

# A RARE MUTATION MODEL IN A SPATIAL HETEROGENEOUS ENVIRONMENT

ANNA LISA AMADORI<sup>1,2</sup>, ROBERTO NATALINI<sup>2</sup>, DAVIDE PALMIGIANI<sup>2,3</sup>

**ABSTRACT.** We propose a stochastic model in evolutionary game theory where individuals (or subpopulations) can mutate changing their strategies randomly (but rarely) and explore the external environment. This environment affects the selective pressure by modifying the payoff arising from the interactions between strategies. We derive a Fokker-Plank integro-differential equation and provide Monte Carlo simulations for the Hawks vs Doves game. In particular we show that, in some cases, taking into account the external environment favors the persistence of the low-fitness strategy.

## 1. INTRODUCTION

Evolutionary Dynamics describes biological systems subject to Darwinian Evolution by taking into account the main mechanisms and phenomena of Evolution itself. In [11], Maynard Smith and Price propose an instance of this approach by considering a population modified according to the replicator dynamics. A population is formed by  $d$  types, or behaviors,  $E_1, \dots, E_d$ , with fractions corresponding to relative abundance in the vector  $x = (x_1, \dots, x_d)$ , which corresponds to a point in the simplex

$$\mathcal{S}^d = \left\{ x = (x_1, \dots, x_d) \in \mathbb{R}^d : x_k \geq 0, \sum_{k=1}^d x_k = 1 \right\}.$$

The selection and adaptation mechanism is described by means of a system of differential equations in the following form:

$$(1.1) \quad \frac{\dot{x}_k}{x_k} = f_k(x) - \bar{f}(x),$$

as  $k = 1, \dots, d$ . The rate of increment  $\dot{x}_k/x_k$  of the type  $E_k$  is given by its absolute fitness, denoted with  $f_k$ , balanced with the average fitness of the population  $\bar{f}$ , which has the form

$$\bar{f}(x) = \sum_{k=1}^d x_k f_k(x).$$

In evolutionary **matrix** game theory the vector of absolute fitness  $f = (f_1, \dots, f_d)$  is defined as

$$f(x) = \mathcal{U}(x) x,$$

where  $\mathcal{U}(x)$  is the matrix of payoff that rules the interplay between different strategists (and possibly depends by the frequencies of different species themselves). In

---

*Key words and phrases.* Evolutionary game theory; mutations; spatial games; Monte Carlo simulation.

The first author is member of the GNAMPA group of the Istituto Nazionale di Alta Matematica (INdAM).

this regard, the fitness of the type  $E_k$  is defined as the result that an individual of that type gets colliding against another individual on average, i.e.

$$f_k(x) = [\mathcal{U}(x)x]_k = \sum_{i=1}^d u_{ki}(x)x_i.$$

However, it is clear that the basic element for the generation of evolutionary novelties are mutations. [The quasispecies equation, dating back to the 1970s, modifies the growth rate of each species by considering the dispersion due to the birth of mutated offspring.](#)

The same underlying idea has been included in the evolutionary games setting in [16] with the replicator-mutator equation:

$$(1.2) \quad \dot{x}_k = \sum_{i=1}^d f_i q_{ik} x_i - \bar{f} x_k.$$

Here the coefficient  $q_{ik}$  express the proportion of offspring of  $k$ -type from a progenitor  $i$ , which shows up at any procreation. An important aspect of mutations stands in their randomness, which is quite underrated in (1.2). Since then many more refined models have been proposed to put into the right light randomness; we refer for instance to [5] showing that one single stochastic microscopic process can generate different macroscopic models of adaptive evolution. More recently, in [2], it has been proposed a macroscopic stochastic model where mutations occur at a different time scale than selection. This approach goes into the direction of adaptive dynamics, but differentiates from trait substitution sequence because it is not assumed that there is complete adaptation (namely invasion or extinction of the mutant trait) between subsequent mutations. [Within the framework of social dilemma, where the types  \$E\_i\$  are read as strategies, a "mutation" happens when a player changes his strategy. The model in \[2\] assumes that such events happen on rare and random occasions, even more than once before the system reaches its stable state.](#) See also the numerical paper [3], focused on Prisoner's Dilemma.

In this paper we take a step further and address our attention to the environment, seen as a place where individuals can evolve but also as a factor that can influence the dynamics of interaction between strategists. The model presented in [2] is then expanded to take into account how the natural environment can modify the interactions between individuals, changing selective pressures; we add a new variable  $y \in \mathbb{R}^N$  to the variable  $x$ , in the simplex, so that the status of the population is described by the pair  $(x, y)$ . The new variable  $y$  stands for the position of the population or, more widely, for an external parameter that affects the results of the interplay between strategies. It changes according to a velocity, partly deterministic, partly stochastic, and influences the selection mechanism because the payoff matrix depends on  $y$ .

In the following Section 2 we recall the stochastic model for replicator dynamics with point-type mutations introduced in [2]. With the aim of performing Monte-Carlo simulations, we give an alternative (but equivalent) description of the process by using a single Poisson random measure. Starting from this description, we generate an algorithm to simulate our process. Next, the spatial environment is introduced as a further stochastic variable, whose dynamics is ruled by a SDE. Therefore, we end up with two coupled SDE for the character-position variables  $(x, y)$ : see (2.5), (2.6).

In Section 3 we derive a Fokker-Plank integro-differential equation for (2.5), (2.6), (see (3.4) later on). The classical regularity assumptions requested by the Hormander theory are not satisfied because of the presence of a non-local term,

which is the deterministic counterpart of the point process modeling mutations. We therefore read it in the viscosity sense, even if the problem (3.4) does not fit plainly in the standard framework of viscosity solutions for integro-differential equations: the main difficulty comes from the domain where it is set, which is closed. Actually, the model does not justify any attempt to impose a boundary condition. Moreover the nonlocal term does not depend continuously on  $x$ . These difficulties are overcome by extending in a suitable way the problem to the whole space (3.5) and noticing that the produced solution can actually be interpreted as a probability density for the couple character-position  $(x, y)$ .

Finally Section 4 provides numerical simulations concerning the two strategist game Hawks vs Doves, used by Maynard Smith to explain the high frequency of conventional displays, rather than all-out fight, among animals (especially within heavily armed species) [7]. We modify the standard model by assuming that the cost for fighting changes according to the location, and perform various simulations for the probability density obtained both by a Monte-Carlo method starting from the stochastic system (2.5), (2.6), and by a finite difference scheme based on the Fokker-Plank equation (3.5). The equilibrium of the standard replicator-mutator dynamics can be disrupted by effect of either random motion or mutations. In some particular cases, the environment itself allows for the survival of the low fitness species.

## 2. A STOCHASTIC MODEL FOR MUTATIONS IN HETEROGENEOUS ENVIRONMENT

We propose to describe the frequencies of different phenotypes in the population according to a stochastic differential equations (SDE) in the general framework

$$(2.1) \quad X_t = X_0 + \int_0^t a(X_s) ds + \int_0^t b(X_s) dW(s) + \int_0^t \int_E K(X_{s-}, \xi) \mathcal{N}(ds \times d\xi).$$

Here  $X_t$  is a process on a probability space  $(\Omega, \mathcal{F}, \mathbb{P})$ , where  $a, b, K$  are Borel measurable functions of appropriate dimensions.  $W(s)$  is a standard Brownian motion and  $P(s)$  is a Poisson point process with random measure  $\mathcal{N}(ds \times d\xi)$  on  $\mathbb{R}^+ \times E$ , with mean measure  $l \times \nu$ ,  $l$  Lebesgue measure on  $\mathbb{R}^+$ ,  $\nu$  a  $\sigma$ -finite measure on a measurable space  $(E, \mathcal{E})$ .

The process of classic replicator dynamics (1.1) is obtained when  $X = (x_1, \dots, x_d)$  is the vector of relative frequencies of  $d$  various phenotypes,  $a$  is the vector of relative fitness, i.e.  $a(X) = (\dots, a_k(X), \dots)$ , with

$$a_k(X) = x_k (f_k(X) - \bar{f}(X)),$$

and  $b$  and  $K$  are null, so that (2.1) is totally deterministic.

In [2], mutations are described by means of a pure point process that alters replicator dynamics and the Brownian motion term is zero ( $b = 0$ ). Any mutation has a fixed progenitor (type  $i$ ) and a unique descendant (type  $j$ ): this gives  $2\binom{d}{2} = d(d-1)$  different mutations, precisely all those that transform a type  $i$  in a type  $j$  as

$$(i, j) \in I = \left\{ (i, j) \in \{1, \dots, d\}^2; i \neq j \right\}.$$

The mutation from type  $i$  to type  $j$  is driven by a non-homogeneous point process  $N_t^{ij}$  with stochastic intensity  $\lambda_{ij} f_i(X_{t-})$ . The process  $N_t^{ij}$  makes unit jumps with a frequency depending on the process itself, according to the “genetic distance” between the types  $i$  and  $j$  ( $\lambda_{ij}$ ) and the fitness of  $i$  ( $f_i$ ): the higher the fitness, the higher the rate of reproduction of individuals of that kind, the more they will suffer mutations. A further coefficient  $\gamma_{ij} \in (0, 1)$  measures the proportion of individuals involved in mutations: the population of type  $i$  decreases by a fraction  $\gamma_{ij} x_i$ , while the population of type  $j$  increases by the same amount. This yields a jump of the

population frequency vector of size  $\gamma_{ij}x_i(e_j - e_i)$ ,  $e_i$  standing for the unit vector pointing in the direction  $i$ . The resulting SDE is

$$(2.2) \quad x_{k,t} = x_k(0) + \int_0^t a_k(X_s)ds + \sum_{i \neq k} \int_0^t \gamma_{ik}x_{i,t}dN_t^{ik} - \sum_{i \neq k} \int_0^t \gamma_{ki}x_{k,t}dN_t^{ki}.$$

Let us notice by now that the number of variables depicting the character can be reduced by observing that  $x_d = 1 - \sum_{i=1}^{d-1} x_i$  and setting the problem in the closed set

$$\Sigma^d = \{(x_1, \dots, x_{d-1}) : x_i \geq 0, \sum_{i=1}^{d-1} x_i \leq 1\}.$$

With a little abuse of notations we shall continue to write  $x \in \Sigma^d$  and

$$f_k(x) = f_k(x_1, \dots, x_{d-1}, 1 - \sum_{i=1}^{d-1} x_i),$$

$$a_k(x) = a_k(x_1, \dots, x_{d-1}, 1 - \sum_{i=1}^{d-1} x_i) = (f_k - f_d)(1 - x_k)x_k - \sum_{\substack{i=1 \\ i \neq k}}^{d-1} (f_i - f_d)x_i x_k.$$

In the same paper [2], a Kolmogorov integro-differential equation describing the expected frequencies is derived and investigated analytically, with particular attention to the long term equilibrium. Analytical investigation is satisfactory in the case of constant fitness (quasispecies equation), but there are some gaps concerning variable fitness, that has been tackled by a numeric approach in the subsequent paper [3]. In the present work we are mainly concerned with Monte-Carlo simulations. That is why, before enriching the model by including the effect of heterogeneous environment, it is worth giving an alternative description and present an algorithmic approach.

The SDE (2.2) can be written in standard form (2.1) by taking  $d(d-1)$  independent Poisson random measures  $\mathcal{N}_{ij}(ds \times d\xi)$  on  $\mathbb{R}^+ \times \mathbb{R}^+$ , defining the amplitudes of jumps as

$$(2.3) \quad K_{ij}(X, \xi) = \gamma_{ij}x_i(e_j - e_i)1_{[0, \lambda_{ij}f_i(X)]}(\xi),$$

and then invoking the Poisson embedding [6].

It is possible to set up an equivalent mode (i.e. with the same probability distribution) with only one random measure  $\mathcal{N}(ds \times d\xi)$  on  $\mathbb{R}^+ \times E$  with  $E = \mathbb{R}^+ \times [0, 1]$ . To this aim we look at the sum of the stochastic intensity of each individual process

$$\Lambda(X) = \sum_{i \neq j} \lambda_{ij}f_i(X),$$

split the unit interval into  $d(d-1)$  disjoint intervals  $\mathcal{I}_{ij}$  of length  $\lambda_{ij}f_i(X)/\Lambda(X)$ , and take the amplitude of jumps as

$$(2.4) \quad K(X, \xi) = K(X, u, \theta) = 1_{[0, \Lambda(X)]}(\theta) \sum_{i \neq j} [\gamma_{ij}x_i(e_j - e_i)1_{\mathcal{I}_{ij}}(u)].$$

The two processes just described coincide indeed.

**Lemma 2.1.** *The processes (2.3) and (2.4) have the same infinitesimal generator, so they have the same probability distribution.*

*Proof.* The generator of 2.4 is

$$\begin{aligned}
& \int_{(0,1)} \int_{\mathbb{R}} \left[ \phi \left( X + 1_{(0,\Lambda(X)]}(\theta) \sum_{i \neq j} \gamma_{ij} x_i (e_j - e_i) 1_{\mathcal{I}_{ij}}(u) \right) - \phi(X) \right] du d\theta \\
&= \Lambda(X) \int_{(0,1)} \left[ \phi \left( X + \sum_{i \neq j} \gamma_{ij} x_i (e_j - e_i) 1_{\mathcal{I}_{ij}}(u) \right) - \phi(X) \right] du \\
&= \Lambda(X) \sum_{i \neq j} \int_{\mathcal{I}_{ij}} [\phi(X + \gamma_{ij} x_i (e_j - e_i)) - \phi(X)] du \\
&= \Lambda(X) \sum_{i \neq j} |\mathcal{I}_{ij}| [\phi(X + \gamma_{ij} x_i (e_j - e_i)) - \phi(X)] \\
&= \sum_{i \neq j} \lambda_{ij} f_i(X) [\phi(X + \gamma_{ij} x_i (e_j - e_i)) - \phi(X)],
\end{aligned}$$

i.e. the same infinitesimal generator of (2.3), as in [2]. □

This alternative construction, albeit equivalent to the first one, can be turned into a simulation more easily and with a more compact and efficient code, because it involves only one jump process instead of  $d(d-1)$  independent ones. In view of Monte Carlo approximations, we therefore give an intuitive interpretation of this last process, based on the existence theorem for Poisson random measures in [9].

Let  $T > 0$  a fixed time horizon and

$$\Lambda^{\max} = \max_X \Lambda(X).$$

The evolution process can be simulated by the following steps:

- i) Build a priori an homogeneous Poisson process with intensity  $\Lambda^{\max}$ , whose jump times will be denoted by  $T_n$  lower than  $T$ ;
- ii) Simulate the replicator dynamics till  $T_1$ ;
- iii) Extract uniformly a random number  $\xi \in [0, 1]$ ;
- iii.a) if  $\Lambda^{\max} \xi > \Lambda(X_{T_1^-})$  no jump occurs,
- iii.b) if  $\Lambda^{\max} \xi \leq \Lambda(X_{T_1^-})$  a jump occurs indeed.

To decide which kind of mutation occurs, extract another random number  $u \sim \text{Unif}(0, 1)$  and look at which interval  $\mathcal{I}_{\hat{i}\hat{j}}$  it belongs (it is possible because the sets  $\mathcal{I}_{ij}$  form a partition of  $[0, 1]$ ).

Then shift a quantity  $\gamma_{\hat{i}\hat{j}} x_{\hat{i}, T_1^-}$  from  $\hat{i}$  to  $\hat{j}$ .

- iv) Restart from step ii).

**2.1. Heterogeneous environment.** In the present model the only observed variables are the frequencies of the various phenotypes, as well as in the classical replicator equation. The rules of the play are fixed once and for all by means of the payoff matrix  $\mathcal{U}$ , and nothing depends by the physical position of the population, as if the individuals were not able to move, or if the environment were completely homogeneous. A more realistic picture has to take into account that environmental changes affect the results of interaction between different behaviors.

To introduce heterogeneous environment we increase the observed variables so that the status of the population (or of a sub-population) is described by a pair  $X = (x, y)$ : as before  $x = (x_1, \dots, x_{d-1}) \in \Sigma^d$  stands for the *character* of the population, each  $x_i$  being the fraction of individuals of type  $E_i$  (and  $x_d = 1 - \sum_{i=1}^{d-1} x_i$

the fraction of type  $E_d$ ), while the new variable  $y \in \mathbb{R}^N$  stands for the *position* of the population. More widely this new variable can be seen as an external parameter that affects the results of the interplay between strategies. The payoff matrix depends by  $y$ , i.e.  $\mathcal{U} = \mathcal{U}(y)$ , consequently also the respective fitness

$$f_k(x, y) = \sum_{i=1}^{d-1} u_{ki}(y)x_i + u_{id}(y)\left(1 - \sum_{i=1}^{d-1} x_i\right)$$

varies with  $y$ .

The character  $x$  evolves according to a suitable version of equation (2.2):

$$(2.5) \quad x_t = x_0 + \int_0^t a(x_s, y_s) ds + \int_0^t \int_E K(x_{s-}, y_s, \xi) \mathcal{N}(ds \times d\xi).$$

Here

- $a \in R^{d-1}$  stands for the *vector field of the replicator dynamics*. It has the same structure as in the former case, but with an important difference: the fitness are allowed to depend from  $y$ , so that

$$a_k(x, y) = x_k(f(x, y) - \bar{f}(x, y)) \quad \text{as } k = 1, \dots, d.$$

- The jump amplitude  $K$  and the Random measure  $\mathcal{N}$  describe the *mutation process* as before. The location  $y$  affects the mutation process through the fitness, as

$$\Lambda(x, y) = \sum_{i \neq j} \lambda_{ij} f_i(x, y),$$

$$K(x, y, u, \theta) = 1_{[0, \Lambda(x, y))}(\theta) \sum_{i \neq j} \gamma_{ij} x_i (e_j - e_i) 1_{\mathcal{I}_{ij}(x, y)}(u),$$

where the intervals  $\mathcal{I}_{ij}(x, y)$  have length equal to  $\lambda_{ij} f_i(x, y) / \Lambda(x, y)$  and form a partition of the unit interval, as  $i \neq j \in \{1, \dots, d\}$ .

The environmental variable  $y$  changes according to a diffusion with drift:

$$(2.6) \quad y_t = y_0 + \int_0^t v(x_s, y_s) ds + \int_0^t \sigma(x_s, y_s) dW_s,$$

where

- $v \in R^N$  stands for the *velocity field of the population*. For any given  $y$ ,  $v(e_i, y)$  is the drift of the type  $E_i$ , while a composite population described by the character  $x$  is inclined to move according to  $v(x, y)$ .
- $\sigma$  is an  $N \times N$  matrix and  $W_s$  is an  $N$ -dimensional Brownian motion, describing the random component of the displacement.

**Notice that both the drift and the diffusion may depend by the frequency vector  $x$ , allowing retro-actions of population on the environment itself.**

The well posedness of the process (2.5), (2.6) is assured by classical arguments (see [4], [8]). Monte-Carlo simulations do not require substantial changes compared to the non-spatial case: the additional Brownian motion can be effectively simulated in a standard way.

### 3. A FOKKER-PLANK EQUATION FOR THE PROBABILITY DENSITY

The stochastic process (2.5), (2.6) can be described in a deterministic way by means of two Kolmogorov integro-partial differential equations: the backward one, also known as Feynman-Kac equation, (related to expected value) and the forward one, also known as Fokker-Plank equation (related to the density).

With minor changes from [2, Proposition 3.1], one easily sees that the infinitesimal generator of the process (2.5) (settled in  $\Sigma^d$ ), (2.6) is

$$(3.1) \quad \mathcal{L}\phi = a \cdot D_x \phi + v \cdot D_y \phi + \frac{1}{2} \text{Tr} (\sigma \sigma^t D_{yy}^2 \phi) + \mathcal{J}\phi.$$

Here  $D_x$  and  $D_y$  stand for the vectors of first derivatives w.r.t.  $x \in \mathbb{R}^{d-1}$  and  $y \in \mathbb{R}^N$ , respectively,  $D_{yy}^2$  stands for the  $N \times N$  matrix of the second order derivatives w.r.t.  $y$ ,  $a$ ,  $v$ ,  $\sigma$  are the same functions appearing in (2.5), (2.6), and  $\mathcal{J}$  is a non-local functional related to a discrete measure:

$$\begin{aligned} \mathcal{J}(x, y, \phi) &= \int_{\mathbb{R}^{d-1}} (\phi(x+z, y, t) - \phi(x, y, t)) d\mu_{x,y}(z), \\ \mu_{x,y}(z) &= \sum_{\substack{i,j=1 \\ i \neq j}}^{d-1} \lambda_{ij} f_i(x, y) \delta_{\{\gamma_{ij} x_i (e_j - e_i)\}}(z) + \sum_{i=1}^{d-1} \lambda_{id} f_i(x, y) \delta_{\{-\gamma_{id} x_i e_i\}}(z) \\ &\quad + \sum_{i=1}^{d-1} \lambda_{di} f_d(x, y) \delta_{\{\gamma_{di} (1 - \sum_{k=1}^{d-1} x_k)\}}(z). \end{aligned}$$

The expected value at time  $t$  of a population which is at state  $(x, y)$  at time  $t = 0$  is described by  $u(x, y, t)$ , the solution to the Feynman-Kac system

$$(3.2) \quad \begin{cases} \partial_t u_k - a \cdot D_x u_k - v \cdot D_y u_k - \frac{1}{2} \text{Tr} (\sigma \sigma^t D_{yy}^2 u_k) = \mathcal{J} u_k, \\ u_k(x, y, 0) = \begin{cases} x_k & \text{as } k = 1, \dots, d-1, \\ y_{k-d} & \text{as } k = d, \dots, d+N-1. \end{cases} \end{cases}$$

Otherwise, one can be interested into the macroscopic function  $\varrho(x, y, t) \in [0, 1]$ , measuring the probability of finding a population distribution  $(x_1, \dots, x_{d-1}, 1 - \sum_{i=1}^d x_i) \in S^d$  in the position  $y \in \mathbb{R}^N$  at time  $t$ . For instance at time  $t > 0$  the quantity

$$P_i(t) = \iint_{(B_\varepsilon(e_i) \cap \Sigma^d) \times \mathbb{R}^N} \varrho(x, y, t) dx dy$$

depicts the probability of having an high proportion of individuals of type  $i$ , while

$$P_i(t, \delta) = \iint_{(B_\varepsilon(e_i) \cap \Sigma^d) \times B_\delta(0)} \varrho(x, y, t) dx dy$$

depicts the probability of finding an high proportion of individuals of type  $i$  near at the origin.

This can be done if the starting point is one population with character  $x$  in the position  $y$  (that is the initial datum is a Dirac mass centered at  $(x, y)$ ), or if the initial status is a random variable with density function  $\varrho_0(x, y)$ .

A rigorous deduction of the Fokker-Plank equation requests a-priori regularity of the density function. The topic of regularity can be addressed by the classical Hormander theory (see, for instance, the book [13]) and requests some technical assumptions, also in the diffusive setting (i.e. in absence of mutations). In the present setting there is no reason to expect that the density function is smooth enough, due to the anisotropy of diffusion and to the point process modeling mutation. We therefore choose to write the Fokker-Plank equation formally and then to settle it in the framework of viscosity solution theory. This approach has the advantage of asking very few a-priori regularity and producing well-posed solutions even in the degenerate elliptic, integro-differential setting arising from rare mutations.

Following Pavliotis [14] we compute  $\mathcal{L}^*$ , the dual operator in  $L^2(\Sigma^d \times \mathbb{R}^N)$  of the infinitesimal generator:

$$(3.3) \quad \mathcal{L}^* \phi = \frac{1}{2} \sum_{h,k=1}^N \partial_{y_h y_k}^2 ((\sigma \sigma^t)_{hk} \phi) - \operatorname{div}_x (\phi a) - \operatorname{div}_y (\phi v) + \sum_{i=1}^d \mathcal{J}_i^* (f_i \phi),$$

where now

$$\begin{aligned} \mathcal{J}_i^* (x, y, \phi) &= \int_{\mathbb{R}^{d-1}} (\phi(x+z, y, t) - \phi(x, y, t)) d\mu_{x,y}^i(z), \\ d\mu_{x,y}^i(z) &= \sum_{\substack{j=1 \\ j \neq i}}^{d-1} \lambda_{ij} (1 + \gamma_{ij}^*) 1_{\Sigma^d} (x + \gamma_{ij}^* x_i (e_i - e_j)) \delta_{\{\gamma_{ij}^* x_i (e_j - e_i)\}}(z) \\ &\quad + \lambda_{id} (1 + \gamma_{id}^*) 1_{\Sigma^d} (x + \gamma_{id}^* x_i e_i) \delta_{\{-\gamma_{id}^* x_i e_i\}}(z), \end{aligned}$$

as  $i = 1, \dots, d-1$  and

$$d\mu_{x,y}^d(z) = \sum_{j=1}^{d-1} \lambda_{dj} (1 + \gamma_{dj}^*) 1_{\Sigma^d} (x - \gamma_{dj}^* (1 - \sum_{k=1}^{d-1} x_k) e_j) \delta_{\{\gamma_{dj}^* (1 - \sum_{k=1}^{d-1} x_k) e_j\}}(z),$$

for  $\gamma_{ij}^* = \gamma_{ij}/(1 - \gamma_{ij})$ . It turns out that, if  $\varrho_0(x, y)$  is the probability density of the random variable  $X_0 = (x_0, y_0)$  describing the initial distribution of subpopulations, and if the solution  $X_t = (x_t, y_t)$  to (2.5), (2.6) has a sufficiently smooth probability density  $\varrho(x, y, t)$  for  $t > 0$ , then it solves the initial value problem

$$(3.4) \quad \begin{cases} \partial_t \varrho - \frac{1}{2} \sum_{h,k=1}^N \partial_{y_h y_k}^2 ((\sigma \sigma^t)_{hk} \varrho) + \operatorname{div}_x (\varrho a) + \operatorname{div}_y (\varrho v) = \sum_{i=1}^d \mathcal{J}_i^* (f_i \varrho) \\ \varrho(x, y, 0) = \varrho_0(x, y), \end{cases}$$

in the closed set  $(x, y) \in \Sigma^d \times \mathbb{R}^N$  and  $t > 0$ .

Let us explicitly remark that nonlocal operators  $\mathcal{J}_i^*$  are not continuous w.r.t.  $x$ : this fact may have a huge instability effect. We therefore switch to another problem which is settled into all  $\mathbb{R}^{d-1} \times \mathbb{R}^N$  and is continuous. To this end we extend the fitness functions  $f_i$ , the drift  $v$  and the diffusion  $\sigma$  in a bounded smooth way to all  $\mathbb{R}^d \times \mathbb{R}^N$  so that  $f_i \geq 0$  have support contained in a cylinder, say  $B_R(0) \times \mathbb{R}^N$ . Concerning the initial datum  $\varrho_0$ , it can be extended as  $\varrho_0 \equiv 0$  outside  $\Sigma^d \times \mathbb{R}^N$ . We thus look into the problem

$$(3.5) \quad \begin{cases} \partial_t \varrho - \frac{1}{2} \sum_{h,k=1}^N \partial_{y_h y_k}^2 ((\sigma \sigma^t)_{hk} \varrho) + \operatorname{div}_x (\varrho a) + \operatorname{div}_y (\varrho v) + c \varrho = \tilde{\mathcal{J}} \varrho \\ \varrho(x, y, 0) = \varrho_0(x, y), \end{cases}$$

for  $(x, y) \in \mathbb{R}^d \times \mathbb{R}^N$  and  $t > 0$ , where now

$$\begin{aligned} \tilde{\mathcal{J}}(x, y, \phi) &= \int_{\mathbb{R}^{d-1}} (\phi(x+z, y, t) - \phi(x, y, t)) d\mu_{x,y}(z), \\ d\mu_{x,y}(z) &= \sum_{\substack{i,j=1 \\ j \neq i}}^{d-1} m_{ij}(x, y) \delta_{\{\gamma_{ij}^* x_i (e_j - e_i)\}}(z) \\ &\quad + \sum_{i=1}^{d-1} m_{id}(x, y) \delta_{\{-\gamma_{id}^* x_i e_i\}}(z) + \sum_{j=1}^{d-1} m_{dj}(x, y) \delta_{\{\gamma_{dj}^* (1 - \sum_{k=1}^{d-1} x_k) e_j\}}(z), \\ m_{ij}(x, y) &= (1 + \gamma_{ij}^*) \lambda_{ij} f_i(x + \gamma_{ij}^* x_i (e_i - e_j), y), \end{aligned}$$



as  $i, j = 1, \dots, d-1$ , with  $i \neq j$ , and

$$\begin{aligned} m_{id}(x, y) &= \lambda_{id}(1 + \gamma_{id}^*)f_i(x + \gamma_{id}^*x_i, y), \\ m_{di}(x, y) &= \lambda_{di}(1 + \gamma_{di}^*)f_d(x - \gamma_{di}^*(1 - \sum_{k=1}^{d-1} x_k)e_i, y), \end{aligned}$$

as  $i = 1, \dots, d-1$ ,

$$c(x, y) = \sum_{\substack{i, j=1 \\ i \neq j}}^d (\lambda_{ij}f_i(x, y) - m_{ij}(x, y)).$$

It is worth clarify that the equation in (3.5) does not coincide with the one in (3.4) even if  $x \in \Sigma^d$ . Although they do coincide for that functions  $\varrho$  which are zero for  $x$  outside  $\Sigma^d$ . On the other hand if the support of  $\varrho_0$  is contained in  $\Sigma^d \times \mathbb{R}^N$  and  $\varrho(t) \in L^1(\mathbb{R}^{d-1} \times \mathbb{R}^N)$  is nonnegative, then also the support of  $\varrho(t)$  is contained in  $\Sigma^d \times \mathbb{R}^N$ .

To see this fact, let

$$\begin{aligned} A_k &= \{x \in \mathbb{R}^{d-1} : x_k < 0\} && \text{as } k = 1, \dots, d-1, \\ A_d &= \{x \in \mathbb{R}^{d-1} : \sum_{k=1}^{d-1} x_k > 1\}, \\ I_k(t) &= \iint_{A_k \times \mathbb{R}^N} \varrho(t) dx dy && \text{as } k = 1, \dots, d. \end{aligned}$$

It suffices to check that  $\frac{d}{dt}I_k(t) \leq 0$ . For simplicity we perform computations only in the case  $d = 2$ . Integrating the equation in (3.5) on  $A_1 \times \mathbb{R}^N$  gives

$$\begin{aligned} \frac{d}{dt}I_1(t) &= - \int_{\mathbb{R}^N} (a_1\varrho)(0, y) dy + \lambda_{12} \iint_{A_1 \times \mathbb{R}^N} ((1 + \gamma_{12}^*)(f_1\varrho)((1 + \gamma_{12}^*)x, y, t) - (f_1\varrho)(x, y, t)) dx dy \\ &\quad + \lambda_{21} \iint_{A_1 \times \mathbb{R}^N} ((1 + \gamma_{21}^*)(f_2\varrho)(x - \gamma_{21}^*(1 - x), y, t) - (f_2\varrho)(x, y, t)) dx dy \end{aligned}$$

remembering that  $a_1(0, y) \equiv 0$  and performing the obvious transformations in the second and third integrals yields

$$= - \lambda_{21} \int_{\mathbb{R}^N} dy \int_{-\gamma_{21}^*}^0 dx (f_2\varrho)(x, y, t) \leq 0$$

because  $f_2\varrho \geq 0$ . Similarly, since  $a_1(1, y) \equiv 0$  one gets

$$\frac{d}{dt}I_2(t) = - \lambda_{12} \int_{\mathbb{R}^N} dy \int_1^{1+\gamma_{12}^*} dx (f_1\varrho)(x, y, t) \leq 0.$$

It has also to be stressed that, in order to read the solution  $\varrho(t)$  as a probability density, its total mass has to be 1, that is

$$M(t) = \iint_{\mathbb{R}^{d-1} \times \mathbb{R}^N} \varrho(x, y, t) dx dy = 1 \quad \text{for all } t > 0,$$

provided that  $M(0) = \iint_{\Sigma^d \times \mathbb{R}^N} \varrho_0(x, y) dx dy = 1$ . Again, integrating the equation in (3.5) gives

$$\begin{aligned} \frac{d}{dt} M(t) = & \lambda_{12} \iint_{\mathbb{R} \times \mathbb{R}^N} ((1 + \gamma_{12}^*)(f_1 \varrho)((1 + \gamma_{12}^*)x, y, t) - (f_1 \varrho)(x, y, t)) dx dy \\ & + \lambda_{21} \iint_{\mathbb{R} \times \mathbb{R}^N} ((1 + \gamma_{21}^*)(f_2 \varrho)(x - \gamma_{21}^*(1 - x), y, t) - (f_2 \varrho)(x, y, t)) dx dy = 0 \end{aligned}$$

after a trivial change of variables. Hence the total mass is preserved in the modified problem (3.5).

In view of these remarks, we can read as the probability density of the process (2.5), (2.6) a solution  $\varrho(t)$  to the Cauchy problem (3.5) with the properties  $\varrho(t) \in L^1(\mathbb{R}^{d-1} \times \mathbb{R}^N)$  and  $\varrho(t) \geq 0$  for  $t > 0$ . The existence of such a solution is assured in the viscosity framework.

**Theorem 3.1.** *Assume that  $f_i, v \in C^{1,1}(\mathbb{R}^{d-1} \times \mathbb{R}^N)$ ,  $\sigma \in C^{2,1}(\mathbb{R}^{d-1} \times \mathbb{R}^N)$  are bounded together with their derivatives, with  $f_i \geq 0$  and  $\sigma \geq \varepsilon > 0$ . Take  $\varrho_0$  a Lipschitz-continuous, bounded function whose support is compact and contained in the interior of  $\Sigma^d \times \mathbb{R}^N$  such that  $\varrho_0 \geq 0$  and  $\iint \varrho_0 dx dy = 1$ . Then there exists a unique viscosity solution to (3.5). Moreover  $\varrho(t) \in L^1(\mathbb{R}^{d-1} \times \mathbb{R}^N)$  and  $\varrho(t) \geq 0$  for all  $t > 0$ .*

*Proof.* First of all the equation in (3.5) has to be written in the standard form of the viscosity solution framework, which is nonvariational. This can be done if the coefficients  $f_i, v, \sigma$  have the regularity requested by hypothesis. So we write

$$(3.6) \quad \partial_t \varrho + a \partial_x \varrho + b \partial_y \varrho + c \varrho - \frac{1}{2} \sigma^2 \partial_{yy}^2 \varrho = \sum_{i=1}^2 \tilde{\lambda}_i \mathcal{I}_i(\varrho)$$

where now

$$\begin{aligned} \tilde{\lambda}_1(x, y) &= \lambda_{12}(1 + \gamma_1^*) f_1(x + \gamma_1^* x, y), \\ \tilde{\lambda}_2(x, y) &= \lambda_{21}(1 + \gamma_2^*) f_2(x - \gamma_2^*(1 - x), y), \end{aligned}$$

and consequently

$$c(x) = \partial_x a + \partial_y v - \frac{1}{2} \partial_{yy}^2 \sigma^2 + \sum_{i=1}^2 (\lambda_i f_i - \tilde{\lambda}_i)$$

are continuous and bounded. This problem satisfies the assumptions in [1, Theorems 1.1, 1.2], therefore it has a unique continuous viscosity solution  $\varrho(x, y, t)$  which is Lipschitz-continuous w.r.t.  $x, y$  and bounded. Moreover comparison principle holds, in particular one can find suitable parameters  $c_1, c_2, c_3$  so that

$$(3.7) \quad 0 \leq \varrho \leq \exp(c_1 t - c_2 \sqrt{1 + x^2} - c_3 y^2) \quad \text{in } \mathbb{R}^2 \times [0, \infty).$$

In particular  $\varrho(t) \in L^1(\mathbb{R}^2)$  for all  $t$ .  $\square$

**Remark 3.1.** *The assumption  $\sigma \geq \varepsilon > 0$  has only been used to obtain the estimate from above in (3.7) and infer the integrability of the solution and the equation into all  $\mathbb{R}^2$ . The hypothesis can be removed by asking something more to the drift  $v$  in order to assure some decay w.r.t.  $y$ .*

In view of the biological applications, it is suitable to allow the initial density  $\varrho_0$  to be a probability measure. For instance modeling the evolution of one population whose initial state  $(x, y)$  is known deterministically requests to take a  $\rho_0$  as a Dirac mass centered at  $(x, y)$ . This would hugely increase the mathematical difficulty. The

recent paper [10] presents interesting results in this direction, which are modeled on the fractional Laplacian and therefore do not include the discrete non-local operator appearing here. We also mention [15] for some transport problem involving measures.

#### 4. HAWKS AND DOVES: A NUMERICAL STUDY

In this section we take as a case study the two strategy game Hawks vs Doves ( $d = 2$ ), with the following payoff matrix:

$$\mathcal{U} = \begin{pmatrix} \frac{G-C}{2} & G \\ 0 & \frac{G}{2} \end{pmatrix},$$

where the coefficients are both positive. The fitness functions for Hawks ( $x_1$ ) and Doves ( $x_2$ ), are respectively

$$f_1 = (G - C)x_1/2 + Gx_2, \quad f_2 = Gx_2/2,$$

then the replicator dynamics (reducing the coordinates only to  $x \in [0, 1]$ , fraction of hawks) is

$$\dot{x} = x(1-x)(f_1 - f_2) = x(1-x)(G - Cx)/2.$$

Besides the pure-strategies equilibria  $x = 0$  (all Doves) and  $x = 1$  (all Hawks), a mixed strategies equilibrium can occur,  $\bar{x} = G/C$ , when  $C > G$ : in this case the real Hawks vs Doves game occurs, with  $\bar{x}$  attractive and the other two values 0 and 1 which become unstable equilibria. Notice that when the cost of the fight  $C$  increases, the percentage of hawks at the equilibrium  $\bar{x}$  decreases; instead, when the cost of fighting is less or equal than the gain,  $C \leq G$ , the only equilibria are the pure-strategies ones, with  $x = 1$  attractive; the population tends to become only hawks.

We add to the two strategies game also the space component, with  $y \in \mathbb{R}$  ( $N = 1$ ). In particular we assume that the cost for fighting depends by  $y$  as

$$C(y) = \frac{3G}{2} \left[ 1 + \frac{2}{\pi} \arctan(y) \right].$$

The function  $C$  is designed so that, at  $y = 0$ , the cost for fighting is  $C = 3G/2 > G$  and we have a coexistence equilibrium  $\bar{x} = 2/3$ . At  $y < 0$  the cost lowers until it becomes equal to the gain for  $y = -\sqrt{3}/3$ , so for smaller values of  $y$  the coexistence equilibrium disappears, hawks increase and the only attracting equilibrium is  $\bar{x} = 1$ . Otherwise if  $y > 0$  environment is more favorable to doves, because the cost increases up to  $3G$ , so that the fraction of hawks at equilibrium  $\bar{x}(y)$  is a decreasing function of  $y$ , tending towards  $1/3$  as  $y \rightarrow +\infty$ . [Summing up, for any fixed  \$y\$ , the standard replicator dynamics has its equilibrium at](#)

$$(4.1) \quad \bar{x}(y) = \begin{cases} 1 & y < -\sqrt{3}/3, \\ G/C(y) & y \geq -\sqrt{3}/3, \end{cases}$$

which is well known to be a global attractor. In particular the initial state  $(x_0, y_0) = (2/3, 0)$  is an equilibrium for the standard replicator dynamics (i.e. neither mutations or motions are allowed), and also when a deterministic motion with  $v(2/3, 0) = 0$  is considered. All the simulations that follow represent the probability density  $\rho(x, y, t)$  evolving from the same initial state  $(x_0, y_0) = (2/3, 0)$ , and show that the equilibrium can be disrupted by Brownian motion in an eterogeneous environment and/or by mutations. They have been obtained in MATLAB using Monte-Carlo methods and, in the last section, using a numerical method for the I.P.D.E. (3.5).

**Monte Carlo simulations.** Roughly speaking, large number of independent runs of the stochastic process is performed, to statistically estimate the density.

- Fixed the final time,  $T$ , we discretize the time interval  $[0, T]$  in, at least,  $N = 2^8$  sub-intervals with the same length; fixed an accuracy  $\alpha$ , the number  $N$  increases up to make sure that the probability of the event “up to one jump in each interval” is greater than  $(1 - \alpha)\%$ ;
- We choose the number of iterations of the method,  $\text{itermax}$ ; we fix two values,  $N_x, N_y$  and the interval  $[y_{min}, y_{max}]$  in which we want to display the density; then we create a grid on  $[0, 1] \times [y_{min}, y_{max}]$ , dividing the first interval in  $N_x$  parts, the second in  $N_y$  ( $y_{min} = -5, y_{max} = 5, N_x = N_y = 50$ ); we define the array  $H$  in three dimensions,  $N_x \times N_y \times N$ , that will contain the following information:

$$H(i, j, t) = \frac{\#\{\text{processes s.t. at time } t \text{ are in the cell grid } (i-1, i) \times (j-1, j)\}}{\text{itermax}};$$

- For each iteration, we generate a Brownian motion on the  $N$  time points; then we generate a homogeneous Poisson process with intensity  $\lambda_{max} \geq \max_x \lambda(x)$  on  $[0, T]$ ; let  $\{T_1, \dots, T_k\}$  be the jump times;
- We simulate, with Euler-Maruyama method, the stochastic process without jumps, until the nearest time  $T_i$ ;
- Following the definition of the jump process and the intuitive interpretation presented before, we decide (acceptance-rejection) if the jump of the homogeneous process should be counted or not for the non-homogeneous one: if not, we continue Euler-Maruyama until the next jump; if so, we modify the population fractions in appropriate manner;
- We update the array  $H$ .

**Numerical methods for the Fokker-Planck equation.** We implement a numerical method for the equations (3.5), that in this case has the form:

$$\begin{aligned} \partial_t \varrho - \frac{1}{2} \sigma^2 \varrho_{yy} + (\varrho a)_x + (\varrho v)_y &= \mathcal{J}_1(\varrho, x, y) + \mathcal{J}_2(\varrho, x, y), \\ \mathcal{J}_1(\varrho, x, y) &= \lambda_{12} \left[ \frac{1}{1 - \gamma_{12}} (f_1 \varrho) \left( \frac{x}{1 - \gamma_{12}}, y, t \right) 1_{[0, 1 - \gamma_{12}]}(x) - (f_1 \varrho)(x, y, t) \right], \\ \mathcal{J}_2(\varrho, x, y) &= \lambda_{21} \left[ \frac{1}{1 - \gamma_{21}} (f_2 \varrho) \left( \frac{x - \gamma_{21}}{1 - \gamma_{21}}, y, t \right) 1_{[\gamma_{21}, 1]}(x) - (f_2 \varrho)(x, y, t) \right]. \end{aligned}$$

We obtain a finite differences scheme by discretizing with central difference the second order diffusive term and the transport term in  $y$ , and with a upwind method, that varies depending on the sign of the function  $a$ , for the transport term in  $x$ . The time is discretized using an explicit method. We denote with  $\Delta x$  and  $\Delta y$  the space steps, with  $\Delta t$  the time step, with  $x_i, y_j$  the grid points and  $t_n$  the discrete times. Without considering the integral term (related to jumps) the method is conservative, and has the following form:

$$\begin{aligned} \frac{\varrho_{i,j}^{n+1} - \varrho_{i,j}^n}{\Delta t} &= \frac{\sigma^2}{2(\Delta y)^2} (\varrho_{i,j+1}^n - 2\varrho_{i,j}^n + \varrho_{i,j-1}^n) \\ &- \frac{1}{2\Delta y} \left( (v\varrho)_{i,j+1}^n - (v\varrho)_{i,j-1}^n \right) \\ &- \frac{1}{2\Delta x} \left[ (a\varrho)_{i+1,j}^n - (a\varrho)_{i-1,j}^n - \left( \left| (a\varrho)_{i+1,j}^n \right| - 2 \left| (a\varrho)_{i,j}^n \right| + \left| (a\varrho)_{i-1,j}^n \right| \right) \right], \end{aligned}$$

where  $\varrho_{i,j}^n = \varrho(x_i, y_j, t_n)$ .

Regarding the non-local jump terms  $\mathcal{J}_1, \mathcal{J}_2$  the functions  $f_1, f_2$  are well defined

on non-grid points, but we have to approximate the value of  $\varrho^n$  in  $x_i/(1-\gamma_{12})$ , so we follow [3], using linear interpolation between the grid points  $x_{\hat{i}}$  and  $x_{\hat{i}+1}$ , where  $\hat{i} = \min\{j : x_j \leq x_i/(1-\gamma)\}$ :

$$\varrho^n \left( \frac{x_i}{1-\gamma_{12}} \right) = \frac{(\varrho_{\hat{i}+1}^n - \varrho_{\hat{i}}^n)}{\Delta x} \left( \frac{x_i}{1-\gamma_{12}} - x_{\hat{i}} \right) + \varrho_{\hat{i}}^n.$$

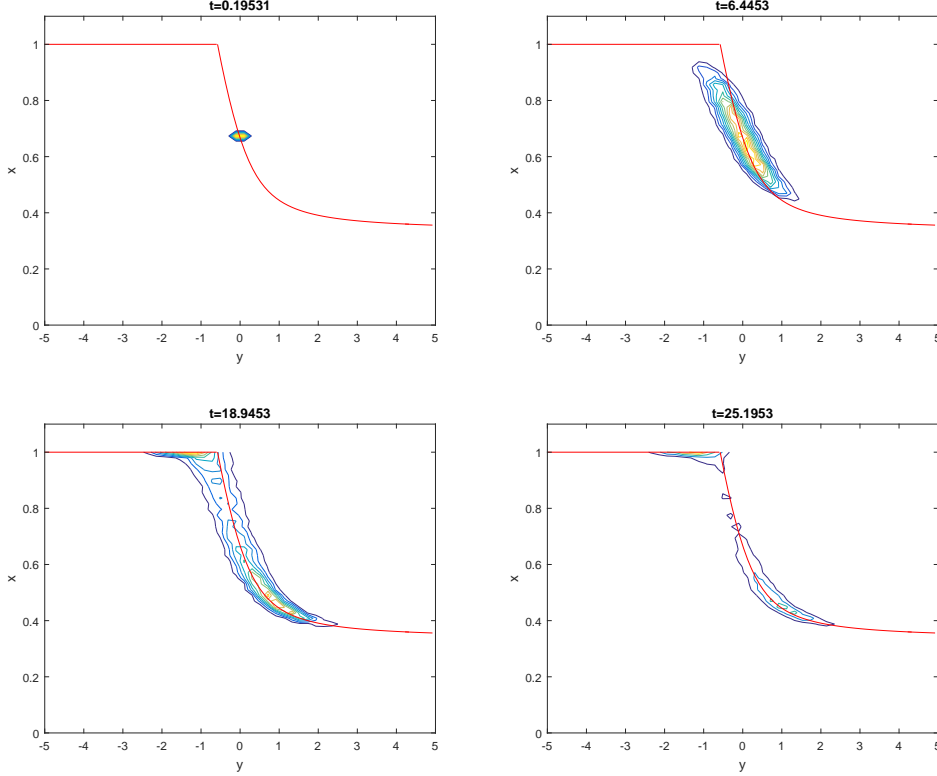


FIGURE 1. Replicator Dynamics perturbed by random motion, simulated by  $10^5$  iterations of the Monte Carlo method. The population moves randomly in space, subject to the selection of a changing environment. The red line is the function  $\bar{x}(y)$ , fraction of hawks at the equilibrium for the standard Replicator Dynamics starting at  $y$ . The deterministic speed is zero,  $v = 0$ , jumps are absent, the coefficient of the Brownian motion is  $\sigma = 0.2$ . Other parameters:  $T = 30$ ,  $N = 2^8$ ,  $y_{min} = -5$ ,  $y_{max} = 5$ ,  $N_x = N_y = 50$ .

**4.1. Replicator Dynamics perturbed by random motion.** In this Monte Carlo simulation the population just moves randomly in space, subject to the selection of a changing environment. To do this, we imagine that jumps are absent, i.e.  $K = 0$  in (2.5), and that (2.6) gives an homogeneous Brownian motion for the variable  $y$ , i.e. the drift  $v$  is zero and the diffusion coefficient is  $\sigma = 0.2$ . If the Brownian motion were absent, the character  $x_t$  of a population starting at  $(x_0, y_0)$  would tend as  $t \rightarrow +\infty$  towards the attractor  $\bar{x}(y_0)$  introduced in (4.1) and depicted by a red line in Figure 1. But now  $y_t$  follows (2.6), which reduces to an

homogeneous Brownian motion, so that its marginal density is a Gaussian function with expected value  $y_0$ , kernel of the heat equation,

$$\varrho_{(y)}(y, t) = \frac{1}{\sqrt{2\pi\sigma^2 t}} \exp\left\{-\frac{(y - y_0)^2}{2\sigma^2 t}\right\}.$$

Meanwhile the SDE (2.5) reduces to the standard replicator dynamics and moves  $x_t$  towards the asymptotically stable equilibrium  $\bar{x}(y_t)$ , which depends by  $y_t$  and therefore by time. We can see how, with  $t \gg 0$ , the density is approximately

$$\varrho(x, y, t) \sim \bar{x}(y)\varrho_{(y)}(y, t)$$

with an expected global frequency of hawks given by  $\int_{\mathbb{R}} \bar{x}(y)\varrho_{(y)}(y, t)dy$ , see Figure 1.

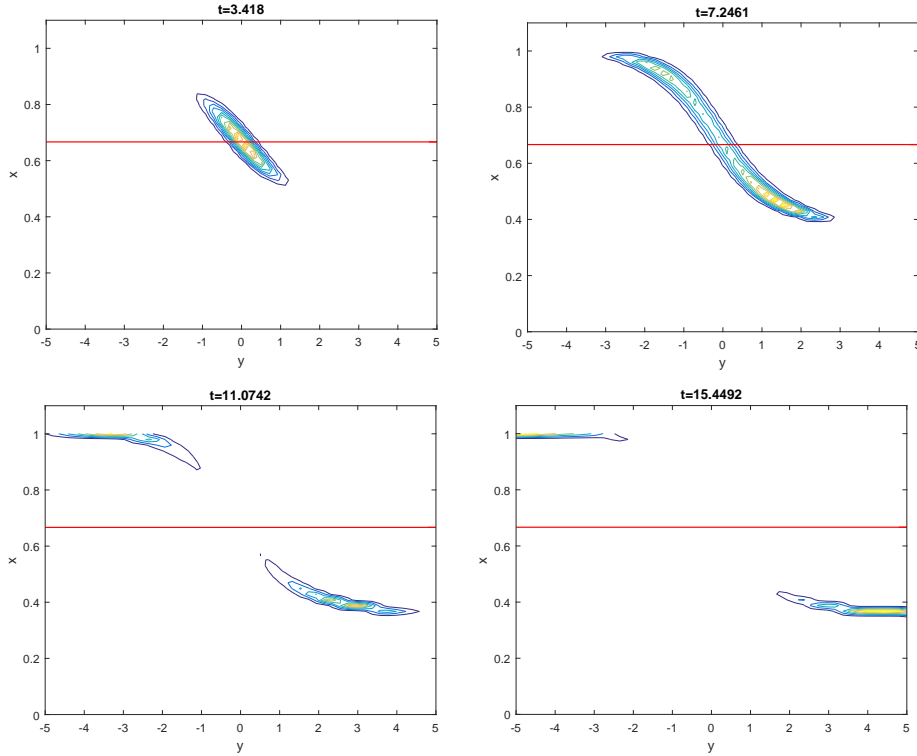


FIGURE 2. Replicator Dynamics plus Brownian motion with drift, simulated by  $10^5$  iterations of the Monte Carlo method. The vector  $x$  evolves according to the game Hawks vs Doves with  $G$  function of  $y$ . The red line represents the expected value of hawks for  $t \rightarrow \infty$ , that is equal to the initial value of hawks. The deterministic speed is chosen as  $v = 1 - \frac{3}{2}x$ , jumps are absent, the coefficient of the Brownian motion is  $\sigma = 0.2$ . Other parameters:  $T = 30$ ,  $N = 2^8$ ,  $y_{min} = -5$ ,  $y_{max} = 5$ ,  $N_x = N_y = 50$ .

**4.2. Replicator Dynamics plus Brownian motion with drift.** We assume again that the character  $x_t$  follows the replicator dynamics with no jumps, i.e. we take  $K = 0$  in (2.5). But now we take a nonnull drift in the environmental dynamics (2.6), depending on the character of the population:

$$(4.2) \quad v(x) = 1 - 3x/2.$$

The drift is decreasing as a function of  $x$  (the proportion of hawks): it has its maximum,  $v = 1$ , at  $x = 0$  (high concentration of Doves) and its minimum,  $v = -1/2$ , in  $x = 1$  (high concentration of Hawks). Moreover the drift is null at  $x = 2/3$ , which is taken as the initial state. As noticed at the beginning of this section, if the Brownian component were absent the initial state  $(x_0, y_0) = (2/3, 0)$  would be an equilibrium and the resulting dynamics would be trivial. In the simulation depicted in Figure 2 the dynamics is not trivial, and we can identify two different behaviors of the process, because of the presence of the Brownian component with  $\sigma = 0.1$ . The support of the probability density function splits in two different regions, and it means that the population moves either towards negative values of  $y$ , or towards positive values, respectively with probability  $p_1$  and  $p_2$ . In the first case, the proportion of hawks at the equilibrium increases (as a function of  $-y$ ), until the process oversteps the value  $y = -\sqrt{3}/3$ , after which  $x = 1$  is the only equilibrium (all hawks); we can see the gradual extinction of each dove. In the other case, the cost of the fight increases with time, the density tends to concentrate toward the coexistence of both strategies, with greater concentration of doves ( $x = 1/3$ ). However, the expected value of the proportion of hawks for  $t \rightarrow +\infty$  (highlighted by a red line in Figure 2) is the same as the initial one,  $2/3$ . In fact, as we can see numerically, each of the two regions have mass  $1/2$ , so  $p_1 = p_2$  and

$$\lim_{t \rightarrow +\infty} \mathbb{E}[x_t] = 1 \cdot p_1 + \frac{1}{3} \cdot p_2 = \frac{2}{3}.$$

**4.3. Point-type mutations plus Brownian motion with drift.** We take now a point-type mutation process for  $x_t$ , with  $\lambda_{12} = \lambda_{21} = 0.2$ ;  $\gamma_{12} = \gamma_{21} = 0.1$  in (2.4). Concerning motion, we take here  $\sigma = 0.2$  and  $v$  given by (4.2), so that the position  $y_t$  changes deterministically with speed  $v$  and stochastically because of the Brownian motion. Let us remark that at each time that a mutation occurs, the probability that hawks (respectively doves) suffer a mutation only depends by fitness. At the initial state  $(2/3, 0)$ , the probability that hawks are the first to suffer mutations is  $1/2$ , just like doves. In this sense mutations produce random perturbations similar to the Brownian motion introduced in the previous example 4.2. The simulations presented in Figure 3 show two different regions also in this case. It is remarkable that the fact that at the equilibrium hawks are more abundant than doves brings as a consequence that mutations favor doves, so that the region of the probability density moving rightwards will have higher mass (the ratio between right region and left region is 2:1 ca.), i.e. the coexistence of both strategies occurs with higher probability ( $p_1 < p_2$ ), unlike example 4.2. The expected value of the proportion of hawks for  $t \rightarrow +\infty$  (highlighted by a blue line in Figure 3) is lower than the initial one:

$$\lim_{t \rightarrow +\infty} \mathbb{E}[x_t] = 1 \cdot p_1 + \frac{1}{3} \cdot p_2 \approx \frac{5}{9}.$$

We therefore see that including the physical space can favour the persistence of the low-fitness strategy, when mutations can happen in both directions.

**4.4. Monte Carlo and Finite Differences simulations.** Here we compare the Monte Carlo algorithm, showed in the previous cases, and the finite differences approximation, presented at the beginning of Section 4. Let us take as study case the same problem as above, in Subection 4.3. After the flattening of the initial datum (Dirac delta), which is slightly faster in the I.P.D.E. approximation, the two simulations run parallel (see Figure 4) creating the two regions with different masses, moving towards opposite directions. In the I.P.D.E. case, as in the Monte

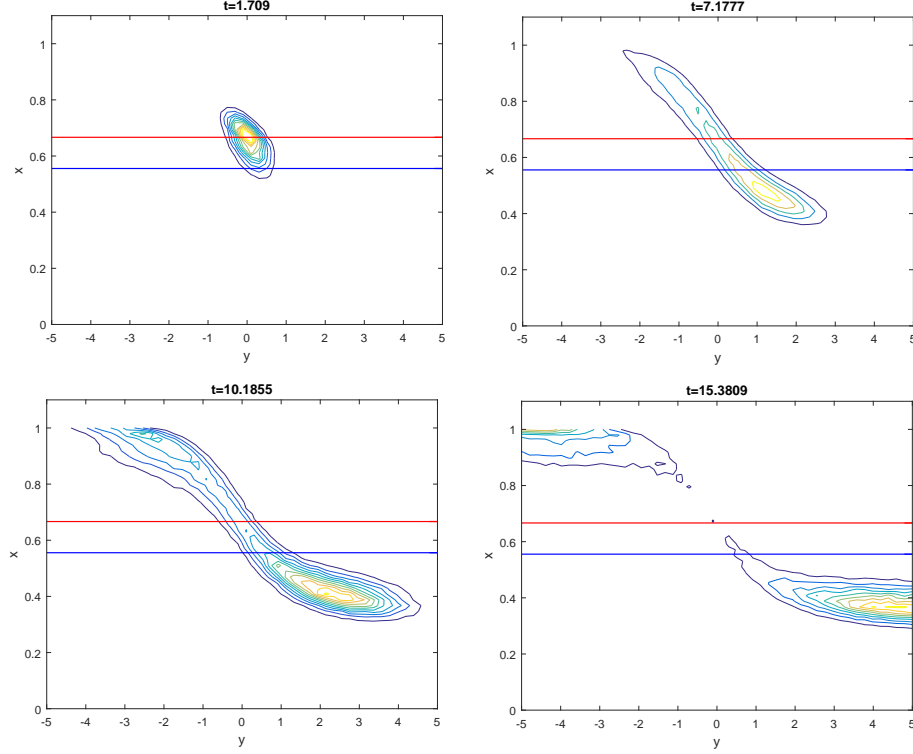


FIGURE 3. Point-type mutations plus deterministic and Brownian motion, simulated by  $10^5$  iterations. The vector  $x$  evolves according to the game Hawks vs Doves with  $G$  function of  $y$ . The red line, as in Figure 2, represents the initial value of hawks and the expected value of hawks for  $t \rightarrow \infty$  in absence of mutations. The blue line is the same expected value for  $t \rightarrow \infty$  in presence of mutations. The deterministic speed is chosen as  $v = 1 - \frac{3}{2}x$ , Brownian motion has  $\sigma = 0.2$ , the parameters of the jump process are  $\lambda_{12} = \lambda_{21} = 0.2$ ,  $\gamma_{12} = \gamma_{21} = 0.1$ , that is one tenth of the population mutate each jump and we have fair jumps. Other parameters:  $T = 30$ ,  $N = 2^8$ ,  $\alpha = 0.1$ ,  $y_{min} = -5$ ,  $y_{max} = 5$ ,  $N_x = N_y = 50$ .

Carlo one, the ratio between the right region and left region masses is 2:1 ca. Even if we choose a thick grid for the I.P.D.E. algorithm (500 cells of size  $\Delta x$ , 1000 cells of size  $\Delta y$ , 6000 time steps), its execution is about 5 times faster than the Monte Carlo simulation with  $10^4$  iterations. However, despite the speed, this algorithm, approximating the non-local jump term with linear interpolation, do not preserve the mass for the whole simulation; in a simulation, the mass at time  $T = 15$  is 90% ca. of the initial one. Then, the choice of a singular initial point as a Dirac delta causes numerical dissipation in the transport terms, especially noticeable in simulations in which the Brownian motion is absent. For these reasons, Monte Carlo simulations have been privileged in sections 4.1, 4.2 and 4.3.

## 5. CONCLUSIONS AND FURTHER DEVELOPMENTS

We presented the mathematical framework for a stochastic model in evolutionary dynamics which describes the dynamics of population frequencies according to



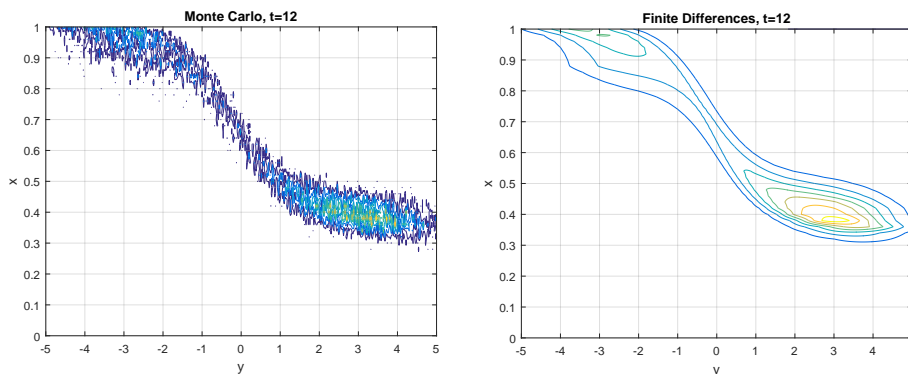


FIGURE 4. Replicator Dynamics plus Brownian motion, with drift and jumps, with different algorithms, both at time  $t = 12$ . On the left the graphic for Monte Carlo method, simulated by  $10^4$  iterations (the grid is dense, to show the single runs). On the right the scheme for the partial difference equation, with  $\Delta x = \Delta y = 0.02$ .

- selection, which is ruled by game theory,
- mutation, depicted by a multi-dimensional pure point process,
- environment, seen as another stochastic variable that modifies the game matrix and therefore the selection rules.

As the stochastic dynamics for the environment depends by the population frequencies, this model can in principle take into account retro-effects of the population on the environment itself.

We have also proposed an alternative formulation of the same process (with the same probability distribution) which allows to describe mutations by means of only one point process, and we have introduced a modified Fokker-Plank equation that relates the probability density to a degenerate-elliptic integro-differential equation and settled it in the framework of viscosity solutions. The Fokker-Plank formulation is far from standard because the same nature of the stochastic process (anisotropic diffusion plus a pure jump process) causes two obstructions: (i) the probability density is generally non-smooth, so that standard Theorems do not apply, (ii) the -formally derived- Fokker-Plank equation contains a non-local term and therefore has to be suitably extended from effective state space (a simplex) to the whole space.

We then have performed simulations by Monte Carlo methods, using the alternative formulation of the process, for a classical Hawks and Doves game. We compared the results with a finite difference method for the Fokker Planck equation, showing that they represent the same phenomenon.

Starting from this model it may be also possible to describe the evolution of a population composed by subpopulations that live in distinct environmental patches, initially distributed according to a density  $\varrho_0(x, y)$ , evolving according to different selection pressures. From this viewpoint it is expected that, when two subpopulations get at the same location, they interact by means of the selection rule. In addition migration of some individuals from one subpopulation to another may happen. To describe such phenomena it is needed to add to the frequencies dynamics two terms which give account of the melting of different subpopulations, and this in turn requests to follow not only the frequencies of various species, but also

their abundance. This aspect certainly deserves a further investigation, and shall be the subject of a future work.

#### REFERENCES

- [1] A.L. Amadori. (2007) Obstacle problem for nonlinear integro-differential equations arising in option pricing, *Ricerche di Matematica*, 56 (1): 1-17. DOI: 10.1007/s11587-007-0001-x
- [2] A.L. Amadori, A. Calzolari, R. Natalini, and B. Torti. (2015) Rare mutations in evolutionary dynamics. *Journal of Differential Equations*, 259 (11): 6191-6214. DOI: 10.1016/j.jde.2015.07.021
- [3] A.L. Amadori, M. Briani, and R. Natalini. (2016) A non-local rare mutations model for quasispecies and prisoner's dilemma: Numerical assessment of qualitative behaviour *European Journal of Applied Mathematics*, 27 (1): 87-110. DOI: 10.1017/S0956792515000352
- [4] K. B. Athreya, W. Kliemann, and G. Koch. (1987) *On sequential construction of solutions of stochastic differential equations with jump terms*. Systems Control Lett..
- [5] N. Champagnat, R. Ferrière, S. Méléard. (2006) Unifying evolutionary dynamics: From individual stochastic processes to macroscopic models *Theoretical Population Biology*, 69 (3): 297-321. DOI: 10.1016/j.tpb.2005.10.004
- [6] D. J. Daley and D. Vere-Jones. (2008) *An Introduction to the Theory of Point Processes*. Springer
- [7] J. Hofbauer and K. Sigmund. (1998) *Evolutionary games and population dynamics*. Cambridge: Cambridge University Press.
- [8] N. Ikeda and S. Watanabe. (1981) *Stochastic Differential Equations and Diffusion Processes*. North-Holland, Amsterdam.
- [9] Ken-Iti Sato. (1999) *Levy Processes and Infinitely Divisible Distributions*. Cambridge: Cambridge University Press.
- [10] T. Kuusi, G. Mingione, Y. Sire. (2015) Nonlocal Equations with Measure Data. *Communications in Mathematical Physics*, 337 (3): 1317-1368. DOI: 10.1007/s00220-015-2356-2
- [11] J. Maynard Smith and G. R. Price. (1973) The logic of animal conflict. *Nature*, 246:15-18.
- [12] M. A. Nowak. (2006) *Evolutionary dynamics. Exploring the equations of life*. Cambridge, MA: The Belknap Press of Harvard University Press.
- [13] D. Nualart. (2006) *The Malliavin Calculus and Related Topics* New York, Springer Science+Business Media.
- [14] G. A. Pavliotis. (2014) *Stochastic Processes and Applications*. New York, Springer Science+Business Media.
- [15] B. Piccoli, F. Rossi. (2014) Generalized Wasserstein Distance and its Application to Transport Equations with Source *Archive for Rational Mechanics and Analysis*, 211 (1): 335-358. DOI: 10.1007/s00205-013-0669-x
- [16] P. Stadler and P. Schuster. (1992) Mutation in autocatalytic reaction networks. *Journal of mathematical biology*, 30(6):597-632.

<sup>1</sup>DIPARTIMENTO DI SCIENZE APPLICATE, UNIVERSITÀ DI NAPOLI "PARTHENOPE"

<sup>2</sup> ISTITUTO PER LE APPLICAZIONI DEL CALCOLO "M. PICONE", CONSIGLIO NAZIONALE DELLE RICERCHE

<sup>3</sup> DIPARTIMENTO DI MATEMATICA, UNIVERSITÀ DI ROMA "LA SAPIENZA"