

Nonlinear group survival in Kimura's model for the evolution of altruism



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ARTICLE INFO

Article history:

Received 21 September 2013

Received in revised form 3 January 2014

Accepted 9 January 2014

Available online 25 January 2014

Keywords:

Population genetics

Diffusion approximation

Migration

Group selection

Evolution of altruism

ABSTRACT

Establishing the conditions that guarantee the spreading or the sustenance of altruistic traits in a population is the main goal of intergroup selection models. Of particular interest is the balance of the parameters associated to group size, migration and group survival against the selective advantage of the non-altruistic individuals. Here we use Kimura's diffusion model of intergroup selection to determine those conditions in the case the group survival rate is a nonlinear non-decreasing function of the proportion of altruists in a group. In the case this function is linear, there are two possible steady states which correspond to the non-altruistic and the altruistic phases. At the discontinuous transition line separating these phases there is a non-ergodic coexistence phase. For a continuous concave survival function, we find an ergodic coexistence phase that occupies a finite region of the parameter space in between the altruistic and the non-altruistic phases, and is separated from these phases by continuous transition lines. For a convex survival function, the coexistence phase disappears altogether but a bistable phase appears for which the choice of the initial condition determines whether the evolutionary dynamics leads to the altruistic or the non-altruistic steady state.

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1. Introduction

The question of the evolution and maintenance of altruism or, as Wilson [1] put it bluntly “the surrender of personal genetic fitness for the enhancement of personal genetic fitness in others”, has been subject of stern dispute since the 1960s (see, e.g., [2,3]). The central point of this debate is the potential of intergroup selection, whose underlying mechanism is the differential population (group) extinction, to counteract individual selection. Of particular historical relevance to this matter was Wynne-Edwards' suggestion that in order to control population growth animals would limit their own fertility for the sake of group survival [4,5]. In fact, if the extinction of groups occurs at a rate depending on their composition, then such extinctions will, in principle, favor the existence of individuals that increase the probability of survival of the group they belong to. The difficulty is that the group extinction rates should have a magnitude comparable to that of individual selection, a condition that, seemingly, lacks empirical support [1].

The issue boils down then to the identification of the range of the parameters associated to the relevant evolutionary processes – differential reproduction rate of individuals, differential extinction

rate of groups, migration and group size (genetic drift) – necessary to maintain an altruistic trait in the population. Such a trait is defined as one that is detrimental to the fitness of the individual who expresses it, but that confers an advantage to the group of which that individual is a member. Hence the mathematical analyses of the large variety of group selection models for the evolution of altruism presented in the literature have provided the basic information one needs to access the relevance of intergroup selection as an evolutionary force in nature [6,7]. Moreover, the challenging mathematical models used to describe the resulting two-level selection problem are viewed as an attraction on their own and have kept a recurrent theoretical interest on this controversial theory [8–14].

In this paper we offer exact numerical and approximate analytical solutions to perhaps the most elegant mathematical formulation of the intergroup selection problem proposed yet, namely, Kimura's diffusion model of intergroup selection [11]. The key quantity at the group selection level is the group survival function $c(x)$ which essentially determines the rate at which a group containing a fraction x of altruists survives extinction. Whereas Kimura has considered the case that $c(x)$ increases linearly with the frequency x of altruists within the group, i.e., $c(x) = cx$, where c is a positive constant (see also [15]), here we explore the effects of an additional quadratic term, i.e., $c(x) = cx + dx(1 - x)$, where $|d| \leq c$, whose effect is to engender convexity to the survival function.

The biological interpretation of the convexity of the survival function is similar to that of epistatic interactions between

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mutations or genes in genetics [16]. In particular, in the linear case ($d = 0$), the beneficial effects that the altruists accrue to the group are purely additive, i.e., they do not interact with each other. In the case of concave functions ($d > 0$), we have a situation akin to positive or synergistic epistasis in which the group benefit is greater than the additive effects of the single altruists, whereas in the case of convex functions ($d < 0$) the presence of the altruists together have a smaller effect than expected from their effects alone, a situation known in genetics as negative or antagonistic epistasis. Hence the linear case studied by Kimura occurs when the individuals do not interact with each other in the group, which is a somewhat unrealistic assumption since individuals within the same group should exhibit some sort of interaction.

In the case the group survival function is concave ($d > 0$) we find an ergodic coexistence phase in addition to the altruistic and non-altruistic phases, whereas in the case of a convex survival function ($d < 0$) the coexistence phase is eliminated altogether but a bistable regime sets in for sufficiently large values of $|d|$. Overall we conclude that a non-decreasing concave group survival function of the frequency of altruists can increase significantly the region in the parameter space where the altruistic trait can be maintained, albeit in combination with the non-altruistic one.

The rest of the paper is organized as follows. In Section 2 we describe the evolutionary events that comprise the life cycles of the individuals and groups, and derive the partial differential equation that governs the time evolution of the proportion of groups $\phi(x, t)$ carrying a fraction x of altruists at time t . In Section 3 we re-examine the problem studied by Kimura, $c(x) = cx$, and offer rigorous arguments to locate the transition line between the altruistic and non-altruistic phases as well as to characterize the non-ergodic coexistence regime at the transition line. In Section 4 we consider the effect of adding the quadratic term $dx(1 - x)$ to the linear term considered by Kimura. The resulting phase-diagram is studied in detail for the concave case ($d > 0$) and the continuous transition lines separating the ergodic coexistence phase from the altruistic and non-altruistic phases are determined numerically and analytically. Our arguments to prove the existence of a bistable regime in the case $d < 0$ are presented in Appendix. In Section 5 we describe succinctly the results for a Heaviside survival function and show that the continuous transition between the non-altruistic and coexistence phases observed in the case of a concave survival function becomes discontinuous for the Heaviside function. Finally, in Section 6 we summarize our main results and present some concluding remarks.

2. The model

We consider a meta-population composed of an infinite number of competing groups. Each group encompasses exactly N haploid, asexually reproducing individuals. There are two alleles at a single locus that determine whether an individual is altruist (allele A) or not (allele B). The fitness of the individuals are fixed solely by this trait - altruists are assigned fitness 1 and non-altruists fitness $1 + s$, where $s \geq 0$ is a parameter on the order of $1/N$. We assume that N is sufficiently large so that the frequency of altruists within a group, denoted by x , can be viewed as a continuous variable in the closed interval $[0, 1]$. The meta-population is described by the proportion of groups $\phi(x, t)dx$ whose frequency of altruists lies in the range $(x, x + \Delta x)$ at time t . Our goal is to determine how the probability density ϕ is affected by the three evolutionary processes: the individual competition within a group, the migration of individuals between groups and the competition between groups. In the following we discuss these processes in detail.

2.1. Individual selection

If we assume that a group contains j altruists (hence $N - j$ non-altruists), then the probability that there will be exactly i altruists after reproduction is given by the Wright–Fisher process [17]

$$r_{ij} = \binom{N}{i} w_j^i (1 - w_j)^{N-i} \quad (1)$$

where $w_j = j/[N + s(N - j)]$ is the relative fitness of the subpopulation of altruists in the group. The way this process affects the probability density $\phi(x, t)$ is derived using the diffusion approximation of population genetics, which consists essentially on the calculation of the jump moments $\langle (x' - x) \rangle_r$ and $\langle (x' - x)^2 \rangle_r$ where $x = j/N$ and $x' = i/N$ are the frequencies of altruists before and after reproduction, respectively. Here $\langle \dots \rangle_r$ stands for an average using the transition probability r_{ij} . These moments contribute to the drift and the diffusion terms of a Fokker–Planck-like equation for ϕ (see Eq. (11)). We refer the reader to [18,19] for a detailed discussion of the diffusion approximation. More pointedly, direct evaluation of the jump moments using the transition probability (1) yields

$$\langle (x' - x) \rangle_r = w_j - x \approx -sx(1 - x) \quad (2)$$

and

$$\langle (x' - x)^2 \rangle_r = \frac{1}{N} w_j (1 - w_j) + (w_j - x)^2 \approx \frac{1}{N} x(1 - x) \quad (3)$$

where we have kept only terms of the first order in $1/N$ (recall that the fitness advantage s of the non-altruists is on the order of $1/N$).

2.2. Migration

Following Wright's island model we assume that J individuals of each group are replaced by migrants in the time interval Δt and that the frequency of altruists among the migrants is equal to the average frequency of altruists in the entire meta-population, i.e., $\bar{x} = \int_0^1 x \phi(x, t) dx$ [20]. The probability that a group with j altruists ($x = j/N$) becomes a group with i altruists ($x' = i/N$) due to the migration process is then [10]

$$m_{ij} = \sum_{k=k_l}^{k_u} \frac{\binom{j}{k} \binom{N-j}{J-k}}{\binom{N}{J}} \binom{J}{i-j+k} \bar{x}^{i-j+k} (1 - \bar{x})^{J-i-j-k} \quad (4)$$

where $k_l = \max(j - i, 0, J - N + j)$ and $k_u = \min(j, J - i + j, J)$. This somewhat formidable expression has a simple interpretation: the hyper-geometric component yields the probability that exactly k altruists and $J - k$ non-altruists are eliminated from the group to make room for the J migrants, whereas the binomial part yields the probability that there are exactly $i - j + k$ altruists among the J migrants. Note that after migration the number of altruists in the group is given by the sum of the altruist originally in the group ($j - k$) and the number of altruists among the migrants ($i - j + k$). The first two jump moments are given by

$$\langle (x' - x) \rangle_m = m(\bar{x} - x) \quad (5)$$

and

$$\langle (x' - x)^2 \rangle_m = \frac{m}{N} \bar{x}(1 - \bar{x}) + m^2(\bar{x} - x)^2 + \frac{m(1 - m)}{N - 1} x(1 - x) \quad (6)$$

where $\langle \dots \rangle_m$ stands for an average using the transition probability m_{ij} and $m = J/N$ is the fraction of the local population that is replaced by migrants. Assuming that m is on the order of $1/N$, i.e., that the number of migrants J remains finite and limited when N grows large, we can neglect the second jump moment which is $O(1/N^2)$. In addition, the first jump moment becomes of the same order of

the drift contribution due to the selective advantage of the non-altruists, Eq. (2).

2.3. Intergroup selection

Since x represents the fraction of altruists in a group, we define the group survival rate $c(x)$ as a monotone non-decreasing function of x . Assuming that a proportion $1 - [a - c(x)]\Delta t$ of the groups carrying the fraction x of altruists survives extinction during time interval Δt we can write

$$\phi(x, t + \Delta t) = [1 - [a - c(x)]\Delta t]\phi(x, t)\zeta \quad (7)$$

where a is some arbitrary rate. Here ζ is such that $\int_0^1 dx \phi(x, t + \Delta t) = 1$, i.e., $\zeta = 1/[1 - (a - \bar{c})\Delta t]$ with

$$\bar{c} = \int_0^1 c(x)\phi(x, t)dx \quad (8)$$

The enforcement of the normalization of ϕ after the extinction process is akin to assume that the extinct groups are recolonized or replaced by the surviving ones in proportion to their frequencies. Finally, taking the limit $\Delta t \rightarrow 0$ we obtain the change in ϕ due to the extinction and recolonization processes,

$$\Delta\phi = [c(x) - \bar{c}]\phi(x, t)\Delta t \quad (9)$$

from where we can see that the arbitrary rate a has no effect at all on the intergroup selection process. Eq. (9) implies that the process of extinction followed by recolonization amounts to an effective competitive interaction between groups.

For the most part of the paper, we will focus on the group survival function

$$c(x) = cx + dx(1 - x) \quad (10)$$

with $c > 0$. Clearly, $c(x)$ is non-decreasing in the interval $[0, 1]$ provided that $c \geq |d|$, in which case the model can be said to describe the competition between individual selection favoring non-altruistic individuals ($s > 0$) and intergroup selection favoring altruistic individuals. In addition, $c(0) = 0$ and $c(1) = c$ regardless of the value of d .

We note that the sole role of d in Eq. (10) is to generate convexity. The case $d = 0$ was studied by Kimura in the context of the evolution of an altruistic character [11], whereas we have recently considered the case $c = 0$ (and $m = 0$ as well) in a prebiotic evolution scenario for the coexistence of self-replicating molecules [21]. The motivation behind prescription (10) is to understand the effect of a weak nonlinearity, modeled here by the quadratic term $-dx^2$, on the linear case studied by Kimura. In addition, in Section 5 we will consider briefly the effect of a strong nonlinearity where $c(x)$ is given by a Heaviside function.

2.4. Evolution equation for $\phi(x, t)$

Combining the changes in $\phi = \phi(x, t)$ due to the three processes described above we obtain [11]

$$\frac{\partial}{\partial t}\phi = \frac{1}{2N}\frac{\partial^2}{\partial x^2}[x(1-x)\phi] - \frac{\partial}{\partial x}[a(x, t)\phi] + [c(x) - \bar{c}(t)]\phi \quad (11)$$

where

$$a(x, t) = -sx(1-x) - m[x - \bar{x}(t)] \quad (12)$$

is the drift term,

$$\bar{x}(t) = \int_0^1 x\phi(x, t)dx \quad (13)$$

is the mean frequency of altruists in the meta-population, and

$$\bar{c}(t) = \int_0^1 c(x)\phi(x, t)dx \quad (14)$$

is the mean group survival rate. In addition, the normalization condition $\int_0^1 \phi(x, t)dx = 1$ holds for all times t .

We note that in the deterministic limit $N \rightarrow \infty$ the diffusion term of Eq. (11) can be neglected and Kimura's partial differential equation reduces to a particularly simple realization of the deterministic model of group selection studied in [14].

2.5. Equation for the steady state

In the limit $t \rightarrow \infty$ the system reaches equilibrium so that $\partial\phi/\partial t = 0$ and the steady-state equilibrium probability density $\phi(x, t) \rightarrow \hat{\phi}(x) = \hat{\phi}$ satisfies

$$\frac{\partial^2}{\partial x^2}[x(1-x)\hat{\phi}] + \frac{\partial}{\partial x}[A(x)\hat{\phi}] + [C(x) - \bar{C}]\hat{\phi} = 0 \quad (15)$$

where $A(x) = Sx(1-x) + M(x - \bar{x})$ and we have introduced the rescaled parameters $S = 2Ns$ and $M = 2Nm$, as well as the rescaled survival rate $C(x) = 2Nc(x)$. In addition,

$$\bar{x} = \int_0^1 x\hat{\phi}(x)dx \quad \bar{C} = \int_0^1 C(x)\hat{\phi}(x)dx. \quad (16)$$

For $M > 0$, Eqs. (15) and (16) are satisfied both by $\hat{\phi} = \delta(x)$ and $\hat{\phi} = \delta(x-1)$, and they may also be satisfied by a regular function $\hat{\phi} = \hat{\phi}_r(x)$. However, the migration term prohibits solutions that are combinations of these three possibilities, since in this case those equations are violated in at least one of the two extremes, $x = 0$ or $x = 1$. In other words,

$$\hat{\phi}(x) = A_0\delta(x) + B\hat{\phi}_r(x) + A_1\delta(x-1) \quad (17)$$

can be a solution only if one of the three coefficients A_0, B or A_1 equals one and the other two equal zero. As a result, there are three potential phases at the steady state: a non-altruistic phase $\hat{\phi} = \delta(x)$, an altruistic phase $\hat{\phi} = \delta(1-x)$, and a coexistence phase $\hat{\phi} = \hat{\phi}_r(x)$ where the two individual types cohabit a same group.

However, the linear combination (17) with two or three non-vanishing coefficients is a solution of Eq. (15) in the case of isolated groups, $M = 0$ [21]. This situation is useful to elucidate the nature of the averages involved in the derivation of Eq. (15). In fact, because the number of groups is infinite, stochasticity occurs only in the processes that take place inside the groups. For example, in the absence of group selection (i.e., $c(x) = 0$ for $x \in [0, 1]$), each group represents an independent realization of the Wright–Fisher process and since in this case the intragroup dynamics leads to the fixation of one of the individual types in the group we can interpret A_0 in Eq. (17) either as the fraction of groups in which occurred fixation of the egoistic type or as the probability that the egoistic type fixates in a given group. Hence the metapopulation, which is composed of A_0 purely egoistic and A_1 purely altruistic groups, is the ensemble of the realizations of the Wright–Fisher process. A similar interpretation holds in the presence of group selection $c(x) > 0$, except that the groups are no longer independent in this case which results in a biased ensemble of the intragroup stochastic process.

It is instructive to mention that if a regular solution exists, then integration of Eq. (15) over the interval $[0, 1]$ yields

$$\frac{d}{dx}(x\hat{\phi}_r) - M\bar{x}\hat{\phi}_r \Big|_{x=0} = 0 \quad (18)$$

and

$$\frac{d}{dx}[(1-x)\hat{\phi}_r] + M(1-\bar{x})\hat{\phi}_r \Big|_{x=1} = 0 \quad (19)$$

which imply that for x close to 0 one has $\hat{\phi}_r \sim x^{M\bar{x}-1}$, whereas for x close to 1 one has $\hat{\phi}_r \sim (1-x)^{M(1-\bar{x})-1}$.

3. Linear group survival rate

This is the case considered in the seminal paper of Kimura [11] and corresponds to the choice $d = 0$ in Eq. (10) so that $C(x) = Cx$ with $C = 2Nc$. A simplifying feature of the linear case is that the dynamical variable (14) becomes $\bar{C}(t) = C\bar{x}(t)$ and so Eq. (11) exhibits only one non-local dynamical variable, namely, $\bar{x}(t)$. Here we offer a much simpler approach than that presented by Kimura, which does not involve the numerical solution of the steady-state equation. Kimura's approach was based on the presence of a small mutation rate between the alleles A and B which guarantees the existence of a regular solution for all values of the model parameters.

We begin by multiplying both sides of Eq. (11) by $e^{Cx/M}$ and integrating over the interval $[0, 1]$, which yield

$$\frac{\partial}{\partial \tau} \int_0^1 e^{Cx/M} \phi dx = \frac{CR}{M^2} \int_0^1 e^{Cx/M} x(1-x) \phi dx \quad (20)$$

where $\tau = t/2N$ and $R \equiv C - MS$.

If we assume that $R \neq 0$, then the right hand side of (20) must equal zero at the steady state $\phi(x, \tau) \rightarrow \hat{\phi}(x)$. Since $\int_0^1 e^{Cx/M} x(1-x) \hat{\phi} dx$ is strictly positive unless $\hat{\phi} = \delta(x)$ or $\hat{\phi} = \delta(1-x)$, we must conclude that only these two singular steady-state solutions are allowed. Next, let us assume that Eq. (20) holds with $R > 0$. Then the right hand side is always positive (provided the initial distribution $\phi(x, 0)$ is not a Dirac delta centered at 0 or 1), and so $\int_0^1 e^{Cx/M} \phi dx$ increases until it reaches, for $\tau \rightarrow \infty$, the maximum value $e^{C/M}$ which implies that $\hat{\phi} = \delta(x-1)$. Analogously, assuming that Eq. (20) holds with $R < 0$ the same reasoning leads to the conclusion that $\int_0^1 e^{Cx/M} \phi dx$ decreases with increasing τ until it reaches the minimum value 1, which entails that $\hat{\phi} = \delta(x)$. In sum, Eq. (20) implies that $\phi(x, \tau) \rightarrow \delta(x-1)$ for $R > 0$ (provided the initial condition is not $\phi(x, 0) = \delta(x)$) and that $\phi(x, \tau) \rightarrow \delta(x)$ for $R < 0$ (provided the initial condition is not $\phi(x, 0) = \delta(x-1)$).

It remains to analyze the model at the transition surface $R = 0$. In this case we can easily verify that the steady-state solution of Eq. (15) is the Beta distribution

$$\hat{\phi}_k(x) = kx^{M\bar{x}-1}(1-x)^{M(1-\bar{x})-1} \quad (21)$$

where the normalization factor k is the reciprocal of the standard Beta function, i.e., $k = 1/B[M\bar{x}, M(1-\bar{x})]$. Since Eq. (16) are satisfied for any choice of \bar{x} , the value of this parameter must be determined by the initial distribution $\phi(x, 0)$. In fact, setting $S = C/M$ in Eq. (20) we find that $\int_0^1 e^{Sx} \phi(x, t) dx$ is constant in time and so

$$\int_0^1 e^{Sx} \phi(x, 0) dx = \int_0^1 e^{Sx} \hat{\phi}_k(x) dx \quad (22)$$

which provides the necessary condition to determine \bar{x} univocally from the knowledge of the initial distribution $\phi(x, 0)$ and parameters C and M . For example, in the limit $S \rightarrow 0$ Eq. (22) yields $\bar{x} = \int_0^1 x \phi(x, 0) dx$, i.e., \bar{x} is a constant of movement in this case.

In conclusion, in the case of the linear survival rate we have three steady-state phases: a non-altruistic phase for $R = C - MS < 0$, an altruistic phase for $R = C - MS > 0$ and a non-ergodic coexistence phase at the transition surface $R = 0$.

4. Quadratic group survival rate

Here we consider the complete prescription (10) for group survival, which is written in terms of the rescaled parameters as

$$C(x) = Cx + Dx(1-x) \quad (23)$$

with $D = 2Nd$. Since for $D > 0$ the extra term $Dx(1-x)$ favors coexistence we expect that the coexistence phase, which for $D = 0$ is restricted to the surface $S = C/M$, expands to occupy a finite volume

in the space of parameters of the model. This is the reason in the following analysis we will invest heavily on the analysis of the regular steady-state solution of Eq. (15). Unless stated otherwise (see sub-Section 4.4) we assume $D > 0$.

4.1. Numerical analysis

Since $\hat{\phi}_r(x)$ must be positive we write the regular solution of Eq. (15) in the form

$$\hat{\phi}_r(x) = \hat{\phi}_k(x)e^{y(x)} \quad (24)$$

where $\hat{\phi}_k$ is given by (21) and corresponds to the solution for the case $R = 0$ and $D = 0$. In addition, in contrast to $\hat{\phi}_r$, the function y is always finite at the extremes $x = 0$ and $x = 1$. In terms of the auxiliary function $z = dy/dx$ we have

$$x(1-x)(z' + z^2 + Sz + D) + (x-\bar{x})(R-Mz) = \bar{D} \quad (25)$$

where

$$\bar{x} = \int_0^1 dx x \hat{\phi}_k(x) e^{y(x)} \quad (26)$$

$$\bar{D} = D \int_0^1 dx x(1-x) \hat{\phi}_k(x) e^{y(x)} \quad (27)$$

and

$$y(x) = y(0) + \int_0^x d\xi z(\xi) \quad (28)$$

Here the initial value $y(0)$ is chosen in order to ensure the normalization, i.e. $\int_0^1 dx \hat{\phi}_k(x) e^{y(x)} = 1$. We note that the values of $z(x)$ at the two extremes $x = 0$ and $x = 1$ are completely specified by Eq. (25),

$$z(0) = \frac{R}{M} + \frac{\bar{D}}{M\bar{x}} \quad (29)$$

and

$$z(1) = \frac{R}{M} - \frac{\bar{D}}{M(1-\bar{x})} \quad (30)$$

At this stage the problem is ready for a numerical approach. For fixed \bar{x} and \bar{D} we solve Eq. (25) by propagating the Runge-Kutta algorithm from $x = 0$ to $x = 1$ using the initial condition (29). Of course, the choice of an arbitrary value of \bar{D} will not satisfy the boundary condition (30) so we adjust \bar{D} in order that condition is satisfied. This is essentially an application of the well-known shooting method to solve boundary values problems [22]. Note that this procedure actually accounts for replacing Eq. (27) by the boundary condition (30). Once this is achieved, we have solved the problem for a fixed \bar{x} . We then calculate \bar{x} using (26) and return to Eq. (25) repeating the process until we reach the convergence for \bar{x} .

Fig. 1 summarizes the main results obtained using the above numerical scheme. In the coexistence phase, the mean frequency of altruists is well described by a straight line and to a good approximation it seems to be independent of D for $R = 0$. The coexistence index \bar{D}/D provides information on the mean balance of the coexistence within groups: it reaches the maximum value 1/4 for well-balanced groups, i.e., $\hat{\phi} = \delta(x-1/2)$ and it vanishes outside the coexistence phase.

4.2. Transition lines

According to Fig. 1 we identify three phases in the steady-state regime: the non-altruistic phase (NA) for which $\bar{x} = 0$, the coexistence phase (C) for which $0 < \bar{x} < 1$, and the altruistic phase (A) characterized by $\bar{x} = 1$.

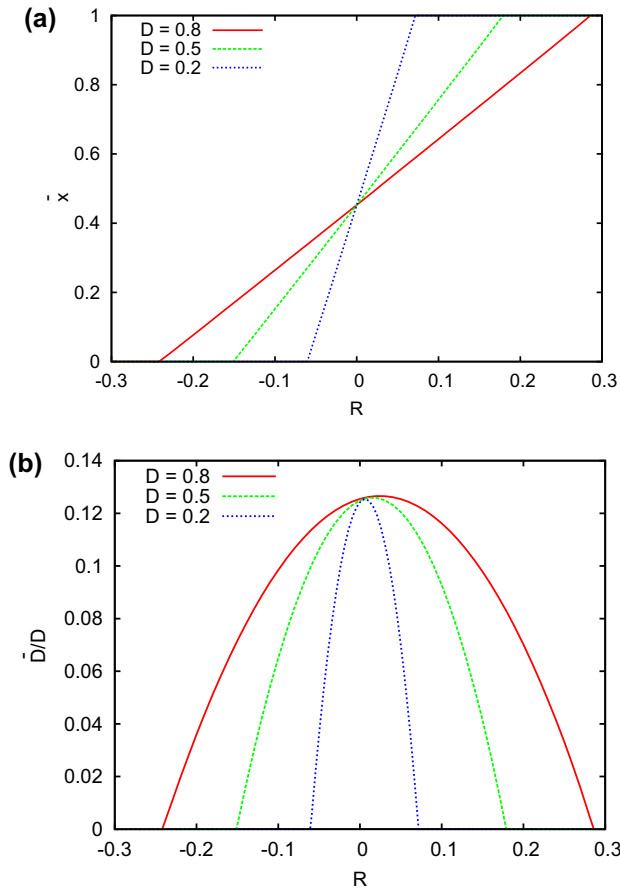


Fig. 1. Mean frequency of altruistic individuals \bar{x} (upper panel) and coexistence index \bar{D}/D (lower panel) at the steady state as function of $R = C - MS$ for $C = 1, M = 1$ and $D = 0.2, 0.5, 0.8$ as indicated in the figure. At $R = 0$ we find $\bar{x} \approx 0.452$ and $\bar{D}/D \approx 0.124$. In the linear group survival case ($D = 0$), \bar{x} exhibits a sharp transition from 0 to 1 at $R = 0$, at which its value depends on the initial condition.

The transition line that separates phases NA and C can be obtained by considering the limits $\bar{x} \rightarrow 0$ and $\bar{D} \rightarrow 0$ of the regular solution $\hat{\phi}_r$. In this case Eq. (25) reduces to

$$(1 - x)(z' + z^2 + Sz + D) + R - Mz = 0 \quad (31)$$

that must be solved using the boundary condition at $x = 1$, Eq. (30), which rewrites

$$z(1) = \frac{R}{M} \quad (32)$$

This boundary value problem yields easily to a numerical approach (e.g., the shooting method [22]) which then allows us to obtain the function $z(x)$ and, in particular, its value at the left boundary, $z(0)$, for arbitrary values of the parameters S, M, C and D . However, since Eq. (31) is valid at the transition line only we need another condition to constraint the values of these parameters. This supplementary condition is provided by Eq. (29) which, after insertion of Eqs. (26) and (27), reads

$$\begin{aligned} z(0) &= \frac{R}{M} + \frac{D}{M} \frac{\int_0^1 dx e^{y(x)} (1-x)^M}{\int_0^1 dx e^{y(x)} (1-x)^{M-1}} \\ &= \frac{R}{M} + \frac{D}{M+1} \frac{\int_0^1 dx e^{y(x)} \rho_{M+1}(x)}{\int_0^1 dx e^{y(x)} \rho_M(x)} \end{aligned} \quad (33)$$

where we have introduced the probability density

$$\rho_M(x) = M(1-x)^{M-1} \quad (34)$$

Notice that the above expressions do not depend on the normalization factor $y(0)$, which actually diverges in the limits $\bar{x} \rightarrow 0$ and $\bar{x} \rightarrow 1$. The transition line is obtained by fixing S, M and C and adjusting D such that the value of z at the $x = 0$ boundary of Eq. (31) coincides with the value obtained using expression (33).

Now we turn to the transition line that separates phases C and A which is obtained by considering the limits $\bar{x} \rightarrow 1$ and $\bar{D} \rightarrow 0$ of the regular solution $\hat{\phi}_r$. In this case Eq. (25) reduces to

$$x(z' + z^2 + Sz + D) - R + Mz = 0 \quad (35)$$

which must be solved using the boundary condition (29), i.e.,

$$z(0) = \frac{R}{M} \quad (36)$$

The procedure is identical to the sketched above for the transition line between the NA and C phases and so the transition line is obtained by equating the value of $z(1)$ that results from the solution of the boundary value problem with the value given by Eq. (30),

$$\begin{aligned} z(1) &= \frac{R}{M} - \frac{D}{M} \frac{\int_0^1 dx e^{y(x)} x^M}{\int_0^1 dx e^{y(x)} x^{M-1}} \\ &= \frac{R}{M} - \frac{D}{M+1} \frac{\int_0^1 dx e^{y(x)} \rho_{M+1}(1-x)}{\int_0^1 dx e^{y(x)} \rho_M(1-x)} \end{aligned} \quad (37)$$

As before, the above expressions do not depend on the (divergent) normalization factor $y(0)$.

Fig. 2 exhibits the phase diagram of the model for $C = 1$ and $M = 1$. The transition lines are well fitted by straight lines (see Section 4.3) because of the constraint that $D < C$. In fact, allowing arbitrarily large values of D yields significant deviation from those straight lines (data not shown).

4.3. Theoretical analysis

A remarkable feature of the phase diagram exhibited in Fig. 2 is that the transition lines are well-fitted by straight lines within the region of interest, namely, $D \leq C$. This finding motivates the search for an analytical solution of Eq. (15) in the regime where the parameters $R = C - SM$ and D are small, i.e., close to the transition

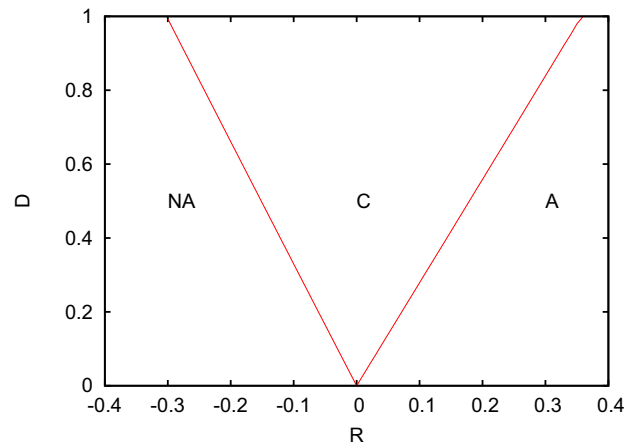


Fig. 2. Phase diagram of the model with the quadratic group survival function $C(x) = Cx + Dx(1-x)$ for $M = 1$ and $C = 1$ showing the non-altruistic (NA), ergodic coexistence (C) and altruistic (A) phases in the space of parameters $D \leq C$ and $R = C - MS$. In the linear group survival case (the $D = 0$ axis), the coexistence phase is limited to the point $R = 0$ and it is non-ergodic.

line of the linear problem (see Section 3). The other parameter S , M and C , however, are not necessarily small.

The starting point of our approximation scheme is the identity

$$R \int_0^1 e^{Sx} \hat{\phi}(x)(x - \bar{x}) dx + \int_0^1 e^{Sx} \hat{\phi}(x)[Dx(1-x) - \bar{D}] dx = 0 \quad (38)$$

which is derived by multiplying both sides of Eq. (15) by e^{Sx} and then integrating over the interval $[0, 1]$. Here \bar{x} and \bar{D} are given by Eq. (16) with $C(x) = Cx + Dx(1-x)$. We note that Eq. (38) is satisfied both by $\hat{\phi}(x) = \delta(x-1)$ (phase A) and $\hat{\phi}(x) = \delta(x)$ (phase NA). In addition, if there is coexistence, it must also be satisfied by a regular function $\hat{\phi}(x) = \hat{\phi}_r(x)$ (phase C).

Close to the transition point $R = D = 0$ in the coexistence phase (see phase diagram of Fig. 2) we can replace $\hat{\phi}_r(x)$ in Eq. (38) with $\hat{\phi}_k(x)$, which is given by Eq. (21). In doing so we neglect terms of second order on D and R . The solution (21) has \bar{x} as free parameter but close to the transition lines one must have $\bar{x} \rightarrow 0$ (transition from phase C to NA) and $\bar{x} \rightarrow 1$ (transition from phase C to A).

Let us consider first the case $\bar{x} \rightarrow 0$. It can be easily verified that for any arbitrary regular function $f(x)$ we can write

$$\int_0^1 f(x) \hat{\phi}_k(x) dx \simeq f(0) + \bar{x} \int_0^1 \frac{f(x) - f(0)}{x} \rho_M(x) dx \quad (39)$$

where ρ_M is given by Eq. (34) and we have neglected terms of higher order in \bar{x} . Note that the normalization condition ($f(x) = 1$) and the mean ($f(x) = x$) are preserved in this approximation scheme. The other moments are correct to first order in \bar{x} . Hence, we can rewrite Eq. (38) as

$$R \int_0^1 (e^{Sx} - 1) \rho_M(x) dx + \frac{DM}{M+1} \int_0^1 (e^{Sx} - 1) \rho_{M+1}(x) dx = 0 \quad (40)$$

which immediately gives the (positive) critical value D_N at the transition line separating the coexistence and the non-altruistic phases in terms of the (negative) parameter R ,

$$D_N = -\alpha_N R \quad (41)$$

where $\alpha_N = \alpha_N(C, M)$ is given by

$$\begin{aligned} \alpha_N &= \frac{M+1}{M} \frac{\int_0^1 (e^{Sx} - 1) \rho_M(x) dx}{\int_0^1 (e^{Sx} - 1) \rho_{M+1}(x) dx} \\ &= \frac{1}{M} \frac{\sum_{n=0}^{\infty} \zeta_{n+1}(M) (C/M)^n}{\sum_{n=0}^{\infty} \zeta_{n+2}(M) (C/M)^n} \end{aligned} \quad (42)$$

where

$$\zeta_n(M) = \prod_{i=1}^n \frac{1}{M+i} \quad (43)$$

and we have replaced S by C/M which is inconsequential to first order in R . These calculations can be repeated in a completely analogous way to derive the critical value D_A at the transition line separating the coexistence and the altruistic phases. Recalling that at this line we have $\bar{x} \rightarrow 1$, we find

$$D_A = \alpha_A R \quad (44)$$

where $\alpha_A = \alpha_A(C, M) = \alpha_N(-C, M)$. For $C = M = 1$, Eq. (42) yields $\alpha_N = 3.29$ and $\alpha_A = 2.78$, which match perfectly the slopes of the straight lines shown in the phase diagram of Fig. 2. Note that only for $C = 0$ (and hence $S = 0$) we have symmetry around the $R = 0$ axis, i.e., $\alpha_A = \alpha_N = (M+2)/M$, and in this case the coexistence phase is confined to the region

$$D > \frac{M+2}{M} |R| \quad (45)$$

Now we set out to establish analytical approximations for the mean coexistence group pressure \bar{D} and for the mean frequency of altruists \bar{x} away from the transition lines. The expression for \bar{D} to first order in D follows immediately from Eq. (27),

$$\bar{D} = D \int_0^1 \hat{\phi}_k(x) x(1-x) dx = D \frac{M}{M+1} \bar{x}(1-\bar{x}) \quad (46)$$

However, the calculation of \bar{x} to the leading order in R and D is somewhat more involved. We begin by noting that, according to Fig. 1, the value of \bar{x} at $R = 0$ appears to be independent of the parameter D . Alas, by setting $R = 0$ in Eq. (38) we can see that this conclusion is not correct since the regular steady-state solution $\hat{\phi} = \hat{\phi}_r$ does depend on D . Next, assuming that D is small we can use Eq. (46) to eliminate \bar{D} in Eq. (38), which to the lowest order in R and D is rewritten as

$$\int_0^1 e^{Cx/M} \hat{\phi}_k(x) \left[\frac{R}{D} (x - \bar{x}) + x(1-x) - \frac{M}{M+1} \bar{x}(1-\bar{x}) \right] dx = 0 \quad (47)$$

where we have replaced S with C/M and $\hat{\phi}$ with the Beta distribution $\hat{\phi}_k$ given in (21). For the purpose of numerical evaluation Eq. (47) is rewritten as

$$\sum_{i=1}^{\infty} \frac{(C/M)^i}{(i-1)!} \frac{B(\alpha+i, \beta)}{M+i} \left[\frac{R}{D} + \frac{(M+1)\beta - (M+i)\alpha}{(M+1+i)(M+1)} \right] = 0 \quad (48)$$

with $\alpha = M\bar{x}$, $\beta = M(1-\bar{x})$ and $B(\cdot, \cdot)$ is the Beta function. Solving Eq. (48) yields \bar{x} in terms of the parameter M and of the ratios C/M and R/D . In fact, this equation explains the observed, though not strict, lack of dependence of \bar{x} and \bar{D}/D on the parameter D for $R = 0$ (see Fig. 1). In particular, for $C = M = 1$ and $R = 0$ we find $\bar{x} = 0.453$ and, inserting this value in Eq. (46), $\bar{D}/D = 0.124$, which is in good agreement with the results of Fig. 1. In addition, varying R/D and solving Eq. (48) for \bar{x} yields results that are indistinguishable from those exhibited in the upper panel of Fig. 1. The coexistence indexes exhibited in the lower panel of Fig. 1 are equally very well described by inserting the values of \bar{x} into Eq. (46). For $C \rightarrow 0$ (and hence $S \rightarrow 0$) Eqs. (48) and (46) yield

$$\bar{x} = \frac{1}{2} + \frac{(M+2)R}{2MD} \quad (49)$$

and

$$\bar{D}/D = \frac{M}{4(M+1)} \left[1 - \left(1 + \frac{2}{M} \right)^2 \frac{R^2}{D^2} \right] \quad (50)$$

We recall that the transition lines $D_N = -\alpha_N(C, M)R$ and $D_A = \alpha_A(C, M)R$ were derived by taking the limits $\bar{x} \rightarrow 0$ and $\bar{x} \rightarrow 1$, respectively, in Eq. (47). Hence the values of \bar{x} obtained by solving the clumsy equation (48) or, equivalently, Eq. (47), tend to the correct limits at those transition lines.

We can derive a handy approximation for \bar{x} with the aid of Fig. 1 by considering the equation of the straight line that joins the points $(-D/\alpha_N, 0)$ and $(D/\alpha_A, 1)$, i.e.,

$$\bar{x} = \frac{\alpha_A}{\alpha_A + \alpha_N} + \frac{\alpha_A \alpha_N}{\alpha_A + \alpha_N} \frac{R}{D} \quad (51)$$

with $\alpha_N(C, M) = \alpha_A(-C, M)$ given by Eq. (42). For $C = M = 1$ this approximation scheme yields $\bar{x} = \alpha_A/(\alpha_A + \alpha_N) \approx 0.458$ at $R = 0$, which is very close to the result obtained by solving Eq. (48) with $R = 0$. Note that the slopes of the approximate straight lines illustrated in the upper panel of Fig. 1 are proportional to $1/D$ and therefore diverge at $D = 0$.

4.4. The case $D < 0$

Up to now we have considered the case where the nonlinear contribution to the group survival rate explicitly favors coexistence, i.e., $0 < d < c$ (or, in terms of the rescaled parameters, $0 < D < C$) in Eq. (10). This choice amounts to saying that the group survival $C(x)$ is a non-decreasing concave function of the frequency x of altruists in the group. Now we address briefly what happens when $C(x)$ is a non-decreasing convex function of x , which corresponds to the choice $0 < -D < C$.

Since a negative value of the parameter D hinders coexistence by construction (see Eq. (10)) and since for $D = 0$ we find coexistence only at the transition line $R = C - MS = 0$ (see Section 3) we expect the coexistence phase to be obliterated for $D < 0$. In the Appendix we offer an analytical argument to support this prospect. However, the effect of $D < 0$ goes beyond destroying the coexistence phase at $R = 0$: it introduces a new (non-ergodic) bistable regime which allows the reaching of the altruistic phase for $R < 0$ and the non-altruistic phase for $R > 0$ provided $|D|$ is sufficiently large compared to $|R|$. The Appendix presents a proof of this result in the limit that the parameters C, S and $|D|$ are small. As the two steady-state phases that exist for $D < 0$ are not described by a regular steady-state solution we lack the tools to determine the boundaries of the region of bistability in the parameter space. A promising approach is to introduce a small symmetric mutation rate v , as done by Kimura to study the linear case [11], and then extrapolate the results for $v \rightarrow 0$. However, because the transition lines obtained in the Appendix for $D < 0$ and small values of the model parameters are identical to the analytical continuation to the region $D < 0$ of the transition lines D_N and D_A derived in subSection 4.3, we conjecture here that the region occupied by the bistable phase in the half-plane $D < 0$ is the mirror of the region occupied by the ergodic coexistence phase in the half-plane $D > 0$.

5. Heaviside group survival rate

Here we consider a somewhat extreme group selection pressure that sets off only in groups in which the altruists are the majority of the group components, i.e.,

$$C(x) = \begin{cases} 0 & \text{if } 0 \leq x < 1/2 \\ C & \text{if } 1/2 \leq x \leq 1 \end{cases} \quad (52)$$

This prescription models the division of labor between the altruists, termed synergism, and it is useful to study the appearance of complex structures that are of value to the organism only when fully formed [23,24]. Using the same transformations introduced in the previous section we write the steady-state equation (15) for the regular solution $\hat{\phi}_r = \hat{\phi}_k(x)e^{y(x)}$ as

$$x(1-x)(z' + z^2 + Sz) - M(x - \bar{x})z + C(x) = \bar{C} \quad (53)$$

where

$$\bar{C} = C \int_{1/2}^1 dx \hat{\phi}_k(x) e^{y(x)} \quad (54)$$

Here \bar{x} and $y(x)$ are defined by Eqs. (26) and (28) respectively. The boundary conditions are $z(0) = \bar{C}/(M\bar{x})$ and $z(1) = (C - \bar{C})/[M(1 - \bar{x})]$. As in the case of the quadratic group survival rate, this boundary value problem can be easily solved using the shooting method and Fig. 3 summarizes the main results. The noteworthy feature of this figure that shows the dependence of \bar{x} on $R = C - MS$ is the appearance of a discontinuous transition for negative R that separates the non-altruistic and the coexistence phases. In particular, the jump in \bar{x} at the transition line increases as the migration rate M increases. Moreover, for positive R there is a

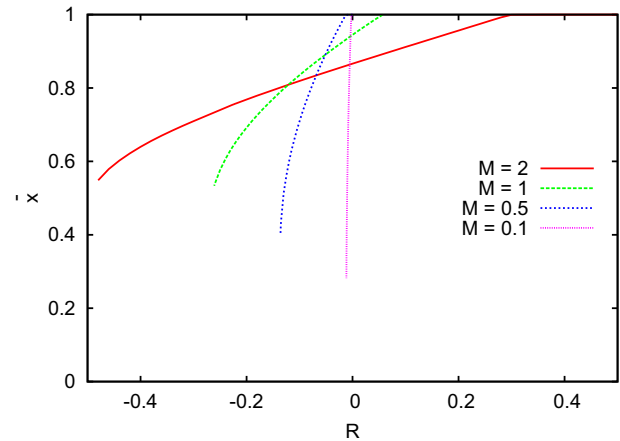


Fig. 3. Mean frequency of altruistic individuals \bar{x} as function of $R = C - MS$ for the Heaviside group survival rate. The parameters are $C = 1$ and M as indicated in the figure.

continuous transition between the coexistence and the altruistic phase. Whereas this continuous transition can be located with good accuracy using the numerical approach of the previous section as both \bar{x} and \bar{C} tend to 1 at that transition, there is no shortcut to determine the discontinuous transition as the values of those two variables are unknown in this case. Since, in addition, we can offer no analytical support to the numerical results, we opt to restrict the study of the Heaviside group survival rate to the exhibition of Fig. 3 which proves our main point: a concave-like nonlinear survival rate, such that the benefit for the group increases slower and slower as the number of altruists increases, favors the coexistence of the two types of individuals inside the group.

We note that provided the initial densities are not $\phi(x, 0) = \delta(x)$ (i.e., only purely egoistic groups) or $\phi(x, 0) = \delta(x - 1)$ (i.e., only purely altruistic groups) the long term evolutionary dynamics will settle in the steady states described in Fig. 3 and, in particular, in the coexistence regime for a proper choice of the model parameters C, M and S . Even the linear combination $\phi(x, 0) = a_0\delta(x) + a_1\delta(x - 1)$ with $a_0 + a_1 = 1$ can lead to coexistence in the long term. In this case, the migration process will play the key role by producing the mixed groups. In addition, if we start with an initial density such that $x < 1/2$ for all groups so that the Heaviside group selection (52) is turned off, then we can invoke Haldane's argument to show that because the groups have a finite size N there is a non-vanishing probability of fixation of the altruists in some groups [25], leading back to the abovementioned linear combination of deltas in the worst case.

6. Conclusion

Building on the diffusion model of group selection proposed by Kimura [11], in this paper we offer an extensive study of the effects of the convexity of the group survival function $C(x) = Cx + Dx(1 - x)$ with $|D| \leq C$ on the steady-state properties of Kimura's model. As in the case that the group survival rate increases linearly with the frequency x of altruists within the group [11], we find that a relevant independent variable in the resolution of the phase diagram of the model is the quantity $R = C - MS$ where M is the rescaled migration rate and S is the rescaled selective advantage of the non-altruists. Typically, the non-altruistic individuals dominate for R large and negative, whereas the altruistic individuals dominate for R large and positive (see phase diagram of Fig. 2). More pointedly, we find that the altruistic trait can be maintained in the population provided that the condition

$$R > -D/\alpha_N \quad (55)$$

is satisfied. Here $D \geq 0$ and $\alpha_N > 0$ is given by Eq. (42). Of course, condition (55) comprehends both the altruistic and the coexistence phase. This condition is important because it reveals that the exchange of individuals between groups favors the non-altruistic trait, whereas in the case the groups are isolated (i.e., $M = 0$) the altruistic trait prevails regardless of the selective advantage of the non-altruists, provided either $C > 0$ or $D > 0$ [8,10].

It is interesting that in the case of the linear survival function the condition for the dominance of the altruists $R > 0$ can be written as $C \frac{1}{M} > S$, which is reminiscent of Hamilton's rule [26,27] since C can be interpreted as the benefit accrued to all individuals in the group and S as the cost (selective disadvantage) paid by the altruists only. In Hamilton's rule the factor $\frac{1}{M}$ should be associated to the average relatedness of the interacting individuals or, more generally, to some measure of the population structure [28]. This interpretation holds true in our case as well, since M is proportional to the number of migrants and so the increase of M results in the increase of interactions involving unrelated individuals, i.e., individuals coming from distinct groups.

We can get a clue on the role of the group size N by reverting to the original parameters $c = C/2N$, $d = D/2N$, $m = M/2N$ and $s = S/2N$, so that the condition (55) for the sustenance of the altruistic trait becomes $c + d/\alpha_N > 2Nms$. This condition shows that the altruistic trait is favored if the groups are small enough so that genetic drift can fix the trait in a few groups, as pointed out by Haldane long ago [25]. It is interesting to note that the effective group size ranges from $N = 10$ to $N = 100$ for most vertebrate species [1]. However, that range increases vastly if one borrows the concepts of intergroup selection to describe the evolution of parasite-host systems [29] and microbial populations [30]. In that case, the hosts are associated with the groups and 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.

In the case the survival rate is a concave function of the frequency of altruists (i.e., $0 < D \leq C$) we find an additional phase – an ergodic coexistence phase which monopolizes the region around $R = 0$, as illustrated in the phase diagram of Fig. 2. This finding contrasts with the linear case $D = 0$ for which the non-ergodic coexistence phase occurs at $R = 0$ only (see Section 3). The coexistence phase is separated from the altruistic and non-altruistic phases by two continuous transition lines, which are very well-described by an approximation scheme based on the first order corrections to the solution of the $D = R = 0$ case. In particular, we find that the average frequency of altruists in the meta-population \bar{x} , which can be viewed as the order parameter of the model, vanishes or tends to unity linearly with the distance to the transition lines as those lines are approached from the coexistence phase. Interestingly, these findings hold true for the case of a discontinuous survival function (see Section 5), except that the transition between the non-altruistic and the coexistence phases becomes discontinuous.

In the case the survival rate is a convex function of the frequency of altruists (i.e., $0 < -D \leq C$) the coexistence phase disappears altogether, as expected. However, a new non-ergodic phase appears for values of $|D|$ large compared to $|R|$ in which either the altruistic or the non-altruistic phases can be reached depending on the initial conditions. We conjecture that this bistable phase occupies a region in the half-plane $D < 0$ which is the reflection over the $D = 0$ axis of the region occupied by the coexistence phase in the half-plane $D > 0$. We stress that coexistence is never allowed for D negative.

The main result of this paper is that the region in the space of parameters where the altruist trait can be sustained in the population (see Eq. (55)) is enlarged significantly if the group survival rate is a non-decreasing concave function of the frequency of altruists. In addition, we show the utility of Kimura's formulation of

intergroup selection based on the diffusion approximation of population genetics to produce analytically treatable two-level selection models. Following the approach promoted by [3], we gauge the relevance of group selection by the effects of the group-level events (group extinction in our case) on the long term evolutionary dynamics. In that sense, the existence of the coexistence and altruist regimes offers unequivocal evidence of the importance of group selection.

Acknowledgments

The work of J.F.F. was supported in part by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and M.S. was partially supported by PRIN 2009 protocollo n. 2009TA2595.02.

Appendix

Here we present the calculations that unveil a nontrivial effect of negative values of the parameter D , which amounts to a group pressure against coexistence.

In a similar manner we derived Eq. (38), which is valid in the steady-state regime, we can derive its dynamical counterpart by multiplying both sides of Eq. (11) by e^{Sx} and then integrating over x over the interval $[0, 1]$. After rescaling the time and the model parameters we obtain

$$\begin{aligned} \frac{d}{d\tau} \int_0^1 e^{Sx} \phi(x, \tau) dx &= R \int_0^1 e^{Sx} \phi(x, \tau) [x - \bar{x}(\tau)] dx \\ &+ \int_0^1 e^{Sx} \phi(x, \tau) [Dx(1-x) - \bar{D}(\tau)] dx \end{aligned} \quad (56)$$

We will consider the case that $R = C - MS$, $|D|$, and S (or C) are small so we can keep only terms of the leading order on those parameters in Eq. (56), yielding

$$\frac{d\bar{x}(\tau)}{d\tau} = \int_0^1 x[x - \bar{x}(\tau)][R + D(1-x)]\phi(x, \tau) dx \quad (57)$$

If there is a regular solution for the steady state, then it must be, neglecting terms of higher order, the Beta distribution (21) with a given \bar{x} . Using

$$\int_0^1 x^2 \hat{\phi}_k(x) dx = \bar{x}(M\bar{x} + 1)/(M + 1) \quad (58)$$

and

$$\int_0^1 x^3 \hat{\phi}_k(x) dx = \bar{x}(M\bar{x} + 2)(M\bar{x} + 1)/[(M + 2)(M + 1)] \quad (59)$$

we have

$$\frac{d\bar{x}(\tau)}{d\tau} = \frac{\bar{x}(\tau)[1 - \bar{x}(\tau)]}{M + 1} \left[R + D \frac{M}{M + 2} [1 - 2\bar{x}(\tau)] \right] \quad (60)$$

whose stationary solution ($d\bar{x}/d\tau = 0$) is given by

$$\bar{x} = \frac{1}{2} + \frac{(M + 2)R}{2MD} \quad (61)$$

which is identical to Eq. (49). Now, linearization of Eq. (60) around \bar{x} yields

$$\frac{d\delta(\tau)}{d\tau} = -D \frac{2M}{M + 2} \frac{\bar{x}(1 - \bar{x})}{M + 1} \delta(\tau) \quad (62)$$

where $\delta(\tau) = \bar{x}(\tau) - \bar{x} \ll 1$ as usual. Therefore solution (61) is stable for positive D and unstable for negative D .

Let us focus on the case $D < 0$ only. In this case the unstable fixed point (61) exists provided that the condition

$$|D| \geq \frac{M+2}{M} |R| \quad (63)$$

is satisfied. Furthermore, if this condition is satisfied then it can be easily proved that the right hand side of Eq. (60) does not change sign during evolution, so that the final value for \bar{x} is either 0 or 1 depending on the initial condition. Since this bistable phase depends on the existence of the unstable fixed point (61) and that this fixed point tends to 0 or 1 when the equality holds in condition (63) then the transitions between this phase and the two other ergodic phases are continuous. Most importantly, the condition (63) for the existence of the bistable phase in the case $D < 0$ is identical to the condition for the existence of the ergodic coexistence phase in the case $D > 0$, given by Eq. (45) for small S, R and D . Hence, we conjecture that the region occupied by the bistable phase is exactly the reflection over the $D = 0$ axis of the region occupied by the ergodic coexistence phase.

For $R = 0$ we can offer an alternative argument to show that the non-ergodic coexistence regime discussed in Section 3 is destabilized by the parameter $D < 0$. In this case Eq. (56) rewrites as

$$\frac{d}{d\tau} \int_0^1 e^{Sx} \phi(x, \tau) dx = -|D| \text{Cov}[e^{Sx}, x(1-x)] \quad (64)$$

where $\text{Cov}[e^{Sx}, x(1-x)]$ is the covariance between e^{Sx} and $x(1-x)$. Now, assume that $\bar{x}(0)$ is close to 0, or, equivalently, that $\phi(x, 0)$ is concentrated on $x = 0$. In this case, the covariance is positive since in the region of small x , where the density is more concentrated, both e^{Sx} and $x(1-x)$ are increasing functions of x . Hence the integral $\int_0^1 e^{Sx} \phi(x, \tau) dx$ decreases with time which implies that $\bar{x}(\tau)$ decreases and $\phi(x, t)$ becomes more and more concentrated on $x = 0$. Therefore, the covariance remains positive and for large τ the integral $\int_0^1 e^{Sx} \phi(x, \tau) dx$ reaches its minimal value 1, which implies that $\bar{x}(\tau)$ vanishes. Parallel results are derived when $\bar{x}(0)$ is close to 1 and so the covariance in Eq. (64) is negative. In this case, $\bar{x}(\tau)$ increases until it reaches the value 1.

In summary, the pressure against coexistence associated to negative values of the parameter D destroys the coexistence regime altogether, as expected. However, it introduces an unexpected non-ergodic phase where the final outcome of the evolutionary dynamics is the altruistic regime ($\bar{x} = 1$) or the non-altruistic one ($\bar{x} = 0$) depending on the initial conditions. For small values of the model parameters we find that this non-ergodic phase exists in the region (63). Outside this region (i.e., for $|D|$ small compared to $|R|$) we have the ergodic altruistic phase for $R > 0$ and the ergodic non-altruistic phase for $R < 0$. Since none of these phases can be described by a regular steady-state solution, our analysis is limited to the approximation scheme presented in this appendix.

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