approximation.
The (conditional) covariance after a life cycle given \( n^t \) in generation \( t \) is simply given by

\[
\text{Cov} \left( n_i^t, n_j^t \right) = - \sum_k S_{ik} S_{jk} n_k^t \quad i \neq j
\]  

(14)

where \( S_{ij} = (URE)_{ij} \) is the matrix element of the product of the three transition matrices. The case \( i = j \) corresponds to the variance, \( \text{Var} \left( n_i^t \right) = \text{Cov} \left( n_i^t, n_i^t \right) \), and yields

\[
\text{Var} \left( n_i^t \right) = \sum_k S_{ik} \left[ 1 - S_{ik} \right] n_k^t.
\]  

(15)

We note that these quantities can be readily evaluated within the mean-field approach by replacing \( n_k^t \) by its average, \( \nu_k^t \). Of course, the estimate of the magnitude of the fluctuations of the random variables \( n_i \) \((i = 0, \ldots, N)\) around their means is crucial to assess the relevance of the finite \( M \) effects.

4 Analysis of the results

The quantity of interest is the fraction of altruistic individuals in the metapopulation in the stationary regime, defined as

\[
p = \frac{1}{N} \sum_{i=0}^{N} i Y_i
\]  

(16)

where \( Y_i = n_i/M \) is the frequency of demes of type \( i \). Clearly, \( \sum_i Y_i = 1 \). Interestingly, in the case \( i_c = N \), there is a simple relation between \( p \) and the mean fitness of the metapopulation which is defined as \( \bar{\alpha} = \sum_i \alpha_i Y_i \), namely,

\[
\bar{\alpha} = \frac{1}{2} \left( 1 + p \right).
\]  

(17)

To measure the dispersion of the random variable \( p \) we introduce the variance

\[
\sigma_p^2 = \frac{1}{N^2} \sum_{i=0}^{N} i^2 Y_i - p^2
\]  

(18)

which vanishes in the case of an homogeneous metapopulation \((Y_k = 1 \text{ and } Y_i = 0 \text{ for } i \neq k)\), and reaches the maximum value \(1/4\) in the case that the demes are segregated in equal proportions into the two opposite classes \((Y_0 = Y_N = 1/2)\). Since \( p \) and \( \sigma_p^2 \) are random variables, we will focus on
their average values, denoted by $\langle p \rangle$ and $\langle \sigma^2_p \rangle$, respectively. In all simulations discussed in this work, the symbols represent the averages over $2 \times 10^4$ independent experiments. The error bars are calculated by measuring the standard deviation of the average results obtained in 50 sets of experiments, each one involving 40 independent runs. Moreover, in each run the population is left to evolve for $2 \times 10^3$ generations and we average over the quantities under analysis in the last 100 generations. No significant differences were found for longer runs. Throughout our analysis we set $i_c = N = 10$, so that Eq. (17) holds true.

In Figs. 1(a) and 1(b) we present $\langle p \rangle$ and $\langle \sigma^2_p \rangle$, respectively, as functions of the mutation rate $u$ for $\tau = 0.9$ and two representative values for the number of demes, $M = 10$ and $M = 100$. For $u = 0$ the altruistic trait always takes over the metapopulation, provided that there is at least one altruistic deme in the initial state ($n^0_N \geq 1$). Besides the stable fixed point presented in these figures, for large $\tau$ the mean-field recursion equations possess an unstable one, $p = u$, which can be reached by starting the iteration with non-altruistic demes only ($n^0_0 = M$). Thus the effect of finite $M$, as shown by the results of the simulations, is to increase the instability of the altruistic regime against mutations by stabilizing the mean-field unstable fixed point. (We note that the mean-field results actually shown the opposite tendency, which indicates the failure of the approximation in this matter.) This is expected since in a smaller metapopulation, chance plays a greater role, and so deleterious mutations accumulate with a higher probability, causing a more rapid decrease in the mean fitness of the metapopulation. In the case that the size of the metapopulation is not fixed but depends on its mean fitness, this positive feedback, termed mutational meltdown, leads rapidly to the extinction of the metapopulation [10,11]. The agreement between the mean-field predictions and the simulations are very good for $M = 100$, except in the region just after the variance maximum. Up to this maximum the population is composed almost exclusively of altruistic and non-altruistic demes, while beyond it the number of altruistic demes decreases very rapidly, the sole source of altruistic individuals being the mutations within the non-altruistic demes. Clearly, in this scenario we have $p = u$ in agreement with the simulation results. The occurrence of a pronounced maximum in $\sigma^2_p$ indicates the existence of a phenomenon similar to the error threshold transition of Eigen’s quasispecies model for molecular evolution [12]. (The formal similarity between group selection and molecular evolution models has already been pointed out in ref. [8].) We note that even for $M = 10$, the mean-field approximation yields very good results for small $u$. Of course, the agreement between theory and simulations is more problematic for small $M$, since in this case the probability that the altruistic demes are lost from the metapopulation due solely to fluctuations becomes significant, leading to the so-called stochastic escape phenomenon [13,14]. This loss is practically irreversible as the altruistic selective disadvantage is too high to allow for the production of new altruistic demes.
The same quantities, $\langle p \rangle$ and $\langle \sigma^2_p \rangle$, are presented in Figs. 2(a) and 2(b), except that the altruistic disadvantage is reduced to $\tau = 0.2$. In this case, the effects of the finite $M$ fluctuations are almost suppressed as illustrated by the agreement between the mean-field and the simulation results. The stochastic escape phenomenon is not important in this case since new altruistic demes can readily be generated due to the small reproductive disadvantage of the altruistic individuals. The results for $M \to \infty$ are practically indistinguishable from those obtained in the mean-field approximation for $M = 100$. We have verified that changing the values of $i_c$ and $N$ alters the frequency of the altruistic gene smoothly, leaving its qualitative dependence on the mutation rate unaffected.

A more direct measure of the finite $M$ fluctuations is presented in Figs. 3 and 4, which show the variances of the fraction of non-altruistic and altruistic demes, $\text{Var}(Y_0)$ and $\text{Var}(Y_N)$, respectively, as functions of the mutation rate for $\tau = 0.9$. We note that although the mean-field approximation describes very well the fluctuations outside the region where the transition between the altruistic ($p \approx 1$) and non-altruistic ($p \approx u$) regimes takes place, it fails badly in that region. This failure seems more pronounced in Fig. 4 because the range of $u$ coincides with the transition region, but a similar discrepancy occurs in Fig. 3 also, where the variance peaks for small $u$ are completely overlooked by the mean-field approximation. The situation for $\tau = 0.2$ is illustrated in Fig. 5 where we present $\text{Var}(Y_N)$ as a function of $u$. In this case the mean-field approximation reproduces very well the behavior pattern of the simulation results, except for the heights of the peaks which, as expected, are underestimated. The results for $\text{Var}(Y_0)$ are very similar to those shown in Fig. 5. Of course, the disagreement between simulation and theory is expected since we are trying to estimate the size of the fluctuations using an approximation scheme that neglects those very same fluctuations. However, the surprisingly good agreement shown in Fig. 3 for $u$ outside the transition region suggests that a self-consistent iterative scheme, where the covariances calculated in the mean-field approximation are used to improve that approximation, may describe successfully the finite $M$ fluctuations. As expected, these variances tend to zero as the number of demes increases.

5 Conclusion

In this paper we have modified the standard implementation of the group selection mechanism, which considers first the extinction of the demes and then the recolonization of the extinct demes by the surviving ones [1,5,7,8], by assigning a recolonizing deme to each extinct deme immediately after its extinction, according to Eq. (2). The actual replacement of the extinct demes is carried out simultaneously for all demes following the stochastic prescription
given in Eq. (6). This modified extinction-recolonization procedure avoids the otherwise inevitable global extinction of the population. We have verified, however, that this procedure yields qualitatively similar results to those obtained with the standard extinction-recolonization procedure in the case that the metapopulation survives global extinction long enough to reach a metastable state.

It is important to mention that, in contrast to its original and very criticized ecological motivation [15,16], some concepts borrowed from group selection have been successfully applied to describe the evolution of parasite-host systems [17,18]. In this case the hosts are associated with the demes, while the parasites correspond to the individuals inhabiting the demes. The role of the altruistic individuals is played by the less virulent parasites which, by having a lower growth rate, increase the survival probability of the host. Migration of individuals between demes corresponds to horizontal transmission of parasites. The transmission of the parasite between parent and offspring generations is termed vertical transmission. Interestingly, a well-known result is that, in a population of asexual hosts, parasites with vertical transmission alone cannot persist if the infected hosts suffer any fitness cost [19,20]. (This result is readily recognized as Eshel’s [6], although no reference to that author is made in the specialized literature of parasite-host systems.) Our finding that at certain ranges of the mutation rate (around 0.04 in Fig. 1), virulent parasites with vertical transmission alone almost take over the population yields evidences of the major role played by mutations in the evolution of virulence [21]. This dominance becomes more pronounced as the host population decreases. A more thorough formulation of parasite-host dynamics through the classical, discrete time population genetics formalism used to study group selection models is still lacking. Such formulation will certainly help to uncover many more similarities, as well as overlapping results, between these two fascinating research fields.

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Figure captions

**Fig. 1(a)** Average frequency of altruists as function of the mutation rate for $\tau = 0.9$, $M = 10$ ($\triangle$), and $M = 100$ ($\bigcirc$). The solid and dashed curves are the mean-field results for $M = 10$ and $M = 100$, respectively. The straight line is $\langle p \rangle = u$. The error bar is omitted when it is smaller than the symbol size. The parameters are $i_c = N = 10$.

**Fig. 1(b)** Average variance of the frequency of altruists as function of the mutation rate. The parameters and convention are the same as for Fig. 1(a).

**Fig. 2(a)** Same as Fig. 1(a) but for $\tau = 0.2$.

**Fig. 2(b)** Same as Fig. 1(b) but for $\tau = 0.2$.

**Fig. 3** Variance of the fraction of non-altruistic demes, $\text{Var} (Y_0)$, as function of the mutation rate for $\tau = 0.9$. The convention is the same as for Fig. 1(a).

**Fig. 4** Variance of the fraction of altruistic demes, $\text{Var} (Y_N)$, as function of the mutation rate for $\tau = 0.9$. The convention is the same as for Fig. 1(a).

**Fig. 5** Same as Fig. 4, but for $\tau = 0.2$. 
Fig. 1(a)
Fig. 2(a)
Fig. 2(b)
Fig. 3

\[ \text{var}(Y_u) \]
Fig. 4
Fig. 5

\[ \text{var}(Y_N) \]

\[ u \]