Predicting Genetic Drift in 2 × 2 Games

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Abstract. For the analysis of the dynamics of game playing populations, it is common practice to assume infinitely large populations. Infinite models yield predictions of fixed points and their stability properties. However, these models cannot demonstrate the influence of genetic drift, caused by stochastic sampling in small populations. Instead, we propose Markov models of finite populations for the analysis of genetic drift in games. With these exact models, we can study the stability of evolutionary stable strategies, and measure the influence of genetic drift in the long run. We show that genetic drift can introduce significant differences in the expectations of long term behavior.

1 Introduction

1.1 Evolutionary Game Theory

Evolutionary Game Theory (EGT, overviews can be found in [1,2]) studies the dynamics and equilibriums of games played by populations of players. The strategies players employ in the games determine their interdependent payoff or fitness. In contrast with the traditional applications of game theory, the players do not act rationally when choosing their strategies, but act instead according to a preprogrammed behavior pattern. In this paper, a pure strategy is encoded in an individual's genome, which can evolve over time while repeatedly playing a game against other players in a population.

A common model to study the dynamics of frequencies of strategies adopted by these populations is based upon replicator dynamics. Replicator dynamics assumes infinite populations, asexual reproduction, complete mixing, i.e., all players are equally likely to interact in the game, and strategies breed true, i.e., strategies are transmitted to offspring proportionally to the payoff achieved.

We study two models from population genetics – a stochastic model of finite populations and a deterministic model of infinite populations – and compare their predictions in order to study the importance of finite population size when the populations are involved in playing well-known symmetric 2 × 2 games, such as the Hawk-Dove game, and the Prisoners' Dilemma. We show the importance and influence of finite population size on the predicted behavior, as compared to infinitely large populations. Evolutionary games with small search spaces – such as 2 × 2 games – are sufficient to investigate this question. Nowak and Sigmund

[3] recently indicated the importance of finite population effects in EGT, and expect that the observations of finite models might question the importance of evolutionary stability of infinite models.

Both models studied in this paper assume discrete time steps, as compared to the continuous progression through time of the differential equations used in replicator dynamics. The discrete time steps denote the consecutive generations of the evolving populations. Both models are based on the simple or generational Genetic Algorithm (GA) where all individuals in the population of the current generation are replaced by a newly produced population of individuals in the next generation. As this creates a stochastic chain of events over time, where no memory is required, both models can be seen as Markov models. The infinite population model studied in this paper is based on the model studied by Vose in [4], where the finite population model is based on the Fischer-Wright model, originally described in [5,6], and its interpretation for the GA as outlined in [7, 8].

1.2   Finite Populations and Genetic Drift

When modeling evolving populations, the assumption of infinitely large populations vastly simplifies the computation and analysis of the predictions of the models under consideration. A population can be represented as a frequency distribution, a stochastic vector, over the set of strategies or available genotypes. The proportions of strategies at the next generation can easily be computed from a population, using deterministic methods. Each resulting frequency distribution then corresponds to an infinite population. In contrast, when studying finite population models, we have to consider every possible population and compute the limit or fixed point probability distribution over these possible states of the system using stochastic finite Markov chain techniques. The number of possible populations grows exponentially with population size and exceeds the number of possible strategies. This complicates the computation and study of the finite systems' behavior.

As most populations in nature are very large, and infinite populations resemble very large populations, the assumption of infinite populations seems to make sense. Note that predictions of the finite population model approximate predictions of infinite population models if the finite population size is sufficiently large. In this paper, we question the belief that predictions of infinite populations can indeed easily be translated to predictions of models that assume finite populations. When large, but finite populations are considered, the populations are expected to closely follow the dynamics as predicted by the infinite population model. Small perturbations in the frequencies of large populations, caused by elements of chance, are then also assumed to fade away easily in the following generations. A finite population model can test whether these assumptions are indeed acceptable for a given problem and finite population size.

Differences in the behavior of the models are expected due to stochastic sampling effects of finite systems. The element of chance when selecting and generating individuals has to be considered at the construction of each generation. The combinatorial effects of limited population size or variation are more pro-

nounced in models that assume smaller population sizes. This element of chance can result in cumulative changes in the frequencies of evolutionary adopted genotypes or strategies. This effect is known as *genetic drift* and is part of the neutral theory of evolution [9]. With infinitely large populations, this element of chance does not exist. Instead of sampling a distribution over strategies in order to obtain the composition of a finite population at a generation, the distribution itself represents the next expected infinitely large population.

1.3   Games

In this section, we briefly introduce a selection of well-known symmetric 2×2 games: a Neutral game, the Hawk-Dove game and the Prisoners' Dilemma. These games are used to discuss the influence of finite population size and genetic drift on the predictions in finite models. All models assume a limited number of strategies (2) that can be employed. As such, the strategies can be represented as an atomic genotype with 2 alleles representing either strategy, which simplifies our analysis. Extended overviews of these games can be found in [1,2].

Fogel et al [10,11,12] and Ficici et al [13] have studied finite population effects of evolutionary dynamics on the stability of evolutionary stable strategies of the Hawk-Dove game empirically. Using simulations of the evolutionary systems, behaviors have been observed that are unrelated to an evolutionary stable strategy (ESS). They have suggested that ESSs may not provide a good expectation of a finite population's behavior. This paper presents a theoretical, Markov model approach to answer the same questions for a larger set of games, adapting Ficici's initial work [13]. We adopt genetic drift, and the causes of genetic drift, as an explanation of our theoretical observations.

All games are represented by a set of strategies Ω and a square payoff matrix **A**. Each entry $A_{i,j}$ in this payoff matrix gives the payoff value for an individual adopting strategy i when confronted with an individual playing strategy j. We assume that all payoffs in matrix **A** are strictly positive.

Hawk-Dove game. In this game, a bird has a choice of 2 behaviors when a resource needs to be shared with another bird. It can either choose to act as an aggressive hawk or a pacific dove. If both players choose the hawk strategy, they fight and injure each other. If only one of both players chooses hawk, then this player defeats the pacific strategy of the dove. If both players play dove, there is a tie in profit, but the profit is lower than the profit of a hawk defeating a dove.

The Hawk-Dove game is also known as the snowdrift or chicken game.

The game can be modeled as a game with two strategies $\Omega = \{H, D\}$ (Hawk and Dove), with a payoff matrix **A** where $A_{H,H} < A_{D,H} < A_{D,D} < A_{H,D}$. Both pure strategies are unstable fixed points of the game if an infinite population without variation is assumed. There also exists a mixed strategy that is an ESS of the system if the proportion of Hawks in the population equals $\frac{A_{D,D} - A_{H,D}}{A_{H,H} + A_{D,D} - A_{H,D} - A_{D,H}}$.

Prisoners' Dilemma. Imagine two criminals who are arrested under the suspicion of a crime they have committed. The police doesn't have enough proof to convict them. The criminals are separately questioned. Both criminals must choose to either cooperate with each other or to defect. If either one of the criminals gives the police more evidence to convict the other, the defector is freed. If both players cooperate, they receive only a short time in jail. If both players tell out on each other, then the police has enough evidence to convict both. If one player defects her cooperating opponent, the defector receives a high payoff, and the cooperator spends a long time in jail.

Biological examples of the Prisoners' Dilemma can be found in the behavior of bacteriophage $\Phi6$ and the evolution of ATP producing pathways [3].

Consequently, the game can be modeled with two strategies $\Omega = \{C, D\}$ (Cooperate and Defect) with a payoff matrix $\mathbf{A}$ where $A_{C,D} < A_{D,D} < A_{C,C} < A_{D,C}$. Both pure strategies are equilibrium strategies if no variation is assumed. The fixed point where the whole population adopts defection is stable, and the equilibrium where all players cooperate is unstable. There is no mixed strategy equilibrium for this game.

Neutral game. The last game we introduce is used for control measurements, and to show how the population behaves in the absence of selection. These predictions give us an idea of how strong genetic drift can become for certain parameters, as variation and sampling of the population are the only processes at work in systems with neutral selection.

We can model a Neutral game with two strategies $\Omega = \{0, 1\}$ with a payoff matrix $\mathbf{A}$ where $A_{0,0} = A_{0,1} = A_{1,0} = A_{1,1}$. If no variation is assumed, all pure and mixed strategies are fixed points of the game. If a variation operator – which is symmetric for both strategies – is assumed, only the mixed strategy at $1/2$ is a stable fixed point of the game.

2   Models and Methods

In this section, we give an overview of the reproduction schemes used in our evolutionary models. We also define the construction of new populations at a new generation, using sampling techniques if finite populations are considered.

2.1   Populations and Fitness of Individuals

Let P denote a population of individuals of type 0 and 1. These types correspond to the strategies in the games. Let $p(i|P)$ denote the proportion of genome $i \in \Omega$ in P. For now, we do not have to assume a size for the populations, and make the distinction between modeling of finite and infinite populations in a later section.

Let $f(i|P)$ with

$$f(i|P) = \sum_{j \in \Omega} A_{i,j} p(j|P)$$

denote the fitness of individual $i \in \Omega$. The fitness denotes the mean payoff received when the individual is matched against all individuals in the population,

including itself. As such, the fitness of an individual denotes the expected payoff received when players are randomly chosen as opponents.

2.2 Selection

According to this fitness function, we can select an individual $i \in \Omega$ from population P with selection probability $s(i|P)$ with

$$s(i|P) = \frac{f(i|P)p(i|P)}{\sum_{j \in \Omega} f(j|P)p(j|P)}.$$

This selection method renders selected genotypes proportional to their fitness and abundance in population P. The denominator of the fraction is the expected fitness or payoff received by any individual in the population.

2.3 Reproduction

Commonly, the next step in the reproduction process would be to recombine these selected individuals in order to get recombined child individuals. However, since we are dealing with individuals with only one locus, there is no need for discussing recombination here. It suffices to consider mutation. Let $m(i|P)$ represent the probability that an individual $i \in \Omega$ is generated by selecting an individual from P, and then mutating it to i. More formally, if we assume a bit flip mutation probability μ with $0 \leq \mu \leq 1$, we can write $m(i|P)$ as $m(i|P) = \mu s(1-i|P) + (1-\mu)s(i|P)$. Note that $m(1-i|P) = 1 - m(i|P)$ since we only have two possible individuals that can be generated. The resulting probability $m(i|P)$ now denotes the probability that genome i ends up in the population at the next generation.

2.4 Creating New Populations

Infinite populations. In the case of populations with an infinite number of individuals, the above reproduction scheme directly yields the proportion of the individuals in the population at the next generation. As such, population P' is generated from P in one generation with $p(i|P') = m(i|P)$. The reproduction of infinitely large populations is deterministic. The fixed points $\hat{P}$ of this system, with $p(i|\hat{P}) = m(i|\hat{P})$ can be derived, and their stability properties studied in order to investigate the long term behavior of the game under evolutionary selection and variation. The fixed point of 2×2 games can easily be found through iteration of the infinite population model. Note that the population with either $p(0|P) = 1$ or $p(1|P) = 1$ is a fixed point if $\mu = 0$, and not a fixed point otherwise.

Finite populations. In the case of populations with a fixed and finite number of individuals, we have to sample the results of reproduction r times in order to construct a population of size r at the next generation. With the introduction

of a finite population size, the process is no longer deterministic and becomes stochastic. The probability that population P' with population size r is generated through sampling in one generation from population P is equal to

$$\Pr\left[\tau(P) = P'\right] = \binom{r}{rp(0|P')} \prod_{i \in \Omega} m(i|P)^{rp(i|P')}.$$

The binomial coefficient computes the number of possible arrangements for a population of size r whose proportion of 0 genomes equals $p(0|P')$. The other factors denote the probability that such an arranged population is sampled from the reproduction process. Note that $\forall i \in \Omega : rp(i|P') \in \mathbb{N}$, since $rp(i|P')$ represents the number of individuals with genotype i in P'. Note that the finite model thus samples the infinite model r times.

As the number of possible populations, i.e. $r + 1$, is finite, we can study the resulting system as a finite Markov chain, over the state space of populations, with transition probability matrix T with entries $T_{P',P} = \Pr\left[\tau(P) = P'\right]$. As this system is irreducible and aperiodic, or ergodic, as $0 < \mu < 1$, we can obtain the system's limit behavior by computing the unique stochastic eigenvector of T with associated eigenvalue 1. This stochastic vector denotes the limit or steady state distribution over the states or possible populations of the system, and can be used to study the expected behavior of the system as a whole. The limit behavior of the system is undefined if $\mu = 0$ or $\mu = 1$. In the case of $\mu = 0$, the system becomes reducible, and the system ends in one of the populations that consist of a unique genome (i.e., either the population with all 0 or all 1 individuals). In the case of $\mu = 1$, the system becomes reducible and periodic, as the population consisting of all 0's can only become the population of all 1's in the next generation since all selected individuals are mutated from genome 0 to 1. Vice versa, this also holds when the system is started with a population of all 1's, which results in a periodic system. In practice, we only assume $0 < \mu \leq 1/2$, since mutation probabilities above $1/2$ work counterproductive for the evolutionary process. Otherwise, all selected individuals would have a too high probability of being mutated to less optimal genotypes.

2.5   Transitions

Figure 1 depicts the stochastic transition probability matrices of the finite model and the deterministic transition functions of the infinite model, for $r = 20$ and $\mu = 0.1$. The payoffs of the Hawk-Dove game are chosen with $A_{H,H} = 1 < A_{D,H} = 2 < A_{D,D} = 3 < A_{H,D} = 4$, and for the Prisoner's dilemma the utility function used in this paper is given by $A_{C,D} = 1 < A_{D,D} = 2 < A_{C,C} = 3 < A_{D,C} = 4$. Each of the columns of the transition matrices of the finite population models sums up to 1, as each column represents the probability distribution over the states at the next generation. As the population size increases, the sampling of the population at the next generation becomes more stable, and the stochastic model better resembles the deterministic infinite population model. On the other hand, if the rate of mutation is increased, the finite population model resembles the infinite model less. This is due to higher probabilities to end up in other population configurations then the most probable ones.
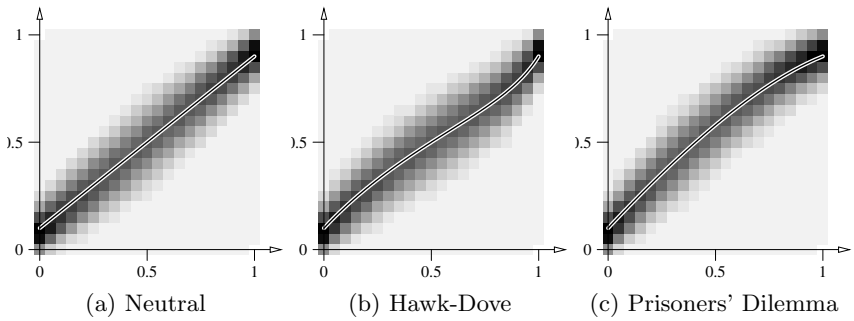
(a) Neutral   (b) Hawk-Dove   (c) Prisoners' Dilemma

Fig. 1. Transition matrices of the finite population model ($r = 20$), overlayed by the deterministic map diagram (graph with white background) of the infinite population model, for $\mu = 0.1$. The horizontal axis represents the current proportion of (a) 0, (b) Hawk or (c) Defect genomes in the population, the vertical axis represents the proportion at the next generation. Each gray scaled box represents the transition probability between states in one generation for the finite model. Darker grays represent higher probabilities.

3   Results

3.1   Neutral Game

Given the Neutral game from section 1.3, figure 2 depicts the limit or fixed point distributions of the finite population model, for a small set of population sizes and mutation rates[1]. For all possible parameters, the weighted mean of the distribution is equal to the predicted fixed point of the infinite model, namely at 1/2. Figure 2(a) shows a typical distribution for (relatively) large population sizes and large mutation rates. In this type, the system is most likely to end up with highly diverse populations. Figure 2(c) shows a typical distribution for systems with a small population size and a small mutation rate. In these cases, a run of the system will most likely end up in either one of the populations filled exclusively with either genome 0 or 1. Note that with these parameter settings, the system prefers extremes of the state space, and avoids the predicted "stable" fixed point of the infinite population model. Figure 2(b) shows a snapshot of the transition from the first type to the second. Note that the behavior depicted in these distributions is structurally very different, although the infinite population model predicts the same stable fixed point for all of these evolutionary systems. These differences in predicted behavior are due to genetic drift around this stable fixed point. Drift is stronger as populations become smaller (more sampling effects) or the mutation rate decreases (convergence due to low genetic diversity).

The weighted standard deviation σ of the steady state distributions' means can be employed to discuss the importance of genetic drift in our games with

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[1] As the predicted stable fixed point of the infinite model equals the weighted mean of the distribution, the lines cannot be distinguished in these figures, but become important as other games than the Neutral game are introduced.
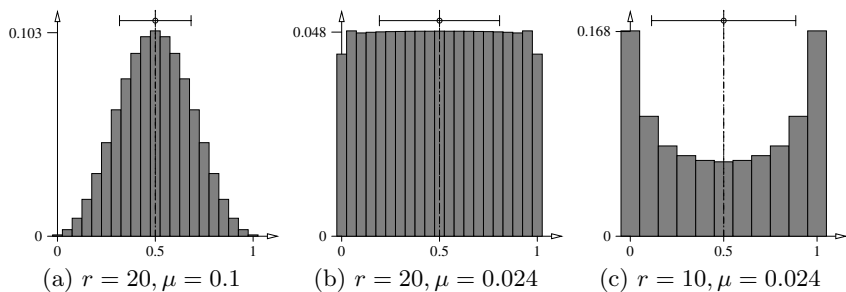
Fig. 2. Limit or steady state distributions for the Neutral game for 3 different parameter settings. The bars denote the probability of ending up in the population with the given proportion of 0 genomes. The dashed vertical line denotes the weighted mean of the distribution, the error bars the weighted standard deviation for this mean. The dash-dotted vertical line gives the fixed point of the infinite population model. Note that there is no standard deviation in the infinite model as the system is deterministic.

finite populations, and we are able to predict how the parameters are influencing the system's behavior. Later on, we use similar techniques to discuss genetic drift in games with selective pressure, and can use the Neutral game as a control for our predictions and expectations.

Influence of population size. Assume a fixed mutation rate μ with $0 < \mu < 1$ throughout this section. As population size r increases, the standard deviation σ decreases. This is due to the genetic drift introduced by stochastic sampling of the finite population, which becomes more deterministic for larger populations. Consequently, as the population size becomes larger, the finite population model behaves more similar to the prediction of the unique stable fixed point of the deterministic infinite population model, where $\sigma = 0$. Indeed, if we keep on increasing the population size, then σ comes closer to 0, and the mean of the distribution converges to the fixed point of the infinite population model[2]. Note that this holds unless μ equals 0 or 1. If $\mu = 0$, the limit behavior of the finite model gives 2 attracting states, where the infinite model predicts a mixed strategy fixed point.

Influence of mutation rate. In this section, we assume a fixed and finite population size r. As the mutation rate in the system of evolving populations for the Neutral game is sufficiently decreased, a run of the system most probably ends up in either one of the populations with only one genome. Indeed, if a mutation rate of 0 is assumed, the transition matrix of the evolutionary system

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[2] In the Neutral game, the fixed point of the infinite model and the mean of the finite population are always the same. This statement is thus trivial for this game, but becomes more important as there will be a difference between these two predictions as other games are considered.

becomes reducible, and the steady state distribution of the Markov chain is no longer unique. If $\mu = 0$, two linearly independent stochastic eigenvectors of the transition probability matrix with corresponding eigenvalue 1 exist, and either one of these eigenvectors represents a distribution where the evolutionary system ends up with a population containing only one genotype. As the mutation rate is sufficiently decreased toward 0, the predictions of the finite population model better resemble the extreme situation where $\mu = 0$, independent of the game considered, as the selective pressure becomes negligible.

As the variational pressure for the Neutral game is increased, more random individuals are generated by the reproduction process. In the extreme case, where $\mu = 1/2$, each generation renders a new random population with the probability of either individual in this population being $1/2$. At each step, a distribution over the state space is constructed that is a binomial distribution. The probability of encountering a population with n out of r individuals being of type 0 is then given by $\binom{r}{n} \frac{1}{2}^r$. As this is the case for each of the generations during a run of the system, it is also the limit or steady state distribution. Consequently, if a mutation rate of $1/2$ is assumed, the expected proportion of either genome is $1/2$, and σ becomes $\frac{1}{2\sqrt{r}}$. As the mutation rate is increased toward $1/2$, the finite population model better resembles the extreme situation where $\mu = 1/2$, independent of the game considered.

3.2   Hawk-Dove

The payoffs of the Hawk-Dove game have been chosen with $A_{H,H} = 1 < A_{D,H} = 2 < A_{D,D} = 3 < A_{H,D} = 4$. The stable fixed point of the infinite model with no variation for these parameters lies at $1/2$. Even more, if variation is assumed, the stable fixed point remains at $1/2$ and no other fixed points exist. Consequently, the evolutionary system with this game is similar to the Neutral game, in only having a stable mixed strategy fixed point at $1/2$. When choosing extremely small or large parameters for population size and mutation rate, so are the predictions. Under those parameters, the forces of genetic drift are much stronger, or much weaker, than those of selection according to the payoffs in the game. In the Hawk-Dove game however, selection is asymmetric to either genome. This allows a finite population to wander away from the infinite model's projected "stable" fixed point, which on its turn may result in genetic drift of the population. We can study this effect, and the balance between selective and variational pressure, by examining the differences in expected behavior.

Figure 3 represents the steady state distribution of the finite population model for the Hawk-Dove game, for three parameter settings of the system. Figures 3(a) and (b) show how the system balances between the selection around the fixed point on one hand, and the influence of genetic drift which forces the population to either extreme of its state space on the other hand. Figure 3(c) shows how genetic drift can force the expected behavior of the finite population model relatively far away from the infinite population's predicted stable fixed point, toward higher proportions of the Dove strategy. As the fixed points, means and standard deviations of the systems have been determined by exact techniques,
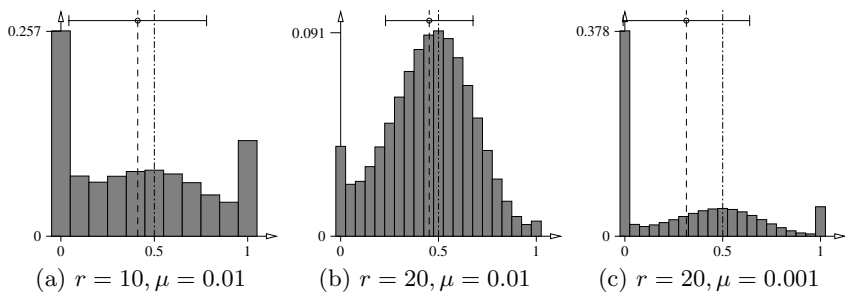
Fig. 3. Limit or steady state distributions for the Hawk-Dove game for 3 different parameter settings. The horizontal axis represents the proportion of Hawk genomes in the population. The vertical dashed line represents the mean of the distribution, where the dash-dotted line represents the fixed point of the infinite model, as in figure 2.

it is clear that genetic drift can introduce significantly different behavior when finite population sizes are considered. These predictions lose significance as population size r or mutation rate μ is increased.

We need an explanation why small populations drift to higher proportions of Dove. Consider two finite systems, with the same population size r and mutation rate μ. The first system is initialized with a population with $r/2 - k$ Hawks, the other is initialized with $r/2 + k$ Hawks, with k strictly positive. The probability of moving from these initial states to the state with a proportion of $1/2$ Hawks in n steps can be computed. The probability of reaching this state is higher when starting with $r/2 + k$ Hawks, where the system started with more Doves remains longer stuck. On average, the overall system thus remains longer in states that have a higher proportion of Doves. Genetic drift pushes the system to higher proportions of Doves as compared to the infinite model. The observation that populations drift toward higher proportions of Dove (and not the other way) is similar to Ficici's [13] observation of this effect in simulation runs and an infinite model of the Hawk-Dove game.

We can thus summarize that predictions of long term behavior differ significantly when infinite and finite models are compared, and that genetic drift gives a viable explanation of these deviations.

3.3   Prisoners' Dilemma

Genetic drift can also be observed in other games, such as the Prisoners' Dilemma. However, the influence of drift differs from the previous games. If no variation is assumed, there is one stable pure strategy (Defect) and there is no mixed strategy ESS. As a result, we expect the populations to contain a lot of the Defect genomes on the long run, even if variation is assumed. The effects of genetic drift observed in the previous games are different in the Prisoners' Dilemma. In the previous games, selective pressure pulls the populations toward diverse populations, as the stable ESS of those games is a mixed strategy. At the other end, genetic drift pushes instantiations of the system to less diverse
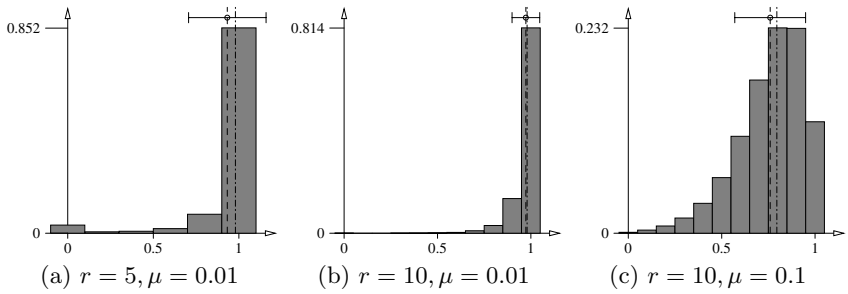
Fig. 4. Limit or steady state distributions for the Prisoners' Dilemma game for 3 different parameter settings. The horizontal axis represents the proportion of Defect genomes in the population.

populations, such that one strategy becomes prominently abundant in the population. In the Prisoners' Dilemma, the behavior in the finite model is expected to concentrate on populations with one strategy (Defect), where genetic drift moves populations to more diverse configurations.

Figure 4 depicts steady state distributions of the finite population model when the individuals are involved in the Prisoners' Dilemma, for a number of parameter settings. As predicted by the infinite model, the distributions are expected to have a large proportion of Defect genomes. As the population size is increased, the expected behavior of the system better resembles the expected infinite population behavior, and the standard deviation σ around the weighted mean of the expected distribution over the states decreases. As we increase the rate of mutation, σ increases, as the generation of random individuals tends to push the populations to more diverse configurations. Note that this observation contrasts with the expected behavior in the previous games, where higher variation resulted in predictions that better resembled the infinite population model. Of course, in these other games, selective pressure and a high mutation rate both guide the system to more diverse populations. For small population sizes and small mutation rates, the predictions of the infinite population model are thus more stable for the Prisoners' Dilemma as compared to the influence of genetic drift in the Neutral and Hawk-Dove game.

In the Prisoners' Dilemma, the Cooperate strategy is rationally the optimal strategy, if all other players in the game also opt for this strategy. In an evolutionary system, however, this pure strategy is an unstable ESS. Only for small population sizes and extremely small mutation rates, the finite population model predicts a noticeable proportion of Cooperate genomes in the populations. Figure 4(a) gives an example of a small probability of ending up in a population filled with the Cooperate genome.

4   Conclusions and Future Work

We have proposed stochastic models of finite populations to study the stability of evolutionary stable strategies for a set of 2×2 games. When the assumption of infinitely large populations in evolutionary models is discarded, statistically significant differences in expected behavior can be observed. In particular, the long term expectations of the finite model differ from the predicted fixed points of the infinite model. We adopted genetic drift to give a viable explanation for the deviation from the fixed points predicted by infinite population models. We have shown that finite population models can be used, and extended, to study the stability of evolutionary "stable" strategies in finitely sized populations.

In future work, we intend to investigate the relationship between mutation rate and population size in terms of genetic drift. We are currently studying larger games and larger populations to check the scalability of our observations. Similarly, we are interested in the influence of differing selective pressure on the amount of genetic drift, where a fixed selective pressure was chosen in this paper.

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