

# DISCRETE STOCHASTIC PROCESSES, REPLICATOR AND FOKKER-PLANCK EQUATIONS OF COEVOLUTIONARY DYNAMICS IN FINITE AND INFINITE POPULATIONS

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**Abstract.** Finite-size fluctuations in coevolutionary dynamics arise in models of biological as well as of social and economic systems. This brief tutorial review surveys a systematic approach starting from a stochastic process discrete both in time and state. The limit  $N \rightarrow \infty$  of an infinite population can be considered explicitly, generally leading to a replicator-type equation in zero order, and to a Fokker-Planck-type equation in first order in  $1/\sqrt{N}$ . Consequences and relations to some previous approaches are outlined.

**1. Introduction.** Evolution is a biological process ubiquitously taking place, acting on several temporal, spatial, and taxonomic scales. Biological organisms are coded by their genetic sequence, and their ability to survive, following Darwin, is largely determined by their genes. However, even the relationship between genotype, phenotype and a fitness (e.g., defined by the reproduction rate) by no means is simple, as it maps an enormously high-dimensional space (the state space of all possible genomes) to a much lower-dimensional phenotype space, and finally to a one-dimensional space of fitness values.

The extinction of species, as observed in the fossil record, follows a complicated behaviour [Eld72] including intermittency-like long periods of stasis, the so-called “punctuated equilibria”. It is still at debate whether external or cosmic influences account for these, or whether a purely dynamic mechanism of the evolutionary and ecological dynamics can produce this stylized fact. In this direction, the Bak-Sneppen model [Bak93] is a pioneering minimal model for the extinction of species, which however is difficult to relate to the biological scenario. On the one hand, it provides an intermediate modeling level, where biological observations can be explained to some extent, but on the other hand,

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a mathematical treatment is still possible [Ban05, Pis97]. On an individual-based level, the Tangled Nature model [Jen04] approaches closer to biology. While the dynamics at large will deserve some further decades of research, simplified situations of coevolutionary dynamics, restricting to a finite number of species can be studied by formal models of evolutionary processes, and can be solved analytically in many cases to allow for an exemplary insight. In this brief tutorial review, coevolutionary dynamics in finite populations is formulated within the framework of evolutionary game theory, providing a convenient common mathematical framework for biological, social and economical evolutionary processes of strategies, or genetic types.

**1.1. Game theory: The strategy of conflict.** Game theory was brought into play by von Neumann and Morgenstern [Neu53] as a minimal model to explain and predict the behaviour of humans in strategic situations, military or economic, assuming fully rational behaviour. In game theory, more specifically in two-player normal form games, agents  $1 \dots N$  “play” a strategy, out of a finite set of possible pure strategies. They interact with a partner also playing one of those strategies, and both receive a (real valued) payoff according to a so-called payoff matrix. This is best illustrated with an example. The most paradigmatic conflict situation described in game theory is the Prisoner’s Dilemma. It is defined by the payoff matrix

$$(1) \quad \pi_{ij} = \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix}.$$

This is to be read as follows. The game is defined between two players, who can adopt two possible strategies: to cooperate (C) or to defect (D). The players act in parallel and are not informed about the opponent’s move. Each player P (row player) playing strategy  $i$  then receives the payoff  $\pi_{ij}$  when meeting a player using strategy  $j$  (column player, O) as opponent. Obviously, here the conflict situation is symmetric, therefore the payoff matrix of the opponent’s payoffs is given by the transpose  $\pi_{ij}^T$ . Often both payoff matrices are combined to

$$(2) \quad (\pi_{ij}^P, \pi_{ij}^O) = \begin{pmatrix} 3, 3 & 0, 5 \\ 5, 0 & 1, 1 \end{pmatrix}.$$

In symmetric conflicts, thereby only redundant information is added. In asymmetric conflicts, for obvious reasons often called *bimatrix games*, the opponent’s payoffs, in general, can be different. We will analyze such cases in Section 6.

In all cases above, the players play their respective strategy with probability one, i.e., they play pure strategies. A straightforward generalization is that players — in a random and uncorrelated manner — can use *mixed strategies*, or *strategy profiles*  $s_n$ , i.e., possess a strategy vector (with components  $(s_n)_i$  summing up to one, thus are elements of a simplex  $S_n$ ), and gain payoffs which are the corresponding linear combination

$$(3) \quad u_n(s_n, s_m) = \sum_{ij} (s_n)_i \pi_{ij} (s_m)_j$$

for playing against one opponent (profile)  $s_n$ , and

$$(4) \quad u_n(s_n, \{s_m\}) = \sum_{ijm} (s_n)_i \pi_{ij} (s_m)_j$$

against a set of opponents indexed by  $m$ . Now, can mixed strategies exist that are successful against all hypothetical sets of opponents? This brings us to the central concept of a Nash equilibrium [Nas51]: A Nash equilibrium is a mixed strategy, in which no single agent can improve its payoff by solely changing its own strategy.

**1.2. Nash equilibria.** A *strict Nash equilibrium* (resp., *Nash equilibrium*) is defined as a strategy profile  $s^* = (s_1^*, \dots, s_N^*)$  for which each agent's strategy  $s_n$  is a best (resp., best or equal) response to the strategies of the other players  $s_{-n}^*$ , i.e.

$$(5) \quad \forall_n \forall_{s \in S_n, s \neq s_n^*} \quad u_n(s_n^*, s_{-n}^*) \geq u_n(s, s_{-n}^*)$$

where  $>$  instead of  $\geq$  must hold for a strict Nash equilibrium.

Hereby  $s_{-n}^* := (s_1, \dots, s_{n-1}, s_{n+1}, \dots, s_N)$  is called a strategy profile of the co-players (formally a set of  $N - 1$  profiles, usually it is understood that playing against all co-players linearly sums the payoffs received playing with each of them; so one can define the co-profile  $(s_{-n}^*)_k := (N - 1)^{-1} \sum_{i \neq n} (s_i)_k$  as a linearly averaged profile of the co-players; or define  $u_n(\cdot, s_{-n}^*)$  as the sum of payoffs against the profile of each co-player).

Nash's theorem [Nas51] ensures that a normal-form game (as defined above) for a finite number of strategies and a finite number of players always possesses a Nash equilibrium. However, it can be degenerate or a mixed strategy (*mixed Nash equilibrium*). In the above Prisoner's Dilemma,  $((1, 0), (1, 0))$ , i.e. both players playing always "defect", is a Nash equilibrium; hence two memory-less agents playing it for one round have no incentive to cooperate. Conversely, the Stag-Hunt game  $\pi_{ij} = \begin{pmatrix} 5 & 0 \\ 3 & 3 \end{pmatrix}$  has two symmetric Nash equi-

libria,  $((1, 0), (1, 0))$  and  $((0, 1), (0, 1))$ , the Hawk-Dove game  $\pi_{ij} = \begin{pmatrix} (V - C)/2 & V \\ 0 & V/2 \end{pmatrix}$  with  $C > V$  has two nonsymmetric Nash equilibria,  $((1, 0), (0, 1))$  and  $((0, 1), (1, 0))$ , the latter is an example of a population where both strategies are present.

**1.3. Evolutionary game theory and evolutionarily stable strategies.** Decades after game theory was invented, Maynard Smith and Price [May73] were the first to utilize its approaches to the understanding of biological conflict situations among whose the emergence of cooperation [Axe84] among animals and humans still is a continuously active field. In the dynamical picture of evolutionary game theory, the concept of the Nash equilibrium has its counterpart in the *evolutionarily stable strategies* (ESS), which are defined as a population in which a single mutant (changing to any of the possible strategies or genotypes) cannot invade the population. In infinite populations, traditionally described within the framework of replicator equations [Tay78, Hof79, Zee80], ESS appear as stable fixed points (see [Hof98] for a systematic treatment). In finite populations, however, this concept has to be refined [Now04, Tay04, Nei04, Wil04, Tra06b]. For a more detailed introduction into the field of evolutionary game theory, and its recent development, see the classical textbooks [Hof84, Hof98] and recent reviews [Sza07, Mie07].

## 2. Microscopic interactions: Game theory based on particle collision models.

The description of social agent behaviour as interaction, or collision, of particles has been studied by Helbing establishing a quite general framework [Hel92a, Hel92b, Hel96],

which at that time had not further been taken up within evolutionary game theory or evolutionary dynamics.

One main limiting assumption of the mean-field type description discussed in the next sections is that any spatial organization can be neglected in a first order approximation. This approximation, as well as neglecting age structure and time delay [Alb04], however is not warranted in general.

**2.1. Patchy ecosystems.** To describe the full dynamics of ecological and evolutionary processes, it can be necessary to split up the population into parts, or patches, and to investigate an intermediate level of subdivided populations [Che03] or metapopulation dynamics [Hår02]. In general, a rich variety of dynamical scenarios can emerge; thus simplified models on lattices and graphs have been investigated widely.

**2.2. Spatial models.** Life typically is organized, to a very rough approximation, as a covering of the surface of earth, in competition for sunlight, solid ground, or hunting territory. So it is natural to investigate evolutionary dynamics of individuals located in a two-dimensional space [Now92], where collective phenomena can emerge [Her94]. Another classical study by Lindgren and Nordahl [Lin94] investigated the spatial Prisoner's Dilemma game with strategies of different memory lengths. Spatial structure has been identified as one possible mechanism to promote cooperation [Now92]. In general, spatial game theory is capable of rich dynamical behaviour [Sza99, Szo04, Sza05, Tra04], as coarsening, segregation, and spiral waves. Likewise, models for opinion dynamics have been studied, as the Sznajd model [Szn00].

**2.3. Evolutionary dynamics on graphs.** The systematic understanding of evolutionary dynamics on graphs is a still developing field. An early investigation of coevolutionary dynamics (i.e., including frequency-dependence) on graphs has been given by Ebel and Bornholdt [Ebe02], investigating the iterated Prisoner's Dilemma on networks. On the small-world architecture, Szabó et al. [Sza04] investigated the Rock-Paper-Scissors game dynamics. In [Lie05, Oht06], fixation properties of evolutionary dynamics on graphs are studied, and special subgraphs have been identified to enhance or suppress fixation. For two strategies and non frequency-dependent fitness, Antal, Redner and Sood [Ant06] have provided exact results for fixation for the case of degree-uncorrelated graphs. Despite this significant progress [Sza07], a general theory of coevolutionary dynamics on graphs remains a formidable challenge.

**2.4. Unstructured population dynamics: Meanfield approach, or Pólya urn models.** The approximation of an unstructured population implies that individuals are undistinguishable (apart from their strategies or genotype), and individuals are chosen randomly from the population, for death, reproduction, and competition. Hence, the population can be viewed as a Pólya urn from which individuals are drawn for the stochastic process. All evolutionary processes discussed for finite populations in the remainder belong to this class of processes.

**3. Microscopic evolutionary processes.** Evolutionary processes have been widely considered in population genetics. For processes in discrete time, an important systematic

distinction has to be made between synchronous or parallel [Baa97] update processes, as the Fisher-Wright process, and processes with overlapping generations, where one individual is replaced in each evolutionary step (see Fig. 1).

**3.1. Fisher-Wright process.** The process defined by Fisher [Fis30] and Wright [Wri31] in its original form is not frequency-dependent; the fitness of the individuals does not depend on the state of the population (given by the number of individuals in each of the strategies). The Fisher-Wright process is defined as follows. In each time step, all individuals reproduce with probabilities proportional to their fitness, until the same population size  $N$  is reached. An important case is given by *neutral evolution*, where all individuals have identical fitness. Hence, the discrete stochastic process that describes the time evolution resembles a random genetic drift, and no Darwinian principle is incorporated.

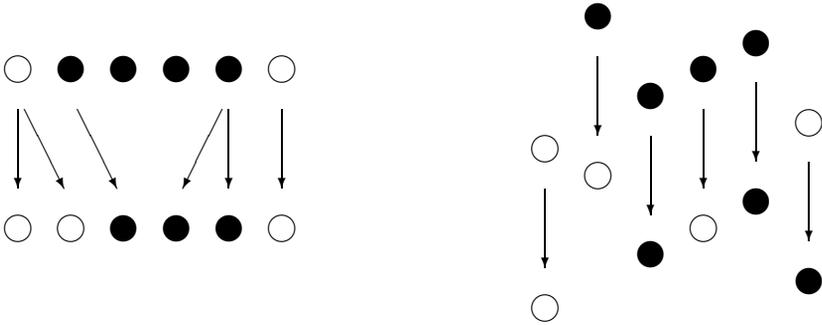


Fig. 1. Discrete stochastic evolution processes: Fisher-Wright process (left) as a typical synchronous update process, and an overlapping generations process (right). In the Moran process and Local update the lifetime of the individuals however is nonidentical, due to the stochastic asynchronous update. For the transition probabilities see text. The open and closed bullets can represent two different strategies (in a social system), or two different alleles at a specific genetic locus (in biology). The generalization to higher numbers of strategies or genetic types is straightforward.

Of course the Fisher-Wright process can be straightforwardly generalized to the case where the fitness of strategies depends on payoff gains obtained from game-theoretic interactions with other individuals. The finite population case has been considered recently by Taylor and Nowak [Tay06]. Here the transition matrix of the Markov process is by no means sparse; apart from the absorbing boundaries all matrix elements can be nonzero.

**3.2. Discrete stochastic processes for overlapping generations.** The evolutionary processes of Moran or Local update type provide us with a transition probability  $T^\pm$  that the number of individuals  $i$  (being in the first strategy) increases or decreases by one, respectively.

For definiteness, we consider explicitly the Moran evolution dynamics in arbitrary  $2 \times 2$  games [Cla05]. Given a finite population of  $N$  agents (two types/strategies A and B) interacting via in a game with the payoff matrix

$$(6) \quad P = \begin{pmatrix} a & b \\ c & d \end{pmatrix}.$$

In the frequency-dependent Moran process, every agent interacts with a representative sample of the population, yielding the payoffs of  $A$  and  $B$  individuals as

$$(7) \quad \pi^A(i) = 1 - w + w \frac{a(i-1) + b(N-i)}{N-1},$$

$$(8) \quad \pi^B(i) = 1 - w + w \frac{c i + d(N-1-i)}{N-1},$$

$i$  is the number of  $A$  individuals, and  $1 - w$  is a background fitness.

**3.3. Moran process.** In its original form, also the Moran process [Mor62] is not frequency dependent. In this birth-death process, in each time step an individual is selected for reproduction, and subsequently a randomly selected individual dies. Here it is ensured that the total number of individuals  $N$  remains constant.

For two strategies, the Moran process therefore is a one-dimensional Markov process with a finite number of states from  $i = 0, \dots, N$ . Taking up the Moran approach, Nowak, Taylor, Fudenberg and Sasaki [Now04, Tay04] investigated a frequency-dependent Moran process, defined as follows: In the frequency-dependent Moran process, selection for reproduction is proportional to the payoff compared to the average payoff,  $\pi^A(i)/\langle\pi\rangle$ . The probability per time step that a copy of an  $A$  agent is newborn then is  $p^+i/N$  (with  $p^+$  as given in Table 1). It replaces a randomly chosen individual. Here, the fitness is evaluated after each individual took interaction according to a payoff matrix with all individuals in the population.

**3.4. Local update and imitation processes.** An apparent limitation of the Moran process with respect to biological situations is that individuals in each update step have to compete with the whole population (or, in real systems with a representative sample) of the population.

A more realistic setting is given by local or pairwise competitive interactions, which can be called imitation dynamics [Hof00] (in the concept of social strategies) or local update. These processes can be defined in a slightly different manner. In a non-symmetric definition of the (linear) local update process [Tra05], one individual is selected for reproduction, and the other for death. Then the strategy of the reproducing individual is changed (or kept) with probabilities that depend linearly on the difference of the payoffs of the two interacting individuals. Here, as is usually assumed in evolutionary game theory, the payoffs are evaluated by playing (on a shorter time scale) with the whole population, so these payoff differences still are evaluated in a global process.

**3.5. Nonlinear response: Local Fermi process.** A variant [Blu93, Sza98, Hau05] of the Local update process arises naturally when the game interaction payoff is one of many additive contributions to the reproductive fitness. In the case where the external contributions are large, and consist of many degrees of freedom that act like an external heatbath, the payoffs of the individuals appear as argument of Boltzmann factors, where a parameter  $w$  can be introduced as for the other processes ( $w \rightarrow 0$  corresponds to weak selection), and here can be interpreted as a temperature. This pairwise comparison process has been studied in detail in [Tra06c, Tra07]. See Table 1 for the transition probabilities  $T^\pm$  of the Moran process, Local update, and Fermi process.

**Table 1.** Comparison of three microscopic update processes and their respective differential equations for  $x := i/N$  obtained in the deterministic limit of  $N \rightarrow \infty$  (see Sec. 5.2).

Moran process	Local update	Fermi process
$p^+ = \frac{1-w+w\pi_i^A}{1-w+w\langle\pi_i\rangle}$	$p^+ = \frac{1}{2} + \frac{w}{2} \frac{\pi_i^A - \pi_i^B}{\Delta\pi_{\max}}$	$p^+ = \frac{1}{1+e^{-w(\pi_i^A - \pi_i^B)}}$
$p^- = \frac{1-w+w\pi_i^B}{1-w+w\langle\pi_i\rangle}$	$p^- = \frac{1}{2} + \frac{w}{2} \frac{\pi_i^B - \pi_i^A}{\Delta\pi_{\max}}$	$p^- = \frac{1}{1+e^{-w(\pi_i^B - \pi_i^A)}}$
$0 \leq w \leq 1$	$0 \leq w \leq 1$	$0 \leq w \leq \infty$
Transition probabilities for increase/decrease of $i$ :		
$T^\pm = p^\pm \frac{i}{N} \frac{N-i}{N}$	$T^\pm = p^\pm \frac{i}{N} \frac{N-i}{N}$	$T^\pm = p^\pm \frac{i}{N} \frac{N-i}{N}$
In the $N \rightarrow \infty$ limit:		
$\dot{x} = \frac{wx(1-x)(\pi_x^A - \pi_x^B)}{1-w+w\langle\pi(x)\rangle}$	$\dot{x} = \frac{wx(1-x)(\pi_x^A - \pi_x^B)}{\Delta\pi_{\max}}$	$\dot{x} = x(1-x) \tanh\left(\frac{w}{2}(\pi_x^A - \pi_x^B)\right)$
<i>adjusted replicator eq.</i>	<i>ordinary replicator eq.</i>	<i>replicator eq. after [Tra06c]</i>

**4. Broadening of distributions in finite populations.** For the Moran process, the strategy distribution is generated only by the inherent stochasticity of the finite population. At the borders, for  $T_{0 \rightarrow 1}$  and  $T_{N \rightarrow N-1}$  we assume a small mutation rate  $\mu$  [Fud04]. While in the infinite population case the population density is peaked at the deterministic trajectory in the sense of a delta distribution, for a finite population it is broadened. Fortunately, the Moran process allows for an analytical treatment. The stationary distribution for an arbitrary payoff matrix can be expressed via Pochhammer symbols, rising factorials or gamma functions, for the general case of  $2 \times 2$  games including nonvanishing background fitness [Cla05]. For illustration, let us consider the special cases of neutral evolution, constant fitness, an ‘anticoordination game’ and the Prisoner’s dilemma,

$$P_n = \begin{pmatrix} a & a \\ a & a \end{pmatrix}, \quad P_c = \begin{pmatrix} a & a \\ c & c \end{pmatrix}, \quad P_{AC} = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}, \quad P_{PD} = \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix}.$$

*Internal (mixed) vs. external (pure) Nash equilibrium.* For frequency dependent fitness and  $w > 0$ , the game can have an internal Nash equilibrium or an equilibrium in one of the absorbing states. A simple example with an internal Nash equilibrium is the ‘anticoordination’ game with  $w = 1$ ,  $P = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$ . The transition matrix here is  $T_{i \rightarrow i+1} = \frac{N-i}{2N}$ ,  $T_{i \rightarrow i-1} = \frac{i}{2N}$ , describing a random walk with a drift towards the deterministic fixed point  $i = N/2$ . In equilibrium, we have  $P_i T_{i \rightarrow i+1} = P_{i+1} T_{i+1 \rightarrow i}$  for every  $i$ , thus

$$(9) \quad P_{i+1} = P_0 \prod_{j=0}^i \frac{N-j}{j+1} = P_0 \binom{N}{i+1}.$$

$P_i$  is a binomial distribution around the equilibrium of the replicator dynamics.

The *Prisoner's Dilemma* has a Nash equilibrium for mutual defection, i.e.  $i = 0$ . At the borders, for  $T_{0 \rightarrow 1}$  and  $T_{N \rightarrow N-1}$  we assume a small mutation rate  $\mu$  [Fud04]. As  $b = 0$ , also state  $i = 1$  is absorbing for  $w = 1$  (two cooperators are needed to promote cooperation). Thus a small mutation rate  $\mu$  has to be assumed also for  $T_{1 \rightarrow 2}$ . Alternatively one could assume  $w < 1$ .

The four cases are summarized in Table 2. For *neutral evolution* the decay is very slow. With *constant fitness*, the probability decays approximately exponentially. For the

**Table 2.** The four payoff matrix cases considered in Fig. 2 under the assumption of a small mutation rate (see text). Without the frequency-dependence introduced by a game, the cases of constant fitness and neutral evolution known from mathematical genetics are recovered; the distribution keeps localized (for low mutation rates, mutants stay rare). For the analytical expressions of the distributions see [Cla05]. The distributions follow approximately a stretched exponential with the fit exponents  $\gamma$  as given in the table.

Payoff matrix	Distribution $\approx \exp(-bx^\gamma)$	Nash equilibrium (NE)?
$a = b = c = d$ Neutral evolution	$P_i \sim \frac{1}{i(N-i)}$	drift $\rightarrow i = 0$ and $\rightarrow i = N$
$a = b < c = d$ constant fitness	$\simeq$ exponential $\gamma = 0.87$	drift $\rightarrow i = 0$
$P_{AC} = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$	$\simeq$ binomial $\gamma = 2.07$	$i = N/2$ "internal NE"
$P_{PD} = \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix}$	$\gamma = 0.63$	$i = 0$ "external NE"

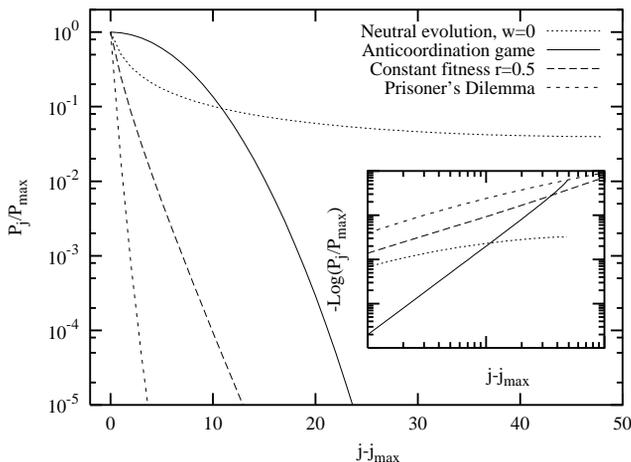


Fig. 2. Reproduced from [Cla05]. The invariant distributions  $P_j$  share different decay tails as a function of the distance  $j - j_{\max}$  from the Nash equilibrium  $j_{\max}$ . Here  $r = 1 - w + wa$ . In the four cases considered here (shown for  $N = 100$ ), the distributions can be approximated by stretched exponentials (which would appear as straight lines in appropriate scaling, the inset shows that the approximation is reasonable). For higher mutation rates see [Tra06a].

Prisoner's dilemma, the decay becomes slower with larger distance, while it becomes faster for the binomial distribution at the internal Nash equilibrium. The distributions are shown in Fig. 2. The decay of the distribution can be fitted by a  $P \approx \exp(-bx^\gamma)$ ,  $\gamma_{AC} = 2.06$ ,  $\gamma_{CF} = 0.87$ ,  $\gamma_{PD} = 0.63$ . This corresponds to random motion in an anharmonic potential.

**5. From microscopic equations to macroscopic equations** Corresponding to the discreteness of states, we first describe the processes by a master equation, then formulate a Fokker-Planck (Kolmogorov forward) equation for large  $N$ , and finally compare the deterministic equations resulting from the limit  $N \rightarrow \infty$ .

**5.1. Limit of large populations: From master equation to Fokker-Planck equation.** The equation of motion (or time evolution equation) for the stochastic process can be formulated in terms of the master equation

$$(10) \quad P^{\tau+1}(i) - P^\tau(i) = P^\tau(i-1)T^+(i-1) - P^\tau(i)T^-(i) \\ + P^\tau(i+1)T^-(i+1) - P^\tau(i)T^+(i)$$

for the probability distribution, i.e.,  $P^\tau(i)$  is the probability to be in state  $i$  at time  $\tau$ . For  $N \gg 1$  we can proceed via a Kramers-Moyal expansion, defining  $x = i/N$  and  $t = \tau/N$ . Then a formal Taylor expansion of  $T$  and  $\rho(x, t) = N P^\tau(i)$  yields, considering only the two leading terms of the Taylor expansion,

$$(11) \quad \frac{d}{dt}\rho(x, t) = -\frac{d}{dx}[a(x)\rho(x, t)] + \frac{1}{2}\frac{d^2}{dx^2}[b^2(x)\rho(x, t)],$$

$$(12) \quad a(x) = T^+(x) - T^-(x),$$

$$(13) \quad b(x) = \sqrt{\frac{1}{N}[T^+(x) + T^-(x)]}.$$

For large, but finite  $N$ , this equation has the form of a Fokker-Planck equation. This allows to generalize the diffusion approximation (see e.g. [Dro01]) to coevolution. Since the internal noise is not correlated in time as subsequent update steps are independent, according to the Itô calculus a corresponding Langevin equation reads

$$(14) \quad \dot{x} = a(x) + b(x)\xi$$

where  $\xi$  is uncorrelated Gaussian noise and  $b(x) = 0$  for  $x = 0$  and  $x = 1$ . We here see that the noise is multiplicative and frequency-dependent.

**5.2. Limit of infinite populations: Replicator equation and adjusted replicator equation.** The leading order term does not vanish and describes the deterministic drift term. Surprisingly, the replicator equation [Tay78, Hof79, Zee81]

$$(15) \quad \dot{x} = \frac{wx(1-x)(\pi_x^A - \pi_x^B)}{\Delta\pi_{\max}}$$

is obtained for the Local update process [Tra05], whereas the adjusted replicator equation

$$(16) \quad \dot{x} = \frac{wx(1-x)(\pi_x^A - \pi_x^B)}{1-w+w\langle\pi(x)\rangle}$$

is the deterministic limit of the Moran process [Tra05]. For other processes, other differential equations may be obtained, see Table 1.

The difference between the two equations may be best illustrated for the Prisoner's Dilemma. Here the (ordinary) replicator dynamics reads  $\dot{x} = -x(1 - x^2)$ , whereas the adjusted replicator dynamics reads  $\dot{x} = \frac{-x(1-x^2)}{\frac{1-w}{w} + 1 + 3x - x^2}$ . In this case, the stability of fixed points is preserved, as the additional denominator can be absorbed into a dynamical rescaling of the time scale, commonly known as velocity transform. However, in asymmetric conflicts the change of time scale matters, as will be detailed in the next section.

**6. Asymmetric and cyclic games.** Cyclicity of evolutionary dynamics intuitively is contradictory to the oversimplified picture of an absolute *fitness landscape*: any species having reached the maximal fitness value within a population will outcompete all others, and no cyclicity or oscillation can emerge. However, in ecological competition, oscillations of populations are quite generic, as known since Lotka [Lot20] and Volterra [Vol26] (see also [Mur04]). Of special interest are cases where species cyclically outcompete each other, as in Dawkins' caricature of mating strategies (see Sections 6.1–6.2), or the children's game *Rock-Paper-Scissors*, where rock crushes scissors, paper covers rock, and scissors cuts paper. This situation has been spotted in the territorial behaviour of lizards [Sin96, Zam00], and also in *E.coli* bacteria in vitro [Ker02] and in vivo [Kir04]. The Fokker-Planck equation, in analogy to Sec. 5.1, for the Rock-Paper-Scissors game has recently been given in [Rei06], and generalizations to other cyclic evolutionary games are straightforward. It is generally claimed that such cyclic coevolution promotes biodiversity [Csa02, Cla08]. However, its relevance in a more general picture of "evolution at large" remains an issue still to be investigated.

**6.1. Asymmetric conflicts (bimatrix games).** As mentioned in the introduction, the payoff matrix for the opponent can be different from that earned by the first player. To set this scenario into work, it is usually required that the game is played between two disjunct populations (as below, female and male), or that the interaction process itself is asymmetric, e.g., that one player is "initiative" and gains payoffs different from those earned in the opponents' role. Many social and economic situations bear such asymmetries, but they are often too weak to be significantly extracted from data.

An illustrative example of biological mating behaviour has been given by Dawkins [Daw76]. Male and female each can occur with two genetic strategies, "fast" (male: philanderer, female: "fast") and "slow" (male: "faithful", female: "coy"). The payoff benefit of a child is assumed to be  $b$  for both parents, the total cost of raising an offspring is  $(-2c)$ , and the prolonged courtship that coy females insists on add a burden of  $a$  to both parents. Coy females and male philanderers produce nothing and gain nothing. The cost  $(-2c)$  is covered by both parents, except for philanderer males and fast females, where the female has to grow up its offspring alone. This translates into the payoff matrix (with usual parameter choices  $a = 3, b = 15, c = 10$ , see also Fig. 3)

$$(17) \quad (\pi_{ij}^M, \pi_{ij}^F) = \begin{pmatrix} (b - c - a, b - c - a) & (b - c, b - c) \\ (0, 0) & (b, b - 2c) \end{pmatrix} = \begin{pmatrix} (2, 2) & (5, 5) \\ (0, 0) & (15, -5) \end{pmatrix}.$$

If the four conditions  $a > 0, c > 0, b - c > 0, 2c - a - b > 0$  are fulfilled, the game is cyclic. These conditions correspond to the arrows in Fig. 3. The cyclicity of the game is



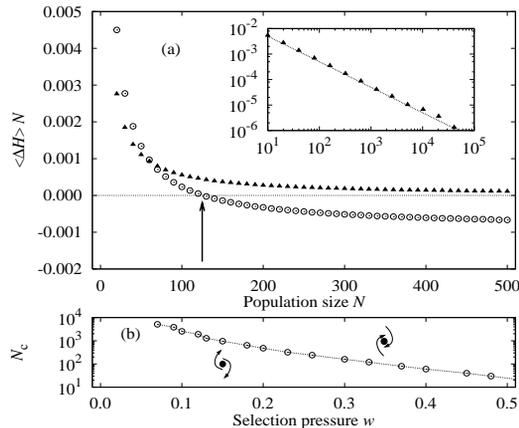


Fig. 4. Reproduced from [Tra05]. Drift reversal in the asymmetric game “Battle of the Sexes”. Shown is the average change of  $H$  (which is a constant of motion in the ordinary replicator equation) for different population sizes. (a) For the Moran process (circles) above a critical population size the average change of  $H$  becomes negative so that trajectories spiral outwards on average. For the Local update, no drift reversal is observed and for  $N \rightarrow \infty$  the change of  $H$  approaches zero (shown in the inset in double logarithmic plot). (b): Scaling of the critical population size with selection pressure  $w$ .

here read

$$(19) \quad \dot{x} = +2 \frac{(x^2 - x)(2y - 1)}{\frac{1-w}{w} + (2y - 1)(2x - 1)},$$

$$(20) \quad \dot{y} = -2 \frac{(y^2 - y)(2x - 1)}{\frac{1-w}{w} - (2y - 1)(2x - 1)}.$$

Hence, if the two populations earn different average payoffs (here they differ by a factor  $-1$ ), the fixed point stability of both types of replicator equations can differ.

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