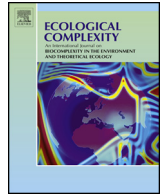




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Original Research Article

A rare mutation model in a spatial heterogeneous environment

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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–Planck 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.

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1. Introduction

Evolutionary dynamics describes biological systems subject to Darwinian Evolution by taking into account the main mechanisms and phenomena of Evolution itself. In Maynard Smith and Price (1973), 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

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

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

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

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 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 Stadler and Schuster (1992) with the “replicator-mutator” equation:

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

here the coefficient q_{ik} express the proportion of offspring of k -type from a progenitor i , which shows up at any procreation. An

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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 Champagnat et al. (2006) showing that one single stochastic microscopic process can generate different macroscopic models of adaptive evolution. More recently, in Amadori et al. (2015), 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 Amadori et al. (2015) 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 Amadori et al. (2016), 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 Amadori et al. (2015) 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 Amadori et al. (2015). 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) and (2.6). In Section 3 we derive a Fokker–Planck integro-differential equation for (2.5) and (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) Hofbauer and Sigmund (1998). 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) and (2.6), and by a finite difference scheme based on the Fokker–Planck 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

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

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}^+ , ν a σ -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 Amadori et al. (2015), 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

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

The mutation from type i to type j is driven by a non-homogeneous point process N_t^{ij} with stochastic intensity $\lambda_{ijf_i}(X_t)$. 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 (λ_{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

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

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

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

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