Discrete \textit{versus} continuous models in evolutionary dynamics: from simple to simpler — and even simpler — models

Fabio A. C. C. Chalub\textsuperscript{*}, Max O. Souza\textsuperscript{†}

September 23, 2013

Abstract

There are many different models—both continuous and discrete—used to describe gene mutation fixation. In particular, the Moran process, the Kimura equation and the replicator dynamics are all well known models, that might lead to different conclusions. We present a discussion of a unified framework to embrace all these models, in the large population regime.

1 Introduction

Real world models need to cover a large range of scales. However, models that are valid in such a large range are hard to obtain and can be very complex to analyze. Alternatively, we might use models that focus on certain scales. Thus, on one hand, we might have a microscopic discrete model that is derived from first principles while, on the other hand, we might also have

\textsuperscript{*}Departamento de Matemática and Centro de Matemática e Aplicações, Universidade Nova de Lisboa, Quinta da Torre, 2829-516, Caparica, Portugal. e-mail:chalub@cii.fc.ul.pt +351 933 313 096

\textsuperscript{†}Departamento de Matemática Aplicada, Universidade Federal Fluminense, R. Mário Santos Braga, s/n, 24020-140, Niterói, RJ, Brasil. e-mail:msouza@mat.uff.br
continuous models that are easier to analyze but are more phenomenological in nature.

When dealing with many descriptions of the same reality, the connection between these various possible descriptions is an important problem. These connections, in the particular case of evolutionary game theory for large populations, will be discussed here after the work in [7]. In particular, we will present a unified theory that covers the Moran process [16], the mean-field theory description by Kimura [10] and the replicator dynamics [9].

In order to develop such a theory, we shall proceed as follows:

1. we prepare a detailed discrete model—the THE MICROSCOPIC MODEL;
2. we identify suitably scalings and the corresponding negligible (small) parameters;
3. we formally find a new model where these variables are set to zero—THE THERMODYNAMICAL LIMIT;
4. we prove that the new model is a good approximation for the previous model, within the given scalings;
5. we study the behaviour of distinguished limiting cases.

It is important to stress that, usually, step three is obtained from phenomenological framework. Thus, even formal connections between discrete and continuous models can be very important in understanding their relationship. Moreover, this allows one to solve the simpler continuous model and thus have the approximate behavior of the solution of the detailed model. This approach is classical in the physical sciences where, for instance, continuous mechanics can be seen as a formal limit of particle dynamics—although the phenomenological derivation has been obtained much earlier [11].

In these derivations, the existence of small parameters is generally natural, but the appropriate scalings are not. For example, models of dilute gas given by Boltzmann equation converge to the Navier-Stokes or Euler equations in fluid dynamics (depending on the precise scaling given) when the re-scaled free mean path is set equal to zero [1 2 14 12]. A similar approach uses kinetic models for modeling cell movement induced by chemicals (chemotaxis) and when the cell free mean path is negligible, their solutions
is comparable to the solutions of the Keller-Segel model \[1, 4, 8, 17\]. In a different framework, relativistic models for particle motion have as the non-relativistic limit (i.e., the limit when typical velocities are small compared to the velocity of light) the Newtonian physics [13, 15], where quantum equations converge again to classical physics when (re-scaled) Planck constant is very small \[3, 15\].

For the Moran Process, it has been recently noticed that the inverse of the population size is the relevant small parameter; cf. [19, 7] for instance.

The outline of this work is as follows: in section 2 we discuss the generalized Moran process. This includes the standard Moran process as a special case, but addresses also the frequency dependent case. In section 3 we review the scalings and thermodynamical limits found in [7]. The connection of some of the thermodynamical limits with the Kimura model is discussed in section 4. After that, we briefly outline some of the mathematical issues involved in the derivation of the thermodynamical models. Relationship between these limits and the Replicator Dynamics is discussed in section 5. We then present a series of numerical simulation to illustrate the theory discussed and compare results in section 7. Some remarks in more general games, where mixed strategies are allowed are given in section 8.

2 The generalized Moran process

![Figure 1: The Moran process: from a two-types population (a) we chose one at random to kill (b) and a second to copy an paste in the place left by the first, this time proportional to the fitness.](image)
Consider a population of fixed size $N$, given by two types of individuals, I and II. The Moran process is defined by three steps:

- we choose one of the individuals at random to be eliminated;
- all the remaining individuals play a game given by the pay-off matrix

$$
\begin{array}{c|cc}
 & \text{I} & \text{II} \\
\hline 
\text{I} & A & B \\
\text{II} & C & D \\
\end{array}
$$

and the individual fitness is identified with the average pay-off. We assume that $C > A > 0$ and $B > D > 0$. This is the only structure of the pay-off matrix that guarantees the existence of non-trivial stable equilibrium. This is known in the literature as the “Hawk-and-Dove” game.

- we choose one of the individuals to be copied with probabilities proportional to the pay-off.

We repeat these steps until a final state is presumably reached. Intuitively, after a long enough time, all individuals will be descendant of a single individual living at time $t = 0$. More precisely, let $P(t, n, N)$ be the probability that at time $t$ we have $n$ type I individuals in a total population of size $N$, and let $c_-(n, N)$ ($c_0(n, N)$, $c_+(n, N)$) be the transition probability associated to $n \to n-1$ ($n \to n$ and $n \to n+1$, respectively). Then, the discrete evolution process is given by

$$
P(t + \Delta t, n, N) = c_+(n - 1, N)P(t, n - 1, N) + c_0(n, N)P(t, n, N) + c_-(n + 1, N)P(t, n + 1, N). $$  \hspace{3cm} (1)

Let us introduce the vector

$$
P(t, N) = (P(t, 0, N), P(t, 1, N), \ldots, P(t, N, N))^\dagger.
$$

Then the iteration can be written in matrix form as

$$
P(t + \Delta t, N) = MP(t, N),
$$
where $M$ is a column-stochastic, tridiagonal matrix. It is also possible to show—cf. [7]—that 1 is an eigenvalue of $M$ with multiplicity two, with associated eigenvectors given by $e_1$ and $e_{N+1}$. Since the spectrum and its multiplicity is unchanged if $M$ is replaced by $M^\dagger$ there are two vectors that are kept invariant by $M^\dagger$. One of them is easily seen to be the vector $1 = (1, 1, \ldots, 1, 1)^\dagger$. Let $F$ denote the remaining one. Then, [7] showed that $F$ yields the stationary fixation probability and also that the quantities

$$\eta_1 = \langle 1, P(t, N) \rangle \quad \text{and} \quad \eta_2 = \langle F, P(t, N) \rangle$$

are invariants of the Moran process. The former is well known and it corresponds to the conservation of probability. The latter, however, seems to be new and it can be interpreted as stating that the correlation coefficient between a possible state of the Moran process and the stationary fixation probability must always be the same of the initial condition.

We can now prove that

$$\lim_{\kappa \to \infty} M^\kappa = \begin{pmatrix}
1 & 1 - F_1 & 1 - F_2 & \cdots & 1 - F_{N-1} & 0 \\
0 & 0 & 0 & \cdots & 0 & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\
0 & 0 & 0 & \cdots & 0 & 0 \\
0 & F_1 & F_2 & \cdots & F_{N-1} & 1
\end{pmatrix}$$

As a direct consequence, for any normalized initial condition

$$P_0 = (P(0, 0, N), P(0, 1, N), \cdots, P(0, N, N)),$$

the final state is

$$\lim_{\kappa \to \infty} P(\kappa \Delta t, N) = \lim_{\kappa \to \infty} M^\kappa P_0 = (1 - A, 0, 0, \cdots, A),$$

where

$$A = \sum_{n=0}^{N} F_n P(0, n, N)$$

is the fixation probability associated to the initial condition $P_0$. Note that, with probability 1, one of the types will be fixed. This means, that in the long range, every mutation will be either fixed or lost.
3 Scaling and thermodynamical limits

The central idea of this section is to find a continuous model that works as a good approximation of the Moran process, when the total population is large. This means that we want to find a continuous model for the fraction of mutants in the limit \( N \to \infty \). The core of this process is to define a correct scaling for the time-step and for the pay-offs. We will show, however, that different scalings will give different thermodynamical limits. But only one of these scalings will be able to capture one essential feature of the discrete process discussed in the previous section: that genes are always fixed or lost. In the continuous setting, this means that, as time increases, the probability distribution should move (diffuse) to the boundaries.

Let us suppose that (formally) there exists a probability density

\[
p(t, x) = \lim_{N \to \infty} \frac{P(t, xN, N)}{1/N} = \lim_{N \to \infty} NP(t, xN, N),
\]

where \( x = n/N \).

Let us also suppose that this function \( p : \mathbb{R}_+ \times [0, 1] \to \mathbb{R} \) is sufficiently smooth that we can expand the evolution equation (1) as to obtain

\[
\frac{p(t + \Delta t, x) - p(t, x)}{\Delta t} = \frac{1}{N} \left[ \left( c_+^{(1)} + c_0^{(1)} + c_-^{(1)} \right) p - \left( c_+^{(0)} - c_-^{(0)} \right) \partial_x p \right] + \frac{1}{N^2} \left[ \frac{1}{2} \left( c_+^{(2)} + c_0^{(2)} + c_-^{(2)} \right) p - \left( c_+^{(1)} - c_-^{(1)} \right) \partial_x^2 p \right] + O \left( \frac{1}{N^3} \right),
\]

where \( c_+^{(i)} = c_+^{(i)}(x), \) \( * = +, 0, -, i = 0, 1, 2, \) are defined by

\[
c_+ (xN - 1, N) = c_+ (n - 1, N) = c_+^{(0)} + \frac{1}{N} c_+^{(1)} + \frac{1}{2N^2} c_+^{(2)} + O \left( \frac{1}{N^3} \right),
\]

\[
c_0 (xN, N) = c_0 (n, N) = c_0^{(0)} + \frac{1}{N} c_0^{(1)} + \frac{1}{2N^2} c_0^{(2)} + O \left( \frac{1}{N^3} \right),
\]

\[
c_- (xN + 1, N) = c_- (n - 1, N) = c_-^{(0)} + \frac{1}{N} c_-^{(1)} + \frac{1}{2N^2} c_-^{(2)} + O \left( \frac{1}{N^3} \right).
\]

So far, we made no assumptions on the behavior of the payoffs \( A, B, C, \) and \( D \) as \( N \to \infty \). Since the appropriate large \( N \) limit will be attained through a
rescaling in time, the fitness should also rescaled accordingly to preserve the expected amount of offsprings. In particular, we must have that the fitness approaches one as $N$ grows large; see discussion in [7]. Equivalently, payoffs must also approach one. The order with they approach unity, however, is a free parameter at this point.

Thus, we impose that

$$\lim_{N \to \infty} (A, B, C, D) = (1, 1, 1, 1), \quad (3)$$

$$\lim_{N \to \infty} N^{\nu}(A - 1, B - 1, C - 1, D - 1) = (a, b, c, d), \quad \nu > 0, \quad (4)$$

we find, after a long computation, that

$$\lim_{N \to \infty} N^{\nu} \left( c_{+}^{(1)} + c_{0}^{(1)} + c_{-}^{(1)} \right) = -3x^2(a - b - c + d) - 2x(a - c - 2(b - d)) + (d - b),$$

$$\lim_{N \to \infty} N^{\nu} \left( c_{+}^{(0)} - c_{-}^{(0)} \right) = x(1 - x)(x(a - c) + (1 - x)(b - d)).$$

The only non-trivial balances, as can be readily observed, are given by time-steps of order $\Delta t = N^{-(\nu+1)}$, for $\nu \in (0, 1]$. In this case, we have that

$$\partial_t p = -\partial_x (x(1 - x)(x\alpha + (1 - x)\beta)p), \quad \nu \in (0, 1) \quad (5)$$

and

$$\partial_t p = \partial_x^2 (x(1 - x)p) - \partial_x (x(1 - x)(x\alpha + (1 - x)\beta)p), \quad \text{if} \quad \nu = 1, \quad (6)$$

where $\alpha = a - c < 0$ and $\beta = b - d > 0$. In the particular case where $\alpha = \beta$ (i.e., when the fitness is independent of the particular composition of the population), the last equation can be shown to be equivalent to a celebrated equation in population genetics known as the Kimura equation [10].

The equations above are supplemented by the following boundary conditions

$$\frac{d}{dt} \int_0^1 p(t, x)dx = 0, \quad \text{for equations (5) and (6)};$$

$$\frac{d}{dt} \int_0^1 \psi(x)p(t, x)dx = 0 \quad \text{for equation (6)}.$$
In the latter condition, $\psi$ satisfies
\[
\psi'' + (\beta + (\alpha - \beta)x)\psi' = 0, \quad \psi(0) = 0 \quad \text{and} \quad \psi(1) = 1. \quad (7)
\]
The function $\psi(x)$ is the continuous limit of the vector $\mathbf{F}$ defined in section 2.

Remark 1. For equation (5), it can be shown that the former condition is automatically satisfied; hence, we can treat it as a problem with no boundary conditions. As for equation (6), the degeneracy at the endpoints with such integral boundary conditions turn it in a very nonstandard problem in parabolic pdes. We discuss some of the issues raised by this problem in section 5.

4 The Kimura connection

Using mean-field Gaussian approximations for the frequency independent case, Kimura [10] has derived a PDE for the evolution of the transient fixation probability, which will presumably evolve to a stationary solution that will then be the standard fixation probability. This equation is now known as the Kimura equation and read as follows:
\[
\partial_t f = x(1-x)\partial_x^2 f + \gamma x(1-x)\partial_x f, \quad f(t,0) = 0 \quad \text{and} \quad f(t,1) = 1. \quad (8)
\]
The stationary state can be readily found as
\[
f_s(x) = \frac{1 - e^{-\gamma x}}{1 - e^{-\gamma}},
\]
which corresponds to $\psi$ given by (7), with $\alpha = 0$ and $\beta = \gamma$.

Let $f = \bar{f}(x) + f_s(x)$, then $\bar{f}$ satisfies (8) with homogeneous boundary conditions. In section 5 it will be shown that $p$ can be written as a sum of a smooth part $q$ with a distributional part with support at the end points. It will be also shown that $q$ satisfies (6) without boundary conditions.

Now let us assume that $f(t,x)$ is sufficiently smooth in $x$. Then a straightforward computation shows that
\[
\int_0^1 [x(1-x)\partial_x^2 \bar{f}(t,x + \gamma x(1-x)\partial_x \bar{f}(t,x)) q(t,x)] dx =
\int_0^1 \bar{f}(t,x) \left[ \partial_x^2 (x(1-x)q(t,x)) - \gamma \partial_x (x(1-x)q(t,x)) \right] dx.
\]
Thus, (8) and (6) with no boundary conditions are formally adjoints with the appropriate inner product.

A further relationship between \( \bar{f} \) and \( q \) should be pointed out, namely that, up to a normalising constant, we have

\[
\bar{f}(t, x) = x(1-x)q(t, 1-x).
\]

The adjointness discussed above also hold when \( \alpha \) is nonzero. In this case, we have the generalized Kimura equation given by

\[
\partial_t f = x(1-x)\partial_x^2 f + \gamma x(1-x)(\beta + (\alpha - \beta)x)\partial_x f,
\]

\[
f(t, 0) = 0 \quad \text{and} \quad f(t, 1) = 1.
\]

5 Mathematical issues

There are a number of important questions related to equations (6) and (5) given the degeneracy at the endpoints and the non-standard boundary conditions.

Note that the last two equations will, generally, have very different qualitative behavior as \( t \to \infty \). In particular, we prove the following, concerning equation (5):

**Theorem 1.**

1. For a given \( p^0 \in L^1([0, 1]) \), there exists a unique solution \( p = p(t, x) \) to Equation (5) of class \( C^\infty (\mathbb{R}^+ \times (0, 1)) \) that satisfies \( p(0, x) = p^0(x) \).

2. The solution can be written as

\[
p(t, x) = q(t, x) + a(t)\delta_0 + b(t)\delta_1,
\]

where \( q \in C^\infty (\mathbb{R}^+ \times [0, 1]) \) satisfies (6) without boundary conditions, and we also have

\[
a(t) = \int_0^t q(s, 0)ds \quad \text{and} \quad b(t) = \int_0^t q(s, 1)ds.
\]

In particular, we have that \( p \in C^\infty (\mathbb{R}^+ \times (0, 1)) \).
3. We also have that
\[
\lim_{t \to \infty} q(t, x) = 0 \quad \text{(uniformly)}, \quad \lim_{t \to \infty} a(t) = \pi_0[p^0] \quad \text{and} \quad \lim_{t \to \infty} b(t) = \pi_1[p^0],
\]
where \( \pi_0[p^0] = 1 - \pi_1[p^0] \) and the fixation probability associated to the initial condition \( p^0 \) is
\[
\pi_1[p^0] = \frac{\int_0^1 \left[ \int_y^1 p^0(x) \, dx \right] \exp \left( -y^2 \frac{\alpha - \beta}{2} - y \beta \right) \, dy}{\int_0^1 \exp \left( -y^2 \frac{\alpha - \beta}{2} - y \beta \right) \, dy}.
\]
Note that this means that the solution will 'die out' in the interior and only the Dirac masses in the end points will survive.

4. Write \( p^0 = a^0 \delta_0 + b^0 \delta_1 + q^0 \in L^1([0, 1]) \) and let \( \lambda_0 \) be the smallest eigenvalue of the associated Sturm-Liouville problem (cf. [7]). If, we assume that \( q^0 \in L^2([0, 1], x(1 - x) \, dx) \) and if \( \| \cdot \|_2 \) denotes the corresponding norm, then we have that
\[
\| q(t, \cdot) \|_2 \leq e^{-\lambda_0 t} \| q^0(\cdot) \|_2.
\]
Moreover, we always have the following \( L^1 \) bounds:

(a) \[
\| q(t, \cdot) \|_1 \leq e^{-\lambda_0 t} \| q^0(\cdot) \|_1;
\]

(b) \[
\pi_0[p^0] - e^{-\lambda_0 t} \| q^0(\cdot) \|_1 \leq a(t) \leq \pi_0[p^0];
\]

(c) \[
\pi_1[p^0] - e^{-\lambda_0 t} \| q^0(\cdot) \|_1 \leq b(t) \leq \pi_1[p^0].
\]

It is important to note that equation (5) is not a good long-term approximation for the discrete process in the case of a Hawk-Dove game, as will see that it presents no diffusion to the boundaries. In this case, the final state of any non-trivial initial condition will be fully determined by the unique non-trivial equilibrium of the game, as the following result shows:
Theorem 2. Consider \( p(t, x) \in (L^1 \cap H^{-1})([0, 1]) \) solution of Equation (5). Then

\[
\lim_{t \to \infty} p(t, x) = \delta_{x^*},
\]

where \( x^* = \beta / (\beta - \alpha) \).

Proof. Consider

\[
\phi(x) = \frac{(x(\alpha - \beta) + \beta) \alpha \beta}{x^{\frac{1}{\alpha}}(1-x)^{\frac{1}{\beta}}} , \quad -\frac{1}{\alpha}, \frac{1}{\beta}, \frac{\alpha - \beta}{\alpha \beta} > 0 .
\]

Then, \( x(1-x)(x(\alpha - \beta) + \beta) \phi'(x) = -\phi(x) \), which implies

\[
\partial_t \int_0^1 p(t, x) \phi(x) dx = -\int_0^1 p(t, x) \phi(x) dx ,
\]

and we conclude that the final state is supported at \( x^* \), the only zero of \( \phi(x) \). Using the conservation of mass, we prove the theorem. \( \square \)

Remark 2. 1. For the case of non Hawk-Dove game, i.e., a game only with trivial stable equilibrium, then we have

\[
\lim_{t \to \infty} p(t, x) = c\delta_0 + (1-c)\delta_1 ,
\]

The constant \( c \) is directly related to the fixation probability, in the following sense. Let \( \pi_0[p_0] \) be the fixation probability found with \( \alpha \) and \( \beta \) replaced by \( \epsilon^{-1} \alpha \) and \( \epsilon^{-1} \beta \) respectively. Then, [6] show that

\[
c = \pi_0[p^0] + O(\epsilon) .
\]

Thus, if \( \alpha \) and \( \beta \) in the original problem are interpreted as scaled down selection parameters, then equation (5) yields the same asymptotic behaviour.

2. For initial conditions in \( L^1([0, 1]) \), an adaptation of the boundary coupled weak solution developed in [7] may be used to show similar results for games with or without a non-trivial equilibrium.

Equation (6) is a good approximation for the discrete case, as can be seen in the following:
Theorem 3. Let $p_{N,t}(x,t)$ be the solution of the finite population dynamics (of population $N$, time step $\Delta t = 1/N^2$), with initial conditions given by $p^0_N(x) = p^0(x)$, $x = 0, 1/N, 2/N, \ldots, 1$, for $p^0 \in L^1_+(\mathbb{R})$. Assume also that $(A - 1, B - 1, C - 1, D - 1) = 1/N(a,b,c,d) + O(1/N^2)$. Let $p(t,x)$ be the solution of equation (6), with initial condition given by $p_0(x)$. If we write $p_i^n$ for the $i$-th component of $p_{N,t}(x,t)$ in the $n$-th iteration, we have, for any $t^* > 0$, that

$$\lim_{N \to \infty} p_{xN}^{tN^2} = p(t,x), \quad x \in [0,1], \quad t \in [0,t^*].$$

Equation (5) is however a good approximation of (6) for intermediate times and strong selection.

In fact,

Theorem 4. Consider $(\alpha', \beta') = \varepsilon(\alpha, \beta)$ and $t' = \varepsilon^{-1}t$. Then, in the limit $\varepsilon \to 0$, we have that the regular part of the solution $q_\varepsilon$ of the re-scaled equation (7) converges to the solution of equation (5) in $L^2(0,T \times [0,1], dt \otimes x(1-x)dx)$, if the initial condition is in $H^1([0,1], x(1-x)dx)$.

Proof. Dropping $'$, and having in mind Theorem 1 we re-write Equation (6) as

$$\partial_t q_\varepsilon = \varepsilon \partial_x^2 (x(1-x)q_\varepsilon) - \partial_x (x(1-x)(x(\alpha - \beta) + \beta)q_\varepsilon) \quad (9)$$

and then we have the a priori estimate

$$\frac{1}{2} \int_0^1 x(1-x)q_\varepsilon^2 dx = -\varepsilon \int_0^1 (\partial_x (x(1-x)q_\varepsilon))^2 dx + \frac{1}{2} \int_0^1 (x\alpha + (1-x)\beta) \partial_x ((x(1-x)q_\varepsilon)^2)$$

$$\leq \beta - \alpha \frac{\varepsilon}{8} \int_0^1 x(1-x)q_\varepsilon^2 dx .$$

We differentiate equation (9) with respect to $t$, proceed as above to find the estimate

$$\int_0^1 x(1-x) (\partial_t q_\varepsilon)^2 dx \leq \Phi_1(t) ,$$
for an $\varepsilon$-independent function $\Phi_1$. In order to find an $\varepsilon$-independent bound for $\int_0^1 x(1 - x) (\partial_x q_\varepsilon) \, dx$, first we prove

$$\frac{1}{2} \partial_t \int_0^1 q_\varepsilon^2 \, dx \leq \frac{1}{2} \int_0^1 [x(1 - x)(x(\alpha - \beta) + \beta) - \varepsilon(1 - 2x)] \partial_x q_\varepsilon^2 \, dx \leq C \int_0^1 q_\varepsilon^2 \, dx ,$$

and this implies an a priori bound for $\int_0^1 q_\varepsilon^2 \, dx$. Then, note that

$$\frac{1}{2} \partial_t \int_0^1 x(1 - x) (\partial_x q_\varepsilon)^2 \, dx \leq$$

$$\int_0^1 \left[ -\frac{3}{2} (\alpha - \beta)x(1 - x) - (1 - 2x)(x\alpha + (1 - x)\beta) \right] \partial_x q_\varepsilon^2 \, dx$$

$$+ \int_0^1 [(x\alpha + (1 - x)\beta) - (\alpha - \beta)(1 - 2x)] x(1 - x) \partial_x q_\varepsilon^2 \, dx$$

$$\leq C_1 \int_0^1 x(1 - x) (\partial_x q_\varepsilon)^2 \, dx + C_2 \int_0^1 q_\varepsilon^2 \, dx .$$

We conclude an a priori bound for $\int_0^1 x(1 - x) (\partial_x q_\varepsilon)^2 \, dx$ and then from Rellich’s theorem, we know that $\int_0^1 x(1 - x) (q_\varepsilon)^2 \, dx$ is in a compact set of $L^2([0, T] \times [0, 1])$. This proves the theorem.

**Remark 3.** Equation (6) and (5) have a very important difference, even in the case where their asymptotic behaviour is the same. For equation (6) the Diracs at the endpoints appear at time $t = 0^+$, while for (5) this is only attained at $t = \infty$. Thus, we have the unusual situation that, at the endpoints, the parabolic problem is more singular than the hyperbolic associated problem.

### 6 The replicator dynamics connection

The replicator dynamics models the evolution of the fraction of a given type of individuals in an infinite population framework. For a payoff matrix given by

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix} ,$$

in its simplest form the replicator dynamics reads as following

$$\dot{X} = X(1 - X)(X(\alpha - \beta) + \beta) .$$
Equation (5) can be written as
\[
\partial_t p + x(1 - x)(\beta + (\alpha - \beta)x)\partial_x p + \\
(\beta + 2(\alpha - 2\beta)x - 3(\alpha - \beta)x^2) p = 0
\]

Its characteristics are given by
\[
\begin{align*}
\frac{dt}{ds} &= 1, \\
\frac{dx}{ds} &= x(1 - x)(\beta + (\alpha - \beta)x), \\
\frac{dz}{ds} &= - (\beta + 2(\alpha - 2\beta)x - 3(\alpha - \beta)x^2) z.
\end{align*}
\]

The projected characteristics in the $x \times t$ plane are given by
\[
\frac{dx}{dt} = x(1 - x)(\beta + (\alpha - \beta)x),
\]
which is just (11).

For smooth solutions, one can then write the solution to (5)—as done in [6]—as
\[
p(t, x) = a^0\delta_0 + b^0\delta_1 + q^0(\Phi_{-t}(x)) \left| \frac{\beta + (\alpha - \beta)\Phi_{-t}(x)}{\beta + (\alpha - \beta)x} \right| \frac{\Phi_{-t}(x)(1 - \Phi_{-t}(x))}{x(1 - x)}, \tag{12}
\]
where $\Phi_t(x)$ is the flow map of (11).

Notice that, when $\alpha - \beta \neq 0$, the first order term does not represent a pure drift, but also a dampening (enhancing) for $\alpha > \beta$ ($\alpha < \beta$, respectively).

Thus, equation (5) can be seen as an Eulerian representation of a quantity associated to the probability density evolution, but not to the probability density itself. If we let $q(t, x) = p(t, x) - a^0\delta_0 - b^0\delta_1$, we see, from (12), that the Lagrangian transported by the replicator flow is
\[
u(t, x) = x(1 - x)(\beta + (\alpha - \beta)x)q(t, x).
\]

Thus, (11) can be see as a Langragian representation of $\nu$, once the initial probability distribution is given. Since, we can recover $q$ from $\nu$, and hence can recover $p$, we have that, when there is no diffusion, solutions to (11) together with initial probability distribution are equivalent to (5).
An interesting question is to quantify how good is the dynamics given by equation (5)—or equation (11) for that matter—as an approximation to the dynamics of (6) in the case of small diffusion, i.e., strong selection. Besides the results already alluded to in section 5, the following results have also been shown in [6]:

1. For games without a non-trivial stable equilibrium, we have that the dynamics of $p$ is well approximated by solutions of (5) over a long time modulated by an envelope on a slow timescale.

2. For games with a non-trivial stable equilibrium, the above holds away of such an equilibrium. Near the equilibrium, we have a balance of diffusive and selective effects. This prevents the Dirac formation at the equilibrium point.

3. Combining the remarks above, we have, for Hawk-Dove games, that a non trivial initial distribution (i.e., that is not peaked at the endpoints) tends to peak at the interior equilibrium, and that such a peak takes a long time to die out. For an example see figure 11 in [7].

7 A numerical tour

For a comparison of the discrete and continuous models, as well as an extensive ensemble of simulations for (6), the reader is referred to [7].

Here, we shall focus on comparing the solutions to (5) with solutions to (6). We present two sets of simulations of (6); with large $\beta$ and large $\alpha$. We then compared the solutions to (5) with rescaled time and coefficients. We also plotted the position with the peak—with rescaled height—with the peak of the solution to (6). For display convenience, we have omitted the very ends of the interval and plotted $\Delta xp$ instead of $p$.

8 Further remarks

The analogy between the Moran process for finite populations and the replicator dynamics can be taken further. More precisely, suppose that the individuals taking part in the Moran process do not play only pure strategies as
Figure 2: Solutions to equation (6), labeled as Moran, and to (5) labeled as Nondiffusive in the frequency independent case, with $\alpha = \beta = 20$ and initial condition $p^0(x) = x(1 - x)/6$.

Figure 3: Evolution of solutions to (6) together with the peaks given by solutions to (5) plotted as points with rescaled height for a convenient display. Same parameters and initial condition of figure 2.
Figure 4: Solutions to equation (6), labeled as Moran, and to (5) labeled as Nondiffusive in the frequency independent case, with $\alpha = -20$ and $\beta = 20$ and initial condition $p^0(x) = 20x^3(1-x)$.

Figure 5: Solutions to equation (6), labeled as Moran, and to (5) labeled as Nondiffusive in the frequency independent case, with $\alpha = -20$ and $\beta = 20$ and initial condition $p^0(x) = 20x^3(1-x)$. 
in the above analysis, but are allowed to play mixed strategies. In particular, let us suppose that the game involves two kind of strategists, $E_{\theta_1}$ and $E_{\theta_2}$, where an $E_\theta$-strategist means that he/she plays pure strategy I with probability $\theta$ and II with probability $1 - \theta$. Then, the pay-off matrix is given by

$$
\begin{array}{c|cc}
E_{\theta_1} & E_{\theta_2} \\
\hline
E_{\theta_1} & \tilde{A} & \tilde{B} \\
E_{\theta_2} & \tilde{C} & \tilde{D}
\end{array}
$$

where

$$
\begin{align*}
\tilde{A} & := \theta_1^2 A + \theta_1 (1 - \theta_1)(B + C) + (1 - \theta_1)\theta_2^2 D , \\
\tilde{B} & := \theta_1 \theta_2 A + \theta_1 (1 - \theta_2)B + (1 - \theta_1)\theta_2 C + (1 - \theta_1)(1 - \theta_2)D , \\
\tilde{C} & := \theta_1 \theta_2 A + (1 - \theta_1)\theta_2 B + \theta_1 (1 - \theta_2)C + (1 - \theta_1)(1 - \theta_2)D , \\
\tilde{D} & := \theta_2^2 A + \theta_2 (1 - \theta_2)(B + C) + (1 - \theta_2)\theta_1^2 D .
\end{align*}
$$

The associated thermodynamical limit is given by

$$
\partial_t p = \partial_x^2 (x(1 - x)p) - \partial_x (x(1 - x)(x(\theta_1 - \theta_2)^2(\alpha - \beta) + (\theta_1 - \theta_2)(\theta_2 \alpha + (1 - \theta_2)\beta p)) .
$$

Figure 6: Evolution of solutions to (6) together with the peaks given by solutions to (5) plotted as points with rescaled height for a convenient display. Same parameters and initial condition of figures 4 and 5.
The final state is given by \( p^\infty = \pi_0[p^0]\delta_0 + \pi_1[p^0]\delta_1 \), where \( \pi_0[p^0] = 1 - \pi_1[p^0] \) and the fixation probability \( \pi_1[p^0] \) is given by

\[
\pi_1[p^0] = \frac{\int_0^1 \int_0^x p^0(x)F(\theta_1,\theta_2)(y)dydx}{\int_0^1 F(\theta_1,\theta_2)(y)dy},
\]

where

\[
F(\theta_1,\theta_2)(y) := \exp \left( -y^2(\theta_1 - \theta_2)^2 - y(\theta_1 - \theta_2)(\theta_2\alpha + (1 - \theta_2)\beta) \right).
\]

Note that the neutral case (i.e., when the two types of individuals are of the same kind) is given by \( \theta_1 = \theta_2 \), and in this case the governing equation is purely diffusive and fixation probability associated to a given initial state is simply given by

\[
\pi_1^N[p^0] = \int_0^1 xp^0(x)dx.
\]  \( \text{(13)} \)

We say that an \( E_{\theta_2} \) strategist dominates an \( E_{\theta_1} \) strategist (\( E_{\theta_2} \succ E_{\theta_1} \)) if the fixation probability of the first type, for any non-trivial initial condition is smaller than the one in neutral case given by equation \( \text{(13)} \). With this definition, we can prove the following theorem:

**Theorem 5.** \( E_{\theta_2} \succ E_{\theta_1} \) if and only if the flow of the replicator dynamics is such that \( \theta_1 \longrightarrow \theta_2 \).

As a simple corollary, we have that if \( \theta^* = \beta/(\beta - \alpha) \in (0, 1) \) (the ESS of the game), then \( E_{\theta^*} \succ E_{\theta}, \forall \theta \neq \theta^* \). This shows that an individual playing a mixed strategy with probabilities equal to the one of the game’s ESS is better equipped to win any context. But, as we saw in the previous sections, for populations of pure strategists we can not expect an stable mixture (even in fractions equivalent to the game’s ESS) to evolve.

**References**

[1] C. Bardos, F. Golse, and C. D. Levermore. Fluid dynamic limits of kinetic equations. II. Convergence proofs for the Boltzmann equation. *Comm. Pure Appl. Math.*, 46(5):667–753, 1993.
[2] C. Bardos, F. Golse, and D. Levermore. Fluid dynamic limits of kinetic equations. I. Formal derivations. *J. Statist. Phys.*, 63(1-2):323–344, 1991.

[3] P. Bechouche, N. J. Mauser, and S. Selberg. On the asymptotic analysis of the Dirac-Maxwell system in the nonrelativistic limit. *J. Hyperbolic Differ. Equ.*, 2(1):129–182, 2005.

[4] F. A. C. C. Chalub and K. Kang. Global convergence of a kinetic model for chemotaxis to a perturbed keller-segel system. *Nonl. Analysis*, 64(4):686–695, 2006.

[5] F. A. C. C. Chalub, P. A. Markowich, B. Perthame, and C. Schmeiser. Kinetic models for chemotaxis and their drift-diffusion limits. *Monatsh. Math.*, 142(1-2):123–141, 2004.

[6] F. A. C. C. Chalub and M. O. Souza. Asymptotic limits of continuous Moran processes: the Kimura equation and the replicator dynamics. In preparation.

[7] F. A. C. C. Chalub and M. O. Souza. The continuous limit of the Moran process and the diffusion of mutant genes in infinite populations. *Pre-print arXiv:math.AP/0602530*, 2006.

[8] T. Hillen and H. G. Othmer. The diffusion limit of transport equations derived from velocity-jump processes. *SIAM J. Appl. Math.*, 61(3):751–775 (electronic), 2000.

[9] J. Hofbauer and K. Sigmund. *Evolutionary Games and Population Dynamics*. Cambridge University Press, Cambridge, UK, 1998.

[10] M. Kimura. On the probability of fixation of mutant genes in a population. *Genetics*, 47:713–719, 1962.

[11] P. A. Markowich, C. A. Ringhofer, and C. Schmeiser. *Semiconductor equations*. Springer-Verlag, Vienna, 1990.

[12] N. Masmoudi. Some recent developments on the hydrodynamic limit of the Boltzmann equation. In *Mathematics & mathematics education (Bethlehem, 2000)*, pages 167–185. World Sci. Publishing, River Edge, NJ, 2002.
[13] N. Masmoudi and K. Nakanishi. Nonrelativistic limit from Maxwell-Klein-Gordon and Maxwell-Dirac to Poisson-Schrödinger. *Int. Math. Res. Not.*, 13:697–734, 2003.

[14] N. Masmoudi and L. Saint-Raymond. From the Boltzmann equation to the Stokes-Fourier system in a bounded domain. *Comm. Pure Appl. Math.*, 56(9):1263–1293, 2003.

[15] N. J. Mauser. Semi-relativistic approximations of the Dirac equation: first and second order corrections. In *Proceedings of the Fifth International Workshop on Mathematical Aspects of Fluid and Plasma Dynamics (Maui, HI, 1998)*, volume 29, pages 449–464, 2000.

[16] P. A. P. Moran. *The Statistical Process of Evolutionary Theory*. Clarendon Press, Oxford, 1962.

[17] H. G. Othmer and T. Hillen. The diffusion limit of transport equations. II. Chemotaxis equations. *SIAM J. Appl. Math.*, 62(4):1222–1250 (electronic), 2002.

[18] C. Sparber and P. Markowich. Semiclassical asymptotics for the Maxwell-Dirac system. *J. Math. Phys.*, 44(10):4555–4572, 2003.

[19] A. Traulsen, J. C. Claussen, and C. Hauert. Coevolutionary dynamics: From finite to infinite populations. *Phys Rev Lett*, 95:238701, 2005.