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**Quasi-stationary distributions in the Moran model with two
strategy games**

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Abstract

Master of Science

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by Philipp MERZ

This thesis studies the behaviour of a fixed size population that engages in two by two games. We use the Moran model and introduce fitness based on average payoff to weight the imitation happening at each step. This leaves us with a birth-death chain or imitation chain which we can compare to the deterministic replicator dynamic.

Such population models have applications in many fields, for example biology or economics and have been studied extensively. Most studies of the long term behaviour and its stability over time for the Moran model, included mutation because this gives a unique stationary distribution with full support. In this thesis we exclude mutation and work with the non-irreducible chain, which needs a different approach. We mostly used numeric approximations when there were no explicit formulas given.

In the limit of infinite populations the deterministic and stochastic models should agree and we could mostly recapture this fact. We studied five different cases of two by two games namely a neutral, a dominated, a coordination, an anti-coordination and what we called an almost-neutral game. We give detailed discussions for each case in terms of the quasi-stationary, pseudo-stationary and the long-term distributions. Also fixation probabilities and average fixation times are given. Additionally we examine what happens if the game matrix is chosen with largely differing values which in some cases gives us degenerated results.

Balanced versions of the classical coordination or anti-coordination games produce really nice stochastic models which incorporate the details of the dynamics. The anti-coordination case has the most paradoxical nature where it seems like the stationary distribution is no longer relevant. But as it turns out the LTD would converge to the stationary distribution but needs excruciatingly huge amounts of time compared to all other cases. One could say it converges so slowly that the quasi-stationary distribution is a more relevant prediction. Additionally the QSD mirrors the interior stable state of the corresponding REP dynamic and therefore recovers the connection between REP and imitation chain.

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Zusammenfassung

Master of Science

Quasi-stationäre Verteilungen im Moran Modell für Spiele mit zwei Strategien

von Philipp Merz

Diese Arbeit befasst sich mit dem Verhalten einer Population, welche in zwei Personen Spielen untereinander interagiert. Wir verwenden das Moran Modell und führen eine Fitness basierte Immitation ein, welche die durchschnittlichen Payoffs der Spieler sowie ihre Frequenz inkludiert. Damit erhalten wir eine Geburts-Todes Kette oder Immitations Kette, die wir mit der deterministischen Replikator Gleichung vergleichen können.

Solche Populations Modelle haben vielseitige Anwendungen, unter anderem in der Ökonomie und der Biologie. Die meisten Arbeiten über das langfristige Verhalten solcher Ketten inkludieren zusätzlich Mutation, wodurch eine eindeutige stationäre Verteilung mit vollem Träger existiert. Eine Motivation dieser Arbeit, war dieses Modell ohne Mutation und daher nicht-irreduzibel zu betrachten, was eine andere Vorgehensweise benötigt. Wenn keine expliziten Lösungen bekannt sind approximieren wir mit numerischen Methoden.

Im Grenzwert für unendlich große Populationen sollte das stochastische mit dem deterministischen Modell übereinstimmen und zum großen Teil konnte dies von uns bestätigt werden. Untersucht wurden fünf verschiedene Typen von zwei Personen Spielen, nämlich Neutrales, Koordinations, Anti-Koordinations, Dominiertes und das von uns benannte fast neutrale (almost neutral) Spiel. Für jeden Fall werden die Quasi-stationäre, die Pseudo-stationäre und die Langzeitverteilung (long-term distribution) detailliert diskutiert. Zusätzlich werden durchschnittliche Absorptionszeiten (average fixation time) sowie die Fixierungs Wahrscheinlichkeit (fixation probability) angegeben.

Ausbalancierte Versionen der klassischen Koordinations und Anti-Koordinations Spiele ergeben Modelle, welche die Eigenschaften und Dynamiken dieser wieder spiegeln. Das Anti-Koordinations Spiel stellte sich als paradox heraus, da hier die Stationäre Verteilung scheinbar keine Rolle für das langfristige Verhalten spielt. Hier liefert die Quasi-stationäre Verteilung die relevantere Prognose, da sie das innere stabile Gleichgewicht der Replikator Gleichung wiedergibt. Dieser Effekt verstärkt sich bei größeren Population noch, daher stimmen hier Replikator Dynamik und Imitations Kette überein.

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Chapter 1

Introduction

This thesis studies the behaviour of a fixed size population that engages in two by two games. We use the Moran model and introduce fitness based on average payoff to weight the imitation happening at each step. This leaves us with a birth-death chain or imitation chain which we can compare to the deterministic replicator dynamic.

Such population models have applications in many fields, for example biology or economics and have been studied extensively. Most studies of the long term behaviour and its stability over time for the Moran model included mutation because this gives a unique stationary distribution with full support. In this thesis we exclude mutation and work with the non-irreducible chain which needs a different approach. We mostly used numeric approximations (the power method) when there were no explicit formulas given.

In the limit of infinite populations the deterministic and stochastic models should agree and we could mostly recapture this fact. We studied five different cases of two by two games namely a neutral, a dominated, a coordination, an anti-coordination and what we called an almost-neutral game. We give detailed discussions for each case in terms of the quasi-stationary, pseudo-stationary and the long-term distributions. Also fixation probabilities and average fixation times are given. Additionally we examine what happens if the game matrix is chosen with largely differing values which in some cases gives us degenerated results.

Chapter 2

Theory

In this chapter we try to mention all the necessary theory to follow the rest of the thesis. First we dive into *Game Theory* and its evolutionary extension, where we talk about the *Replicator equation*. Afterwards basics needed for stochastic processes, more precisely *Markov chains* are established. Following this we can finally introduce our main point of focus namely the *Moran model*. This model brings together two concepts, a two by two game and a *birth-death chain* with two absorbing states.

2.1 Game Theory

Our model aims at combining game theory and population dynamics. First we need to go over the basics of game theory. Our game will be a two person game, hence we only have two players. Both of these players will have two possible strategies. A well known example of a two person game is the prisoners dilemma. We will explain the key components using this example. Both players have two available options, they can either *cooperate* C or *defect* D . The payoffs for each of the four different situations are written in the following matrix:

$$\begin{array}{cc} & C & D \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix} \end{array}$$

Here α is the payoff for Player 1 if he cooperates and his opponent cooperates as well and γ corresponds to the payoff Player 1 receives if he defects and his opponent cooperates. Every entry in this matrix describes a payoff for the row Player. In our case the game is symmetric which means that both players get the same payoff if they are in the same situation. Now this doesn't mean that β and γ are equal, because these are payoffs for different situations. If (C, D) is played where the first entry corresponds to our row player and the second to the column player, the row player receives β and the column player γ . From the column players perspective he played D versus our C . The gist of this is that we see ourselves as the row player most of the time and we only have to track the four values in this matrix, not eight if both sides had different payoffs for every situation. We will see later that this is also necessary for switching to the population perspective.

The following matrix is an example with explicit values for a prisoners dilemma:

$$\begin{array}{cc} & C & D \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix} \end{array}$$

We can observe that the second row has higher values than the first in every entry. If that's the case we call D a dominant strategy. So obviously we should always play D if we are uncertain what our opponent will chose. The dilemma here lies in the detail that the two payoffs of both players combined are greatest if they both cooperate than in any other constellation. So from a societal point of view if there are many such interactions we would want as much cooperation as possible to maximise our summed payoff over the whole population. If one is interested further in this example, the book **The Calculus of Selfishness** by **Karl Sigmund** would be a good read.

2.1.1 Evolutionary game theory

As the name suggests evolutionary game theory tries to apply game theoretic methods and frameworks to an evolutionary viewpoint. Where we before had two players battling it out, we now see only one large population of players. This population consists of two types, namely players of strategy C and players of strategy D . From here on we will refer to the frequency of strategy C players in the population with x . That of course implies that $1 - x$ is the frequency of D players, we will often write them together in one vector like this $(x \ 1 - x)$. For convenience and readability we now can express calculations like the average payoff in the population as

$$(x \ 1 - x) \begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix} \begin{pmatrix} x \\ 1 - x \end{pmatrix} = x^2\alpha + x(1 - x)\beta + x(1 - x)\gamma + (1 - x)^2\delta. \quad (2.1)$$

We can interpret equation (2.1) as the expected payoff if we chose two individuals at random and let them play against each other. Now let's fix our row player as playing C and we only select his opponent randomly from the population, then his expected payoff will be the first entry on the right hand side of the following calculation:

$$\begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix} \begin{pmatrix} x \\ 1 - x \end{pmatrix} = \begin{pmatrix} x\alpha + (1 - x)\beta \\ x\gamma + (1 - x)\delta \end{pmatrix} \quad (2.2)$$

Analogously if we fix the strategy D for our row player the second entry of the right hand side in (2.2) shows our payoff. Now that we have the expected payoff for each strategy and the average payoff in the whole population, it's possible to formulate the dynamics of the development of player densities in our population.

2.1.2 Replicator dynamics

The replicator dynamics of our population are based on equation (2.2) and (2.1) and describe if the density of C or respectively D players will increase or decrease. The replicator equation was first introduced in the book **Evolutionary games and population dynamics, 1998** written by **J. Hofbauer** and **K. Sigmund**, which covers many important concepts regarding evolutionary dynamics. We will often reference them as **REP** equations. It should be noted that our population is of fixed size so our densities always sum to one. Formally we are then interested in the derivative with respect to time of x , the density of C players. The motivation behind these equations is that only a strategy that does better than the average of all players should increase its density and should decrease it otherwise. This leads us to the following equation, where the brackets evaluate to greater zero and thus induce an increase in density if the payoff for C against the population is greater than the average payoff.

Definition 1

$$\dot{x} = \frac{dx}{dt} = x[x\alpha + (1-x)\beta - (x \ 1-x) \begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix} \begin{pmatrix} x \\ 1-x \end{pmatrix}], \quad x \in [0,1] \quad (2.3)$$

We can simplify it a lot by just calculating the average payoff and then rearranging the terms, first taking out $(1-x)$ and then collect x and $(1-x)$ terms as it is shown in the following steps:

$$\begin{aligned} \dot{x} &= x[x\alpha + (1-x)\beta - x^2\alpha - x(1-x)\beta - x(1-x)\gamma - (1-x)^2\delta] \\ &= x(1-x)[x\alpha + (1-x)\beta - (x\gamma + (1-x)\delta)] \\ &= x(1-x)[x(\alpha - \gamma) + (1-x)(\beta - \delta)] \end{aligned} \quad (2.4)$$

The last line gives us a nice equation that can also be interpreted easily. If we will later talk about the replicator equation we will refer to the last line of (2.4). One should note the similarity to a logistic growth equation where the only difference regards the terms in the brackets. If we take a closer look at these we can see that the following holds:

$$\begin{aligned} x(\alpha - \gamma) &> 0 \Leftrightarrow \alpha > \gamma \\ (1-x)(\beta - \delta) &> 0 \Leftrightarrow \beta > \delta \end{aligned} \quad (2.5)$$

This means the density x of C players can only grow among other C players if its payoff against C is greater than the payoff of D against C . Analogous for growth of x among D players the second term needs to be positive as this is the payoff of C against D which needs to be greater than the payoff of D against D . So if both $\alpha > \gamma$ and $\beta > \delta$ hold \dot{x} will always be positive so the amount of C players grows to one. Notice in (2.4) we only used the differences of payoffs, which means our game is only relevant in how large the payoffs in each column are in relation to each other. We will discuss all the different possibilities for the REP dynamics in the next chapter.

2.1.3 Different types of games

We now move on to briefly touch on the different types of symmetric two by two games and how the REP dynamics work in each case. There are four different categories which can be identified by the relations of the payoffs per column.

Neutral case

The trivial case of a game with all entries being equal should be explained at this place, because later on in the stochastic model this becomes our baseline. As already mentioned the following has to be fulfilled

$$\alpha = \beta = \gamma = \delta \quad (2.6)$$

then the resulting replicator equation collapses to $\dot{x} = 0$ and we have no flow at all. It follows that any constant function satisfying the starting condition is a solution.

The phase portrait of the neutral dynamic shows that all states in $[0,1]$ are stable states which is why this case is considered trivial. We explain the structure of a phase portrait in more detail shortly.

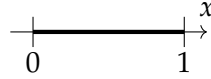


FIGURE 2.1: Phase portrait of a neutral replicator equation.

Dominated strategies

If either

$$\alpha > \gamma \quad \text{and} \quad \beta > \delta \quad \text{or} \quad \alpha < \gamma \quad \text{and} \quad \beta < \delta \quad (2.7)$$

holds then we say that C (strictly) dominates D or vice versa. If that is the case the REP dynamic will be either always positive, if C dominates D , or always negative, if D dominates C . One example for a dominated strategy was given with the prisoners dilemma earlier.

FIGURE 2.2: Replicator Equation for C dominating D

We can also draw the REP dynamic on the interval $[0, 1]$, this is called a phase portrait. We already showed the very easy version in the neutral case. Every state of our population can be plotted here, where 1 means all of our population consists of C players and accordingly being at 0 tells us that we only have D players left. Let's go over the notation used in figure 2.2:

- unstable fixed point
- stable fixed point
- direction of flow

FIGURE 2.3: Legend for the phase portrait

We will also refer to a fixed point as a *rest point*, it should be stated that at any *rest point* $\dot{x} = 0$ has to hold. This obviously means that in our case of two by two symmetric games, we will always have at least two *rest points*, at 0 and 1, due to the factors x and $(1 - x)$ in (2.4).

As we can see from the phase portrait the D players will inevitably die out no matter at what point $x > 0$ we start. The case is completely analogous if D dominates C as in the prisoners dilemma so we omit the discussion for that.

Coordination games

A coordination game is characterized by the need of two or more players to coordinate them to all chose the same strategy. It needs to fulfill the following conditions

$$\alpha > \gamma \quad \text{and} \quad \delta > \beta \quad (2.8)$$

or in other words the largest entry per column needs to be on the diagonal. In our case we will consider two players and the symmetric version, a good example is

given with the *stag hunt*.

A pair of hunters go out to hunt and after some time they find a path where they are certain a stag will come by. So they camp the path for a few days, but no stag shows up. Now a hare comes along and they both have the opportunity to shoot it. But if one shoots the hare the stag will certainly be startled and never show up. So they face the decision of either defecting and shooting the hare, ruining the hunt for the other or of cooperating and continue to wait for the stag, which in our game would surely arrive but they don't know that. This leaves them with the following payoff matrix given in figure 2.4. If they both decide to defect and shoot the hare they will have to share it resulting in payoff 4 for each.



FIGURE 2.4: (Left) Payoff matrix and (Right) phase portrait for the coordination game stag hunt.

These payoffs result in three rest points of the dynamics (2.4). If we switch our perspective back to populations, we see that a population of only C players is stable as it is the case for only D players. This is due to the fact that if everybody plays C then no one would want to switch to D as this would yield a lesser payoff going down from 10 to 8. And vice versa if all play D then a change to C would lead to payoff 0 instead of 4. But what about a mixed population of C and D players? The third rest point lies in between 0 and 1 and is unstable, we denote this point with x^* . We can calculate it easily by setting the terms in the bracket of (2.4) to 0 and solve for x . In figure 2.4 on the right we can see the phase portrait for the stag hunt. We calculate x^* below and recognize that it's closer to 1 than to 0.

$$\begin{aligned} x(\alpha - \gamma) + (1 - x)(\beta - \delta) &= 0 \\ x\alpha - x\gamma - x\beta + x\delta + \beta - \delta &= 0 \quad | -\beta + \delta \\ x(\alpha - \gamma - \beta + \delta) &= \beta + \delta \quad | : (\alpha - \gamma - \beta + \delta) \\ x^* &= \frac{\delta - \beta}{\alpha - \gamma - \beta + \delta} \\ x^* &= \frac{4 + 0}{10 - 8 - 0 + 4} = \frac{2}{3} \end{aligned} \tag{2.9}$$

This means for all populations starting with a density of C players less than x^* that the C players will die out. Only if C players are more frequent than x^* it's the case that they fixate and D dies out. In other words the *basin of attraction* of D is double the size of that of C. It turns out that it's more difficult for a population to coordinate successfully to hunt a stag if the opposing possibility is much more safe, like the hunt for the hare.

Anti-coordination games

There is a third form of two by two games that will be the most important one going forward. It is the counterpart of a coordination game namely an *anti-coordination game*. A game matrix that has its largest entries per column not on the diagonal, in other words satisfies

$$\alpha < \gamma \quad \text{and} \quad \delta < \beta \tag{2.10}$$

is an anti-coordination game. In a coordination game the goal is, that all players play the same strategy, now we aim at getting our players to chose opposing strategies. But let's begin with an example, we stay with the animal theme and discuss the *hawk-dove game* as a typical *anti-coordination game*.

Now the cooperating strategy C is called the dove, seen as the peaceful and pacifist side. The counterpart is the hawk with strategy D , that is aggressive and dangerous. The two sides are fighting over a resource, which yields payoff 6. Two doves will readily share the resource and each gain 3. But a hawk will bully a dove away from the resource and claim it all, which leaves the dove with 0 and the hawk with 6. Now what happens if two hawks fight over the resource? They will harm each other resulting in severe damage 4 which we subtract from their payoff. So if two hawks battle each gets on average payoff -1 as each will win half of its fights, receiving 6 half the time but then the damage is subtracted. We need to choose the damage high enough, to not make D a dominating strategy. This results in the game matrix and the replicator dynamic which we both give in figure 2.5.



FIGURE 2.5: (Left) Payoff matrix and (Right) phase portrait for the hawk-dove-game. Here C is dove, D is hawk.

We again get three rest points, as in a *coordination game* but now both the one at 0 and 1 are unstable and there now exists a mixed stable equilibrium at $x^* = \frac{1}{4}$. This can be explained, with the fact that if only C players or doves exist, then a D player or hawk can easily invade. Analogously only hawks cannot further exist without doves around to take their food, because they would always fight each other. So there needs to be a balance of hawks and doves. Our population is stable with a quarter of doves and three quarters of hawks. The little amount of doves is due to the fact that the damage is relatively low, if we increase it we would decrease the amount of hawks at the mixed equilibrium.

2.2 Birth-death chains

Let's restate briefly what we think of when we say *birth-death chain*. It's a special type of Markov chain, where in one step we cannot go from a state to any other state, but only to neighbouring states. The typical setup includes the following definitions. First we specify the *state space* S as:

$$S := \{0, 1, 2, \dots, N\} \text{ for } N \in \mathbb{N}$$

Later we can interpret this N as our population size.

So if we are in state i we can reach $i + 1$, $i - 1$ and i in one step. Now our *birth-death chain* is a sequence of random Variables X_n where $n \in \mathbb{N}$, is the discrete time index. Each X_n only depends on X_{n-1} and not on the whole history of the chain. The behaviour in the states 0 and N needs to be defined separately as this can differ according to the approach. We define 0 and N as absorbing barriers. Meaning once

$$P = \begin{pmatrix} 1 & 0 & 0 & 0 & \dots & 0 \\ d_1 & r_1 & b_1 & 0 & \dots & 0 \\ 0 & d_2 & r_2 & b_2 & \dots & 0 \\ \vdots & & \ddots & \ddots & \ddots & 0 \\ 0 & \dots & 0 & d_{N-1} & r_{N-1} & b_{N-1} \\ 0 & \dots & 0 & 0 & 0 & 1 \end{pmatrix}$$

FIGURE 2.6: A transition matrix for a birth-death-chain with two absorbing states at 0 and N .

we reach 0 or N we will stay there forever. This leads us to the following transition probabilities:

Definition 2 For $i \in \{1, 2, \dots, N-1\}$ and for $n \in \mathbb{N}$ we define the following:

$$\begin{aligned} b_i &:= \mathbb{P}[X_{n+1} = i+1 | X_n = i] \\ d_i &:= \mathbb{P}[X_{n+1} = i-1 | X_n = i] \\ r_i &:= 1 - b_i - d_i = \mathbb{P}[X_{n+1} = i | X_n = i] \\ 1 &:= \mathbb{P}[X_{n+1} = 0 | X_n = 0] = \mathbb{P}[X_{n+1} = N | X_n = N] \end{aligned} \tag{2.11}$$

We will often call b_i the birth probability and d_i the death probability. We will refer to r_i as the probability to remain.

Now we can define the transition Matrix P .

Definition 3 We call an $(N+1) \times (N+1)$ matrix P a transition matrix if the following holds:

$$P_{ij} = \mathbb{P}[X_{n+1} = j | X_n = i] \quad \forall i, j \in S, \forall n \in \mathbb{N}$$

This means that P is a stochastic row matrix, i.e. $\sum_{j=0}^N P_{ij} = 1$

The definition of a transition matrix is crucial for working with Markov chains, because now we can use linear algebra to study our models. Let v be a $N+1$ dimensional stochastic row vector, i.e. the sum of all its elements is 1. We now identify the i 'th entry of v with the probability of being in the state i . So we can identify v with a probability distribution over S . Now let's say our chain iterates one step starting in each state according to the probability given in v , then we get a new distribution over S which we call v' . We can calculate v' given P and v as:

$$vP = v' \tag{2.12}$$

We just matrix multiply the row vector v with P to get v' . If we want to go multiple steps, say n we can just raise the transition matrix to the power n and multiply with that, see:

$$vP^n = v^{(n)} \text{ where } v_i^{(n)} := \mathbb{P}[X_n = i] \tag{2.13}$$

Further we discuss the classification of our state space.

2.2.1 Types of states

We can separate the states in our state space S into two different categories.

Definition 4 Let X_n be a Markov Chain on a finite, or countable, state Space S . A state $i \in S$ is called recurrent if the following holds:

$$\mathbb{P}[\exists n \geq 1 : X_n = i | X_0 = i] = 1 \quad (2.14)$$

A state i is called transient if the following holds:

$$\mathbb{P}[\exists n \geq 1 : X_n = i | X_0 = i] < 1 \quad (2.15)$$

It's clear from the definition that a state needs to be either transient or recurrent. If we start at a recurrent state we will almost surely visit it again at some point in time. The same is not true for transient states. Once we start at a transient state we might never return to it. An important notion regarding Markov chains is that of irreducibility.

Definition 5 We call a Markov chain X_n on S irreducible if $\forall i, j \in S$, there exists a sequence of possible steps, such that the probability of reaching j from i is positive.

So being irreducible means that it is always possible to reach every other state from any given state no matter how many steps it might take. Another even stronger property is that of a primitive Markov chain.

Definition 6 We call a matrix P primitive, if there exists an integer n such that the matrix P^n has only positive entries. A Markov chain is called primitive if its transition matrix P is primitive.

So every primitive chain is also irreducible, but not the other way round. For example a Markov chain which is periodic with period two or greater can be irreducible but cannot be primitive.

In an irreducible finite Markov chain, all states are recurrent. Now if we don't have irreducibility we can always find a subset of S that is irreducible. For example a birth-death chain with two absorbing states is not irreducible because we can get trapped in either 0 or N , but if we restrict our chain to again either 0 or N it will be irreducible. We will often separate our state space into the set of all recurrent states which we call $R := \{0, N\}$ and the set T of all the transient states $T := S \setminus R = \{1, 2, \dots, N-1\}$. The key concept to take away here is that R and T can be seen as states themselves and we can restructure our perspective on the chain and look only at the probabilities to change between or stay in these states. We show the possible dynamic in 2.7, where we see that we can stay in R and can stay in T and also go from T to R . But once we've entered R we can never leave it and return to T . The labels will be explained below. One question we will try to answer is how long can we stay in T without being absorbed in R . To do that we will need some further concepts from stochastic processes.

2.2.2 Fixation probability

In the context of finite birth-death chains with absorbing states, we get absorbed almost surely. Then one can ask, how likely it is if we start in state i to be absorbed at

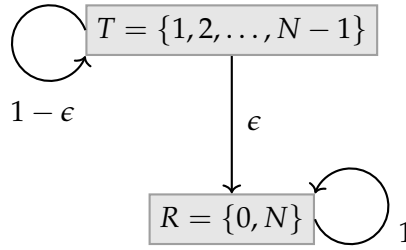


FIGURE 2.7: Transient and recurrent states with the probability of transition from T to R based on the current distribution $v^{(n)}$. Where $\epsilon = d_1 v_1^{(n)} + b_{N-1} v_{N-1}^{(n)}$.

N . We will denote this probability with ρ_i . It follows that if we are trapped with ρ_i at N and the only other trap is 0 we will be absorbed there with probability $1 - \rho_i$. This quantity can be used to determine the mid to long term behaviour of our process and thankfully there is an explicit formula for it in the context of birth-death chains. Obviously $\rho_0 = 0$ and $\rho_N = 1$ and for $i \in T$ we get (Taylor et al., 2004)

$$\rho_i = \frac{1 + \sum_{k=1}^{i-1} \prod_{j=1}^k \frac{d_j}{b_j}}{1 + \sum_{k=1}^{N-1} \prod_{j=1}^k \frac{d_j}{b_j}} \quad (2.16)$$

Later on we will often plot ρ_i for every state i in S which enables us to visualize the dynamic of an imitation chain quite easily.

2.2.3 Stationary distribution

An interesting question to ask about Markov chains is about the existence of a *stationary distribution*. First we quickly define what we understand under the term.

Definition 7 Let X_n be a Markov chain on the states S with the transition Matrix P . We call a $N + 1$ dimensional stochastic vector w a stationary distribution for X_n if the following holds

$$wP = w$$

In other words if w is a left eigenvector of P for the eigenvalue 1.

Every irreducible, finite Markov chain has a unique stationary distribution w with full support. If it is additionally primitive every starting distribution will converge to the stationary distribution in the long run. Meaning no matter at what distribution we start if we take enough steps our distribution will inevitably be arbitrarily close to w at some point. So for every starting distribution $v^{(0)}$ over the states S the following holds for any primitive finite Markov chain:

$$\lim_{n \rightarrow \infty} v^{(0)} P^n = w \quad (2.17)$$

But a Markov chain doesn't have to be irreducible or primitive, for a stationary distribution to exist. For example our birth-death chain with absorbing states 0 and N is not irreducible but every distribution starting only at 0 and N will be absorbed immediately and thus be a stationary distribution. We can use the fixation probability ρ_i to derive the stationary distribution to which we will converge to if we start in

$i \in T$. It is given as the following $N + 1$ dimensional row vector:

$$(1 - \rho_i, 0, \dots, 0, \rho_i) : i \in T \quad (2.18)$$

And if we start with distribution $v^{(0)}$ over the states S we will be absorbed at N with probability $v^{(0)}\rho^T$ in other words the sum of the element wise product of both vectors. This also gives us the mass which will get trapped at N when a chain started at $v^{(0)}$ runs infinitely long.

Now to reiterate we still have some long run convergence determined by the stationary distribution, but it is dependent on the state i . In general one should use the following lemma to relate the long term behaviour to the stationary distribution for a non-irreducible Markov chain.

Lemma 1 *Let X_n be a Markov chain on S with a stationary distribution w . Then for all states i that are transient the corresponding entry of the stationary distribution w is 0, i.e. $w_i = 0$.*

It should be mentioned that the situation becomes a bit more difficult if we also consider *infinite* state spaces. In that case we would need to split the recurrent in *null-recurrent* and *positive-recurrent* states, but in the finite setting all recurrent states are automatically *positive-recurrent*. In lemma 1 we get the theoretic characterisation of our long term behaviour, i.e. a birth-death chain with two absorbing states should get absorbed completely in the long run with 0 mass at the transient states.

2.2.4 Quasi-stationary distribution

The *quasi-stationary distribution* was first introduced by **Darroch and Seneta, 1965** together with the *pseudo-stationary distribution* which we will cover later. In the simplified version of our birth-death chain with two absorbing states, in figure 2.7 we omitted the explanation of the different labels which we give now. We can look at our chain as having only two states T and R . To go from T to R there are two possibilities. Say we are in i with probability $v_i^{(n)}$. Then we are at 1 with probability $v_1^{(n)}$ and a *death* occurs with probability d_1 resulting in the number of C players dropping to 0 which means they died out and we are absorbed. We could also be in the opposite situation with probability $v_{N-1}^{(n)}$ with $N - 1$ players for strategy C and a *birth* happens with probability b_{N-1} leading to the D players becoming extinct, which also leaves us absorbed. Therefore the combined probability to leave the transient states T (in step n) and become absorbed in R is in our case $d_1 v_1^{(n)} + b_{N-1} v_{N-1}^{(n)}$. Once we are in R we can never leave it again which is why we wrote the probability 1 at the arc leaving and entering R . The arc leaving and entering the transient states T is denoted with $1 - d_1 v_1^{(n)} - b_{N-1} v_{N-1}^{(n)}$ as this is the probability to survive one more step at time n .

We denote with Q a matrix derived from the transition matrix P , where we removed for all absorbing states the corresponding row and column, i.e. in our case the first and last row and the first and last column. We can look at Q as a *substochastic* transition matrix operating only on the transient states, furthermore Q is primitive which will become important later.

We now want to ask how long can we stay in T without being absorbed in R ? We will need the following definitions to answer that question.

Definition 8 Let X_n be a Markov chain on S and $v^{(n)}$ be its distribution at time n over the states S . As above we assume the states 0 and N to be recurrent and 1 to $N - 1$ as transient. We define $q_i^{(n)}$ as the probability of being in $i \in T$ conditioned on not being absorbed at 0 or N up to time n :

$$q_i^{(n)} := \frac{v_i^{(n)}}{\sum_{k=1}^{N-1} v_k^{(n)}} = \frac{v_i^{(n)}}{1 - v_0^{(n)} - v_N^{(n)}} \quad (2.19)$$

Furthermore we can write all $q_i^{(n)}$ in one vector which we will denote $q^{(n)}$ and it will be our distribution over T at time n conditioned on survival.

$$q^{(n)} := \frac{(v_1^{(n)}, \dots, v_{N-1}^{(n)})}{1 - v_0^{(n)} - v_N^{(n)}} \quad (2.20)$$

If we already know $q^{(n)}$ and Q derived from P as before we can get to $q^{(n+1)}$ via the following calculation:

$$\frac{q^{(n)} Q}{\|q^{(n)} Q\|_1} = q^{(n+1)} \quad (2.21)$$

where $\|u\|_1 = \sum_{k=1}^{N-1} |u_k|$

At last if a stochastic $N - 1$ dimensional vector q fulfills

$$\frac{qQ}{\|qQ\|_1} = q \quad (2.22)$$

we call it a **Quasistationary distribution** for X_n or short **QSD**.

The last definition (2.22) suggests that the **QSD** q is similar to the stationary distribution independent from the starting distribution. Let's fixate $v^{(0)}$ for the moment as $v_i^{(0)}$ being 1 and all other $v_j^{(0)}$ being 0 for j in T with $j \neq i$, i.e. we start in i . We search for a stationary conditional distribution which satisfies $q^{(n)} = q^{(n+1)} = q$ over T . We can rewrite equation (2.22) in terms of searching for the left eigenvector of Q , where we write r for the leading eigenvalue of Q which is given by the following equation, where the second inequality only holds for birth-death chains.

$$r = \|qQ\|_1 = 1 - d_1 q_1 - b_{N-1} q_{N-1} \quad (2.23)$$

Now we get the following equations for the left and right eigenvectors of Q to the eigenvalue r :

$$qQ = rq \quad (2.24)$$

$$Qp^T = rp^T \quad (2.25)$$

Because Q is a primitive matrix we can guarantee the existence of a positive leading eigenvalue r with corresponding positive eigenvectors q and p by **Perron-Frobenius theorem**. This theorem also gives us a limiting behaviour for primitive matrices again in terms of the eigenvectors q and p and the leading eigenvalue r :

$$\frac{Q^n}{r^n} \xrightarrow{n \rightarrow \infty} \frac{p^T q}{qp^T} \quad (2.26)$$

Now looking at the following equation for the probability to be at $j \in T$ when starting in i and not being absorbed at time n where we can take the limit using (2.26).

$$\begin{aligned} \mathbb{P}[X_n = j | X_n \notin \{0, N\}, X_0 = i] &= \frac{v_j^{(n)}}{1 - v_0^{(n)} - v_N^{(n)}} \\ &= \frac{q_j^{(n)}}{\sum_{k=1}^{N-1} q_k^{(n)}} \xrightarrow{n \rightarrow \infty} \frac{p_i q_j}{\sum_{k=1}^{N-1} p_i q_k} = q_j \end{aligned} \quad (2.27)$$

The first two equations are just our definition of $q^{(n)}$ we then took the limit and cancel the p_i term to arrive at only q_j which is independent from the starting state i . We also used that the q_k sum to 1 over $k \in T$. We can conclude that no matter what starting distribution $v^{(0)}$ is given over T we arrive at the same limiting conditional distribution over T , namely the quasi-stationary distribution q . In some sense this is similar to the ergodic theorem for irreducible finite markov chains.

The equations given with (2.22) become a lot simpler when applied to a birth-death chain defined by the transition matrix in figure 2.6. They then read

$$\begin{aligned} q_i(1 - d_1 q_1 - b_{N-1} q_{N-1}) &= q_{i-1} b_{i-1} + q_i r_i + q_{i+1} d_{i+1} \\ &\text{for } i \in \{2, 3, \dots, N-2\} \\ q_1(1 - d_1 q_1 - b_{N-1} q_{N-1}) &= q_1 r_1 + q_2 d_2, \quad \text{for } i = 1 \\ q_{N-1}(1 - d_1 q_1 - b_{N-1} q_{N-1}) &= q_{N-1} r_{N-1} + q_{N-2} d_{N-2}, \quad \text{for } i = N-1 \end{aligned} \quad (2.28)$$

Here we used that $\|qQ\|_1$ becomes $1 - d_1 q_1 - b_{N-1} q_{N-1}$. We can do this because all q_i sum to 1 which is our last equation. We don't know an explicit formula for the solution to this system of equations, which is why we will approximate the quasi-stationary distribution numerically.

Now after that long definition we finally have a relevant piece we need to talk about different aspects of the long term behaviour of our birth-death chain. The quasi-stationary distribution tells us how our chain is distributed if it's not yet absorbed, so if it takes a long time to get extinct this concept is quite relevant as it differs a lot from the stationary distribution given in 2.18.

2.2.5 Pseudo-stationary distribution

Another interesting concept concentrating more on the medium run behaviour of our imitation chain is given with the *pseudo-stationary distribution* (PSD). As already mentioned this was first introduced in **Darroch and Seneta, 1965** and builds onto the quasi-stationary distribution q . To find q we solved the following equation $qQ = rq$ where r is the leading eigenvalue of Q . Now we need to find the right eigenvector to the leading eigenvalue r of Q , i.e. we need to solve $Qp^T = rp^T$ for the $N-1$ dimensional vector p .

Definition 9 Let q be the quasi-stationary distribution of a birth-death chain X_n on S with absorbing states at 0 and N and transition matrix P and corresponding $Q = P|_{T \times T}$. If a

vector p solves $Qp^T = rp^T$, we define the **pseudo-stationary distribution** as

$$qp \quad \text{with } i\text{'th entry given by } q_i p_i \quad \forall i \in T \quad (2.29)$$

where we normalize qp so it fulfills $\sum_{i=1}^{N-1} q_i p_i = 1$.

We can derive the pseudo-stationary distribution similar to the quasi-stationary distribution. Let m and n be positive integers with $m < n$. Now the probability of being in state j at time m when we started in i and will still not be absorbed in the future at time n is given by the equation below. Here we have to briefly use the notation $q_{ij}^{(n)} := \mathbb{P}[X_n = j | X_n \notin \{0, N\}, X_0 = i]$ to be able to specify the probability going from i to j while conditioning on survival up to n .

$$\begin{aligned} \mathbb{P}[X_m = j | X_n \notin \{0, N\}, X_0 = i] &= \frac{q_{ij}^{(m)} \sum_{k=1}^{N-1} q_{jk}^{n-m}}{\sum_{k=1}^{N-1} q_{ik}^{(n)}} \\ &\xrightarrow[n-m \rightarrow \infty]{m \rightarrow \infty} \frac{r^m p_i q_j r^{n-m} \sum_{k=1}^{N-1} p_j q_k}{r^n \sum_{k=1}^{N-1} p_i q_k} = q_j p_j \end{aligned} \quad (2.30)$$

For the limit we used again (2.26) from **Perron-Frobenius** then we cancel the r terms and p_i and use that the sum of q_k over all k in T is 1. This leaves us with $q_j p_j$ which is the j 'th entry of the pseudo-stationary distribution. Again the PSD is independent of our starting distribution which is a really useful property as we don't have to differentiate the PSD between different starting points of our chain.

Where the quasi-stationary distribution describes the long run behaviour, the pseudo-stationary distribution should be seen as a mid term distribution. It can be interpreted as the distribution we are in if absorption is still a long time away but we've taken already a large amount of steps. So we are conditional on survival a long way into the future.

2.2.6 Expected time until absorption

Another interesting thing to look at when talking about processes with absorbing states, is how long it will take on average to be trapped in one of them. We will call it expected time until absorption or average fixation time and denote it with τ . It is calculated as follows for a birth-death chain with absorbing states at 0 and N where we know Q :

$$\tau = (\mathbf{Id} - Q)^{-1} \mathbf{1} \quad (2.31)$$

Where \mathbf{Id} stands for the identity matrix and $\mathbf{1}$ is a $N - 1$ dimensional column vector filled with 1. Then τ is an $N - 1$ dimensional vector where the i 'th entry τ_i is the expected number of steps until absorption when starting in i .

For birth-death chains there is an explicit formula for τ_i , but as we calculate everything using vectorized functions, it's easier to use the above equation.

We will also calculate the expected time until absorption when one starts in distribution v , which we will denote with τ_v . We can calculate it via:

$$\tau_v = \sum_{i=1}^{N-1} v_i \tau_i \quad (2.32)$$

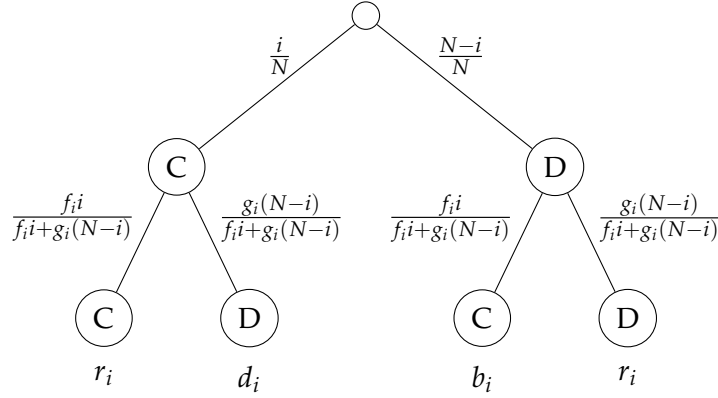


FIGURE 2.8: Tree describing the imitation process.

Often we use the *uniform* distribution as v , then τ_v is just the arithmetic mean of all τ_i and can be seen as the *average time to absorption* if one starts uniformly random over the states T .

2.3 The Moran model

We now focus on a population of N people in which the inhabitants engage in symmetric two person games to determine who has the most fitness. We model our population as a *birth-death chain* on the States S , where the state i represents a population of i many C players and $N - i$ players of strategy D. In our model one player per iteration can change his strategy. Meaning per iteration we first select a random player then choose randomly which player he wants to imitate. This is why the Moran model is also called a population model with imitation. An imitating C player can choose from all other players whom to imitate meaning he can also choose himself and other C players. Sometimes this *self imitation* is excluded but we want that as a possibility, because otherwise the remain r_1 probability is only dependent on the D payoff and if a C player does well against D it should increase his possibility to survive. We will explain the imitation process with a tree pictured in figure 2.8. The first layer chooses the person that will get the choice of whom to imitate in the second layer. The probability of choosing a C player in the first step is simply $\frac{i}{N}$, the number of C players divided by the number of all players. Because we model frequency dependent selection we will include the fitness of a strategy given the current population in the decision process of whom to imitate, so we should first define what we will mean by that.

Fitness in the Moran Model

We have our population of N players total of which i players are running with strategy C. So the other $N - i$ players play strategy D. These strategies belong to the two by two symmetric game given with 2.33 where we restrict the entries to be non-negative. The reason for this will be explained in a moment.

$$\begin{array}{cc} & \begin{matrix} C & D \end{matrix} \\ \begin{matrix} C \\ D \end{matrix} & \begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix} \end{array} \quad (2.33)$$

Now we can derive the average payoff for a C player against the current population which is in the state $(i, N - i)$. So on average he will get payoff α about $\frac{i-1}{N-1}$ of the time and payoff β the rest of the time which is about $\frac{N-i}{N-1}$. The first fraction has $i - 1$ in the numerator because here we exclude the possibility of self-play. This will later lead to an interesting phenomenon if we set s to 1. We will talk about it in 4.2.5.

Definition 10 We denote with F_i the average payoff of a C player in an $(i, N - i)$ population, analogously for a D player the average payoff is denoted by G_i .

$$\begin{aligned} F_i &:= \alpha \frac{i-1}{N-1} + \beta \frac{N-i}{N-1} \\ G_i &:= \gamma \frac{i}{N-1} + \delta \frac{N-i-1}{N-1} \end{aligned} \quad (2.34)$$

Furthermore we define with $s \in [0, 1]$ the selection pressure of the model and call f_i and g_i the fitness of C or respectively D.

$$\begin{aligned} f_i &:= (1-s) + sF_i \\ g_i &:= (1-s) + sG_i \end{aligned} \quad (2.35)$$

The amount the average payoff influences the fitnesses f_i and g_i is controlled with the parameter s . We will often set it to 1 because it makes discussions easier but to be able to do that the game matrix needs to be positive in every entry. Otherwise we might get ill defined probabilities. This is no serious restriction because every game can be transformed by adding the same large enough constant to every entry which then results in a game with the same properties as before but satisfying our condition.

The fitness now becomes a factor in the decision of a player which other player he wants to imitate. The higher the average payoff F_i is, the higher the fitness f_i will be. We want to model the imitation as if the player would look around observing who is doing well and chooses accordingly. So we will weigh the probability of being chosen with the fitness, hence the numerator i times f_i or $N - i$ times g_i in layer two of 2.8. We multiplied the amount of players with their fitness to also weigh in the current population structure in the decision, so if almost no players of a strategy exist their chances of being imitated will be small. With these small assumptions and a normalisation with the total fitness of the population $if_i + (N - i)g_i$ we get the probabilities of being imitated in the second layer of 2.8. It should be noted that if one player type no longer exists it can never be reintroduced, because the probabilities in both layers will be 0 or 1 in this case.

Let's go back to our birth-death chain on the states S , which we use to model the amount of C players in our population. Therefore b_i is the probability of increasing the number of C players by one, when already i many C players exist. This can be derived from the tree 2.8. Only if we first chose a D player which then imitates a C player, will the number of C players increase by one so we denote this path in the tree with b_i . Accordingly the C players only decrease if we first chose a C player, which then imitates a D player so we can write d_i at the bottom of that path in 2.8. The probabilities of the remaining two paths can be added two get the remain probability of the chain r_i . We capture this result below.

Remark 1 Our Moran Model will consist of a symmetric two by two game from which we derive a fitness for each strategy in each state which then gives us transition probabilities for our birth-death chain via an imitation process given in 2.8. For all $i \in \{0, 1, 2, \dots, N\}$ these probabilities are:

$$\begin{aligned}
b_i &= \left(\frac{N-i}{N}\right) \left(\frac{if_i}{if_i + (N-i)g_i}\right) \\
d_i &= \left(\frac{i}{N}\right) \left(\frac{(N-i)g_i}{if_i + (N-i)g_i}\right) \\
r_i &= 1 - b_i - d_i
\end{aligned} \tag{2.36}$$

Usually we set the states 0 and N to be absorbing but in our case they are automatically absorbing following from our imitation process. This leaves us with a well defined birth-death chain on the states S , which we will denote with Y_n and often refer to as the imitation chain.

For the most part we will set s to 1 which then requires a positive game matrix and results in the following transition probabilities for all $i \in \{0, 1, 2, \dots, N\}$:

$$\begin{aligned}
b_i &= \left(\frac{N-i}{N}\right) \left(\frac{i(\alpha_{\frac{i-1}{N-1}} + \beta_{\frac{N-i}{N-1}})}{i(\alpha_{\frac{i-1}{N-1}} + \beta_{\frac{N-i}{N-1}}) + (N-i)(\gamma_{\frac{i}{N-1}} + \delta_{\frac{N-i-1}{N-1}})}\right) \\
d_i &= \left(\frac{i}{N}\right) \left(\frac{(N-i)(\gamma_{\frac{i}{N-1}} + \delta_{\frac{N-i-1}{N-1}})}{i(\alpha_{\frac{i-1}{N-1}} + \beta_{\frac{N-i}{N-1}}) + (N-i)(\gamma_{\frac{i}{N-1}} + \delta_{\frac{N-i-1}{N-1}})}\right) \\
r_i &= 1 - b_i - d_i
\end{aligned} \tag{2.37}$$

This leaves us with a fairly simple setup to model stochastic frequency dependent selection which is governed by interactions in two by two games. We can influence the development of the population of N individuals via our game matrix.

Chapter 3

Methodology

Here we will give a detailed account of which methods were used during the thesis. Precise parameter settings and also the programming language and packages will also be given. The code written for the numerical simulations and plotting is available on github found under <https://github.com/metaconsole/MoranModel>.

For a start we want to give credit to the great open-source community surrounding *python*. All the simulations and all of the plotting was done solely with python using the *spyder IDE* and the *anaconda* distribution and we couldn't recommend them enough. To be more explicit *numpy*, *seaborn* and *matplotlib* were the main packages used.

3.1 Numerical simulation of the replicator dynamic

In 2.4 we defined the replicator dynamics. We will not solve them explicitly but approximate a solution numerically using the *Euler method*.

The Euler method or *forward Euler method* is a very basic algorithm for numerically integrating an *ordinary differential equation* with a given initial value by taking multiple steps according to the differential equation. Let's restate our situation. We have the replicator equation given by

$$\dot{x} = x(1-x)[x(\alpha - \gamma) + (1-x)(\beta - \delta)] \text{ with } t \in \mathbb{R}^+ \text{ and } x(t) \in [0, 1]$$

We can choose an arbitrary initial value $x(0) = x_0$ which will determine in what state the population starts. Now we need a step size h which we will set to 0.01 and an integer that tells us how many steps we will make, here 1000 was sufficient. Then the Euler method tells us to calculate our next data point recursively with the following formula:

$$x_{n+1} = x_n + hx_n(1-x_n)[x_n(\alpha - \gamma) + (1-x_n)(\beta - \delta)] \quad (3.1)$$

This gives us in our case 1001 pairs of (t_k, x_k) which we will plot to approximate the replicator dynamic. We will use this method later to obtain approximations to the different deterministic dynamics generated by different two by two games. In 3.1 the implementation of the euler method is given, where one can see that the only input to the function not already mentioned is the *game* variable which stands for the two by two game matrix. The outputs of the function t_k and x_k both are vectors which combined result in the pairs (t_k, x_k) .

```

1 import numpy as np
2
3 def rep_moran(game, start, h= 0.01, steps = 1000):
4     alpha, beta, gamma, delta = game.flatten()
5
6     x_k = [start]
7
8     for i in range(steps):
9         x_k.append(x_k[-1]+h*x_k[-1]*(1-x_k[-1])*(x_k[-1]*\
10                (alpha-gamma)+(1-x_k[-1])*(beta-delta)))
11
12     t_k = np.arange(0, h*(steps+1), 0.01)
13     return t_k, x_k

```

FIGURE 3.1: The implementation of the euler method with parameters game matrix, the starting condition, the step-size and the number of steps to be taken.

3.2 Simulation of the imitation chain

To simulate the stochastic dynamics of a *birth-death* chain a multi purpose class structure was programmed where future features could be added easily. We will shortly go over the structure of this implementation. It was used mainly for simulating the imitation chain and can be extended to simulate a three by three version of the Moran model as well.

3.2.1 Class structure for a Markov chain

The first thing to code was a structure that could represent a very general Markov chain. This led to a **class MarkovChain** with all the attributes that were necessary for defining a Markov chain. The standard attributes are the population size N , a transition matrix P , a two by two game matrix $game$, the selection parameter s , the sets S , R and T . With these most aspects of the chain itself are specified although we already additionally supplied the game matrix which is only necessary for an imitation chain. We then implement several methods to calculate for example the stationary distribution (if it exists) or an approximation to the quasistationary distribution (the power method).

Then a way was necessary to store path specific data and parameters so a **Path** Object was created. Per **MarkovChain** class Object we can store multiple **Path** objects. Each **Path** needs a starting distribution, a **MarkovChain** Object and an identifier *name*. Now we can run simulations and calculations which are dependent on a specific start.

3.2.2 Long-term distribution method

The most basic approach in the study of stochastic processes has to be a pure simulation. So a method to run our imitation chain as long as possible was implemented. The time horizon wasn't determined at the start, but was rather dynamically set. This is a common approach and was also done by **Harper and Fryer, 2016**.

The goal was to start at a given distribution $v^{(0)}$ over the states S and then to take as many steps with our imitation chain Y_n until no more change in the distribution happens, i.e. until $y^{(n)}$ is equal to $y^{(n+1)}$. For obvious reasons true equality was never really reached so we stopped the run if they became really close according to the euclidean norm. For the most part the following qualified as a maintainable abort condition which gives precise results:

$$\|y^{(n)} - y^{(n+1)}\|_2 < 10^{-10} \quad (3.2)$$

```

1  def qsd_approx_script(self, start, iterations = None, precision = 6):
2      """Calculates the Quasi stationary distribution of a MC starting from a
3      given (N-1) Vector. It multiplies it with Q and then renorms the result to
4      be stochastic again.
5      This will be iterated until the distribution stops changing or a given
6      number of iterations is reached."""
7      n = np.shape(self.Q)[0]
8      if np.shape(start)[0] != n:
9          return 'start vector has wrong dimensions.\n'\
10                 'Need '+str(n)+' entries.'
11      count = 0
12      if iterations is None:
13          cond = True
14      else:
15          cond = iterations > count
16      while cond:
17          step = start.dot(self.Q)
18          step /= sum(step)
19          if la.norm(start - step) < 10**-precision:
20              break
21          start = np.copy(step)
22          count += 1
23          if iterations is not None:
24              cond = count < iterations
25
26      return step, count

```

FIGURE 3.2: Fixed point method for approximation of QSD.

When the abort condition was satisfied the distribution $y^{(n)}$ at that time n was returned. Sometimes but very rarely our abort condition was too strong and never triggered, then the precision was decreased by setting the exponent on the right-hand side to -8 or at minimum -6 . Additionally a condition of at most one million steps was included. This maximum step number was only ever reached in the case of large N and a well balanced anti-coordination game. All other cases came nowhere near this amount of run time.

We will call that distribution over all the states in S that is the result of such a terminated simulation the *long-term distribution* of our imitation chain and abbreviate it by *LTD*. In the cases where the LTD becomes completely absorbed we can compare its result for the amount of mass absorbed at 0 and N to the product of our starting distribution and the fixation probability as described in 2.2.2. If we start uniformly distributed over T we can just take the mean of our fixation probability.

3.2.3 Quasi-stationary distribution approximation

For the imitation chain, or a birth death chain with two absorbing states there is for the most part no explicit formula known for the quasi-stationary distribution. This is why we need to have a method for approximating it.

Power method

We can define the map $v \mapsto \frac{vQ}{\|vQ\|_1}$ which maps the $N - 2$ dimensional probability simplex into itself. With the fact that this map is a contraction the *Banach fixed point theorem* guarantees a unique fixed point. This fixed point is the quasi-stationary distribution q defined in equation (2.22) and solves $qQ = rq$ where r is the leading eigenvalue of Q .

This is commonly known as the *power method* and leaves us with an easy way to numerically approximate the qsd. We just need to iterate the above map, with an arbitrary starting distribution, on T . The algorithm for doing that is given in figure 3.2. We use the same aborting condition given in equation (3.2), but can alternatively also just take a fixed number of map iterations given as a parameter **iterations**. To reiterate we use the power method to find the left eigenvector, corresponding to the leading eigenvalue of Q .

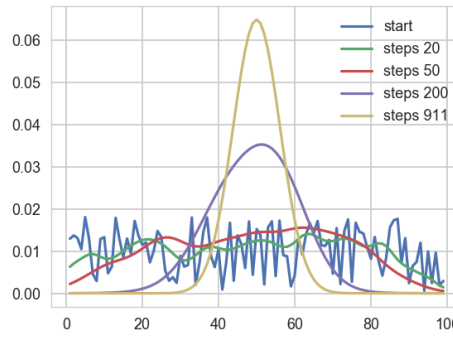


FIGURE 3.3: Convergence to the leading left eigenvector of Q using the power method.

```

1 Tau_unif = []
2
3 x_axis = np.arange(5, 200)
4
5 for N in x_axis:
6     moran = bd.MarkovChain(N, s=1, game=G)
7     Tau_unif.append(np.mean(moran.expected_time_fixation))
8     del moran

```

FIGURE 3.4: Script for calculating the average time until absorption for increasing N .

We also use the power method to find the right eigenvector of the leading eigenvalue of Q . To be precise we find a vector p that solves $Qp^T = rp^T$ as we need it to calculate the pseudo-stationary distribution described in section 2.2.5. We omit the algorithm here because it's essentially the exact same power method as before except used on Q^T , multiplied with q and normalized.

To illustrate we plotted the results of different numbers of iterations in figure 3.3. We started with a vector over T where each entry was chosen uniformly random from $[0, 1]$. We then normalised it with the sum of all elements so that it's a distribution over T . The matrix Q was taken from an imitation chain defined by the game $\begin{pmatrix} 1 & 4 \\ 4 & 1 \end{pmatrix}$ where we set s to 1 and N to 100. The curve plotted in yellow is the distribution that also triggered our abort condition after 911 steps. This calculation finished instantly which shows how efficiently this method performs.

3.2.4 Additional calculations

To further analyse our imitation chain we implemented small methods to derive key parameters. This included the fixation probability, the expected time until fixation, the mass absorbed at N or the interior stable state. One very valuable method was to write mini scripts where everything was fixed and only one parameter was allowed to vary over a given range. Then per value results were calculated and stored. This was used to generate many graphs in chapter 4 and provides deep insights. For example to plot the growth of the *average fixation time* with increasing population size required such a script. We needed to generate the entire model and calculate the average fixation time for each N , which is done in a **for loop**, see figure 3.4.

Chapter 4

Results

We could derive interesting differences between the deterministic model and the stochastic one. It needs to be said that the stochastic models themselves are strongly determined by settings like population size, the game matrix and the selection pressure governing imitation, that's why as a first step a few exploratory trials were conducted to determine which range of these parameters seemed reasonable.

4.1 Experiment to determine population size

First we needed to consider the question of how large the population should be? At one hand our population couldn't be too small because then we got absorbed too fast just by chance, meaning we never experienced long survival times. In theory we could just make it very large but that hinders computation dramatically. Let's get specific, the largest test run had a population size of 2000 which was quite hard to manage. A low end for a reasonable population would be 5 but then you need immensely high selection pressure induced by the game. We arrived at $N = 100$ as a sweet spot for the population size leading to fast run times and being large enough to enable all dynamics of a chain to unfold.

One phenomena we were interested in was the non absorption of the long-term distribution, defined in 3.2.2, in a anti-coordination game setting. So the test run itself consisted of fixing an anti-coordination game matrix G , setting the selection strength s to one and then simulating the imitation chain for different values of N , i.e. finding the long-term distribution. Setting s to one allows us to control the fitness of the population solely with the game G , more precisely with β and γ . During this test we chose the game matrix always to be an anti-coordination game, i.e. we set α and δ to one and β and γ equal and greater one. For example:

$$\begin{pmatrix} 1 & 3 \\ 3 & 1 \end{pmatrix} \quad (4.1)$$

Going forward different values for the off-diagonal of G were set and then tests run with different values of N . We always started in the middle of our population with as many C as D players. If the mass got absorbed completely before the condition (3.2) triggered we considered the N as too small. Because of the anti-coordination game G we want an N that is large enough so the long-term distribution is also bistable meaning only a fraction gets absorbed and most of the mass is over T . As already mentioned this is the case for the above game G and a population of 100, to be precise our run was aborted when only $1.922 * 10^{-10}$ of our mass was absorbed. Here our chain took 2148 steps and was nowhere near full absorption, we will later revisit this in the anti-coordination case where the long term distribution

is already quite stable.

4.2 Deterministic versus stochastic models

Let's now move on to compare how the stochastic and deterministic models fare in providing us with useful information for each kind of game. We will look at a few main avenues to draw information about our models from. First the deterministic prediction, then the different kinds of distributions for our stochastic model, namely the quasi-stationary, the pseudo-stationary and the long-term distribution. We don't need to check the stationary distribution for each game, as it is always the one defined in equation (2.18) which tells us that for $N \rightarrow \infty$ our imitation chain will get absorbed at 0 and N .

4.2.1 The neutral case or no selection

As a baseline we look at the model with no selection pressure. This corresponds to the neutral case in the replicator equations meaning we set the game matrix so that all four entries are equal. Let's first take a look at what our replicator dynamic would predict for this case.

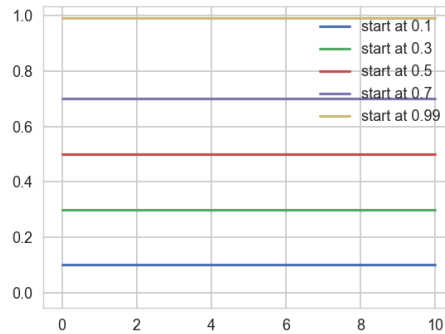


FIGURE 4.1: Replicator dynamics of a neutral game with time on the x-axis and the population state on the y-axis.

In figure 4.1 we see that the trajectories of each population are constant, meaning no absorption or evolution takes place. This makes sense as the replicator dynamic is only dependent on the games payoff differences per column, which in this case are all 0. One can interpret this along the lines of, if the game is completely fair no competition exists and every population is ultimately stable.

Now we compare the stochastic model against this. We set the selection pressure parameter s to 0, which is equivalent to just setting the game to a neutral one. But it's more efficient calculation wise. Now the population size does not really matter that much, so we set it to 100 as this setting will be used again later.

In figure 4.2 we simulate this chain over the time horizon of 5000 iterations. The number 5000 is the average time until absorption when one starts uniformly random in T . It will later turn out that this is by comparison a very long time to be absorbed. We show the *expected time* until absorption, when starting at state i , in figure 4.4 from which we derived the average of 5000. One can also look at the average time until

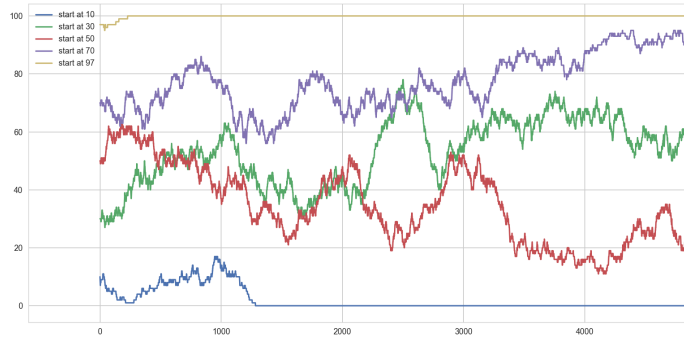


FIGURE 4.2: Paths of a neutral imitation chain.

absorption for different population sizes and as it turns out different games result in different types of growth. In **Antal and Scheuring, 2006** this is studied in detail and we can verify their results here. They state that in the neutral case the average time until fixation grows like $N(N - 1)$ for increasing N , which can be seen in figure 4.3.

Now if we take a look at the long-term distribution, given in figure 4.4, we see that eventually we will be absorbed completely and because we started uniformly distributed we get the same mass of 0.5 at 0 and N . In this plot we used N equal to 40, because then the shape of the pseudo-stationary distribution is easier to distinguish and for this case in particular a larger N just stretches the plot in width. For N equal to 100 we took 59240 steps until the abort condition (3.2) triggered. The long time until the abort is due to the fact that there are almost always a few paths that survive quite a long time.

The neutral case is the only one where we can give an explicit solution to the quasi-stationary distribution. For a neutral imitation chain on the states $S = \{0, 1, 2, \dots, N\}$ the quasi-stationary distribution is approximately given as

$$q_i \approx \frac{1}{N-1} \quad \text{for all } i \in T, \quad (4.2)$$

or in other words the uniform distribution over T . The plot in figure 4.4 of the QSD is actually derived with the power method described earlier, but they obviously give the same result. Now we already know that the QSD gives the distribution prior to absorption, but how can this realistically be the uniform distribution? This is due to the fact that the neutral imitation chain has no focused pull whatsoever, or to be more precise the death and birth probabilities are equal in each step i . We plot them on the left in figure 4.5, where only the green death probability curve can be seen, because it overlaps the birth probability curve perfectly, except for the state 0 where we don't have a possibility of death. The term pull is a heuristic as to how much our probability mass gets shifted around by the chain and in this case the shift goes always equally in both directions, which is why we can start anywhere equally likely as our QSD. After one step everything gets shuffled around and not transported in any designated direction and therefore more or less stays where it is, in the conditional sense of survival. The neutral imitation chain does what we would expect. It moves around quite random, because there is no fitness to guide it and only gets absorbed by chance.

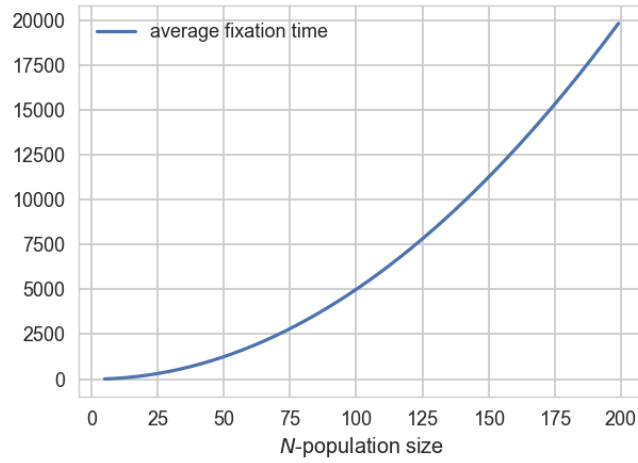


FIGURE 4.3: The average time until absorption in the neutral case, having the shape of a parabola.

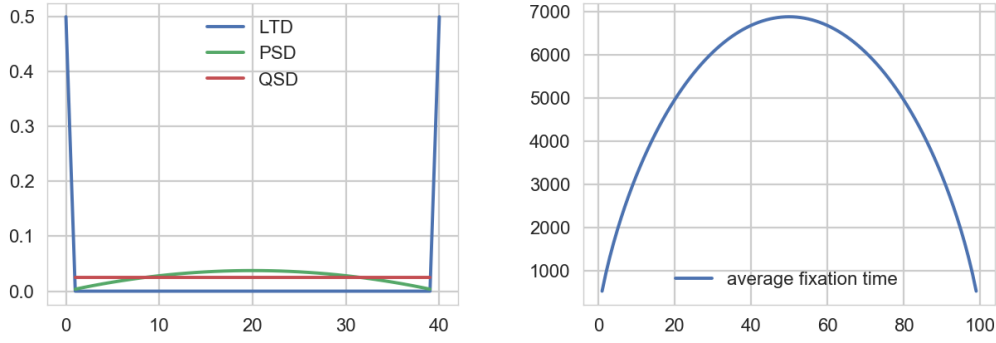


FIGURE 4.4: (Left) The long and mid term behaviour of a neutral imitation chain. (Right) The fixation time shown per state i of a neutral imitation chain.

The pseudo-stationary distribution is quite intuitive, as it shows how we are allocated if extinction is still a long time away. Here that leads to a parabolic formed PSD distribution with the peak in the middle, where we can remain the longest before being absorbed. Then it decreases steadily towards 0 and N , where we find zero mass. The fact that the PSD has significant positive mass at every state in T is quite remarkable and is again due to the lack of focused pull in the movement of our chain. We also recognise this looking at the fixation probability ρ_i on the right in figure 4.5, which only increases linearly from 0 to N . The plot of ρ for every state is an important indicator and it will differ, from case to case, in shape and its non-trivial points, meaning where it is different from 0 or 1. Our heuristic for now is that if ρ_i is non-trivial for a state i then the PSD will have significant mass at that state i .

We now go over the non-trivial games and later revisit the neutral case, when we look at an almost neutral game in 4.2.5.

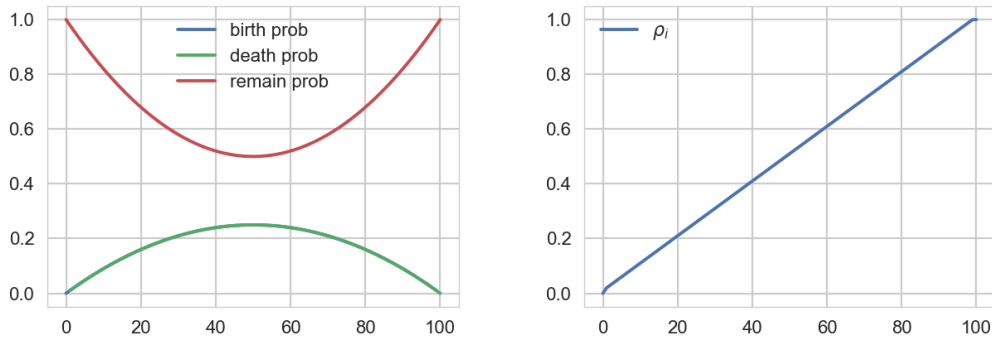


FIGURE 4.5: (Left) The transition probabilities of a neutral imitation chain. (Right) The probability to be absorbed at N when one starts in i , plotted for each state i .

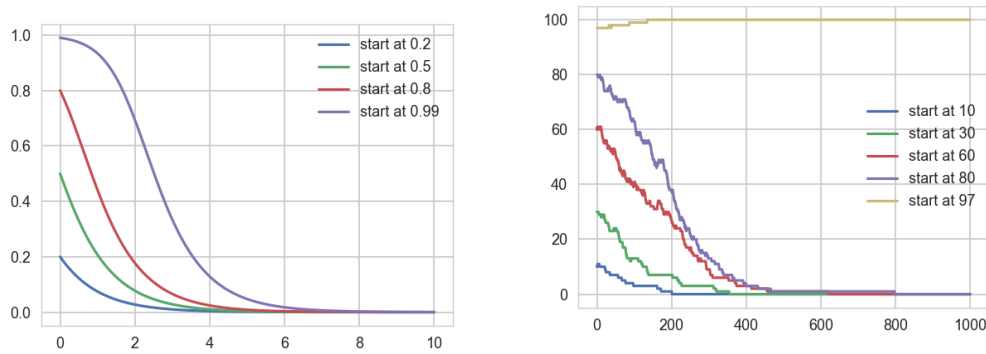


FIGURE 4.6: (Left) REP simulation and (Right) imitation chain paths for the Prisoners dilemma game.

4.2.2 The prisoners dilemma or dominated strategies

We start by examining the case when one strategy dominates the other. We choose the following game matrix G , where we replaced the 0 payoff of C against D with 0.0001, to only have positive entries and still discuss a classic version of the prisoners dilemma.

$$G = \begin{pmatrix} 3 & 0.0001 \\ 5 & 1 \end{pmatrix} \quad (4.3)$$

The replicator dynamics are very clear for this game. At 0 when the extinction of C happens we have our only stable fixed point and we can verify the phase portrait with simulation of four different populations, which we show in the plot 4.6. We can start arbitrarily close to 1 but will still be fixated at 0. This behaviour is only dependent on the differences between the columns of the game matrix, meaning if we had instead chosen the second row as 3.1 and 0.1 so that D still dominates C only not as much as before, we just need to wait longer to see the exact same behaviour as before the change of G .

Next to our replicator equations plot we show five different paths of the imitation chain constructed with the game matrix G given above, the selection strength set to 1 and a population size of 100, so this is the analogous stochastic model. We

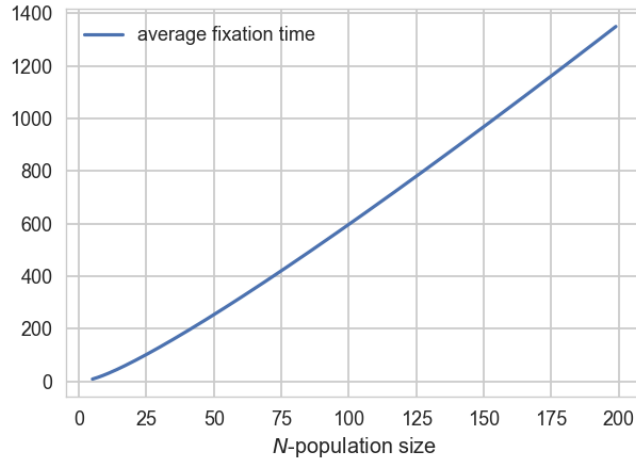


FIGURE 4.7: The average time until absorption for different N in the dominated case.

can see that the behaviour of our chain is quite similar to the REP equation in the sense of the very strong trend to extinction at 0 which captures all paths except the one started at 97. This shows the importance of also considering stochastic models. Let's say we want to ask the question, if one single D player can overtake the whole population of C players? The REP equations answer is always yes because we are deterministic and have to decide in terms of yes or no. In our stochastic version we can start with mass 1 at 99 and then look at the long term distribution generated by that chain. Under these conditions we arrive at the LTD that is completely absorbed but only with mass 0.407935 at 0 and actually mass 0.592064 at 100 after 4544 steps. This means that our stochastic population is quite resilient against the intrusion of a single D player in almost 60% of all cases they defend against the intruder compared to the 0% chance that is given to the C players in the REP equation. Now one should not forget that the REP dynamics considers N infinitely large and can therefore be seen as a limit to our stochastic version. In an infinite population the chance of invasion by only one individual is 0.

The average time until absorption for an *uniform* starting distribution $v^{(0)}$ over T is given as $\tau_{v^{(0)}}$ which is equal to 596.208737. Now the state 0 has trapped almost all the mass (97.584098%) compared to $N = 100$ where only 2.415901% was absorbed. To arrive at this state the chain took 4120 steps, which is a lot longer then the average time until absorption and shows that there are a very small number of paths that survive a really long time. A look at the expected time until absorption plotted for every state T on the right in figure 4.8 confirms this conclusion. The average time until absorption calculated for different population sizes grows like $N \log(N)$ for increasing N , which was also already stated by **Antal and Scheuring, 2006** and can be seen in figure 4.7. It turns out that the dominated case gets absorbed a lot faster than the neutral case, no matter how large the population.

Now consider the quasi-stationary distribution, which reflects our occupation time distribution before being absorbed. We can see our QSD in figure 4.8 and recognize that its mass is concentrated at the states leading to 0, which is our only stable fixed point of the REP dynamics. So the QSD is different than the stationary or long term distribution, but agrees with the deterministic model. Only the states near 0

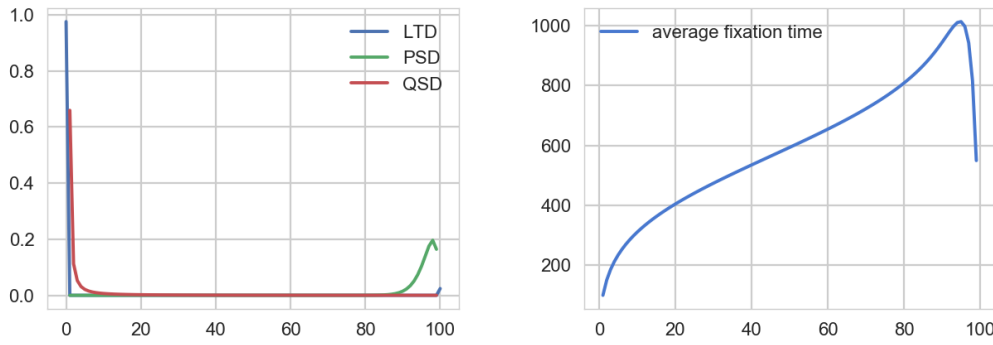


FIGURE 4.8: (Left) QSD for an imitation chain with a prisoners dilemma. (Right) The average fixation time per state, with maximum of 1013.28 at 94.

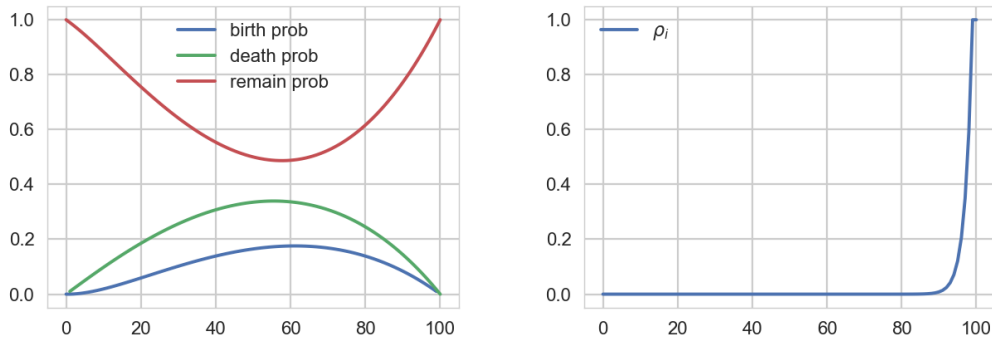


FIGURE 4.9: (Left) The transition probabilities for a dominated imitation chain. (Right) The fixation probability of the same chain, with non-negative values from 87 upward.

are visited frequently before absorption. This can also be seen in the sample paths on the right in figure 4.6, where the bottom four paths have a clear tendency of being absorbed, but are staying longer in the states being closer at 0.

The pseudo-stationary distribution shows where we can stay to not be absorbed for a long time, which in our case means on the farthest point from 0 as we are very likely to be absorbed there, but we also can't go to 100 due to the fact that it has some small amount of pull as we see in 4.9 in the right plot where the ρ_i goes from 0 to almost 1 spanning the states 87 to 98. This interval represents an uncertainty region where we don't know for sure if we get absorbed at 0 or 100. To not be absorbed for a long time into the future one has to stay within this interval, which is why the PSD has its peak at the state 97 where ρ_i is equal to $\frac{1}{2}$.

To reiterate both the transition probabilities and the fixation probability make quite clear how strong the pull towards the state 0 is, in our dominated imitation chain. In figure 4.9 on the left, we see that the death probability is quite a bit higher for every state i , than the birth probability. This results in the almost always 0 fixation probability on the right which shows we will almost always be absorbed at the state 0.

In the case of dominated strategies the overlap between the replicator dynamics and our stochastic model is great. If we start at a state below 94 we will almost certainly be absorbed at 0, which is what the REP dynamics predict, of course the state 94 is no strict boundary. So only the rare case, when starting in a population already quite close to 99 many C players, is not reflected in our deterministic model, because here it's actually more probable to be absorbed at 100 than 0.

4.2.3 Coordination game or bistability

Let's now compare the different dynamics for the case of bistability in the replicator equation, which corresponds to a coordination game in our imitation chain. The following matrix is used in our case study:

$$G = \begin{pmatrix} 3 & 1 \\ 1 & 2 \end{pmatrix} \quad (4.4)$$

The deterministic model is again quite clear. The replicator dynamics now have three rest points at 0, 1 and x^* , where the ones at 0 and 1 are stable. With the given matrix G the unstable interior rest point x^* turns out to be at $\frac{1}{3}$. Every population with a starting frequency of C players less than $\frac{1}{3}$ will be taken over by the D players. Only if the starting frequency of C is higher than $\frac{1}{3}$ they can establish themselves in the population and D dies out. This can be seen in the numerical simulations of the REP dynamic in figure 4.10. Reiterating that the REP dynamics represent an infinitely large population the probability of starting exactly at x^* is 0.

Now comparing our stochastic model in the form of our imitation chain to the REP dynamic, we again see a quantitative overlap between them. We chose N as 100, set s to 1 and used the same game matrix G to define our imitation chain. The simulated paths on the right in figure 4.10, started at 10, 50 and 90, almost look the same as their deterministic counterparts started at 0.1, 0.5 and 0.9. But the closer we get to x^* , which corresponds to the state (33, 67), it's not that clear anymore if both models agree with each other. We can clear up the situation with a look at the fixation probability ρ_i , which gives the chance to be absorbed at N when one starts at i . We plot ρ_i for every state on the left in figure 4.11 and as one can see most of the time it is either 0 or 1. Starting in states 1 to 16 we will almost surely be absorbed at 0 and starting from 52 upward almost certainly at 100. In between these intervals, so from 17 to 51, we get an uncertainty region where we choose randomly where to be absorbed. At one point our chances of being absorbed at 0 or N are even, which marks an important state going forward. It's the state corresponding to x^* of the replicator dynamic. We can find it again as the state where our chance of death d_i and birth b_i are equal. We plot in figure 4.11 on the right the birth, death and remain probabilities of our chain and recognize the intersection of birth and death at approximately 33.

Let's now look at the quasi-stationary distribution (QSD) compared to the long-term distribution (LTD), together with the pseudo-stationary distribution (PSD) which are all plotted in figure 4.14. First the long-term distribution started uniformly distributed is completely absorbed with $\frac{2}{3}$ of its mass at N and only $\frac{1}{3}$ located at 0. So on average we can recapture the replicator dynamic prediction and stay consistent with the fact that our Markov chain should converge to the stationary distribution given enough time.

Now the QSD looks at first a bit counter intuitive, with more of its mass at 0 than

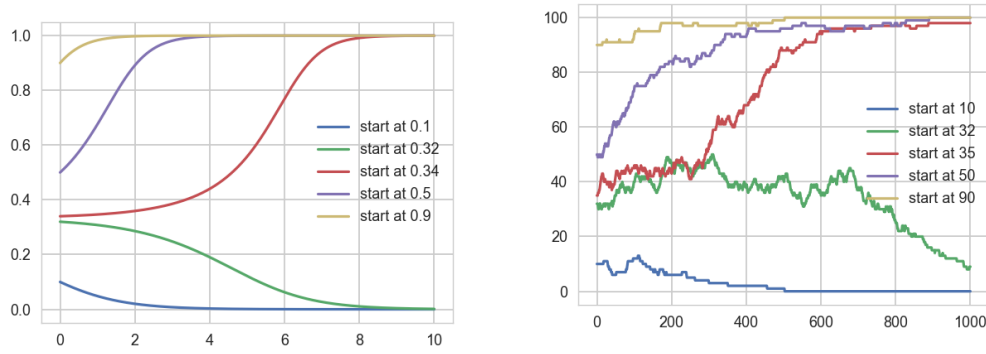


FIGURE 4.10: (Left) Replicator dynamic simulation and (Right) simulated runs of the imitation chain with a coordination game.

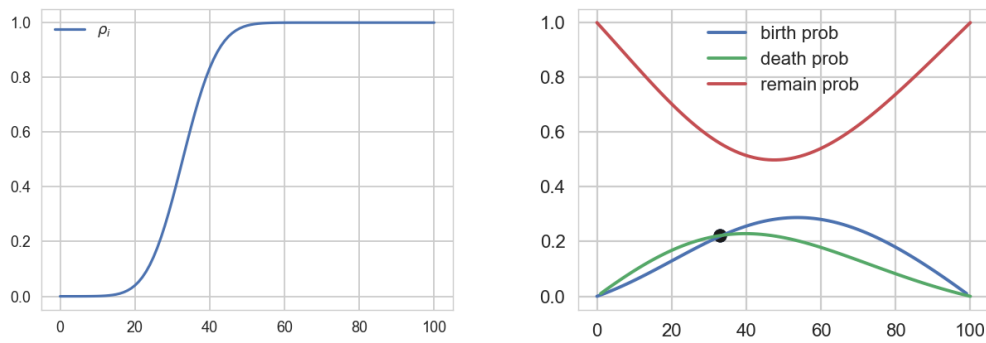


FIGURE 4.11: (Left) Fixation probabilities and (Right) transition probabilities of a coordination game imitation chain.

at N , conflicting the idea that N is the stable state with the greater attraction power, which it definitely is. But we have to interpret the QSD as the distribution our process is in prior to absorption. And the amount of mass the QSD allocates at a state shows how long the chain stays at these states before being absorbed. This means that the higher amount of mass right of 0 is due to the fact that we aren't absorbed as fast there compared to being close to N . The lesser the pull the slower we will be absorbed, although not less certain. We also show again the expected time to fixation which is maximal at 33 the corresponding state to x^* . Here our average fixation time is 676.3698 when starting uniformly distributed. So compared to the neutral case we get absorbed a lot quicker. Now we again plot the average fixation time for different population sizes and see that it grows like $N \log(N)$ in figure 4.12. This is significantly slower than the growth in the neutral case and similar behaviour to the dominated case, suggesting that the pull towards fixation is comparable between coordination and domination case.

The pseudo-stationary distribution describes where we would be allocated, if absorption is still a long time away and we also already made many steps. In our case the place farthest away from any absorbing states is again 33, which is exactly where the peak of the PSD is located. Additionally the mass of the PSD is between the states 4 and 59, which almost aligns with the interval where the fixation probability is non-trivial. The length of this interval was calculated for all N from 20 to 800 and

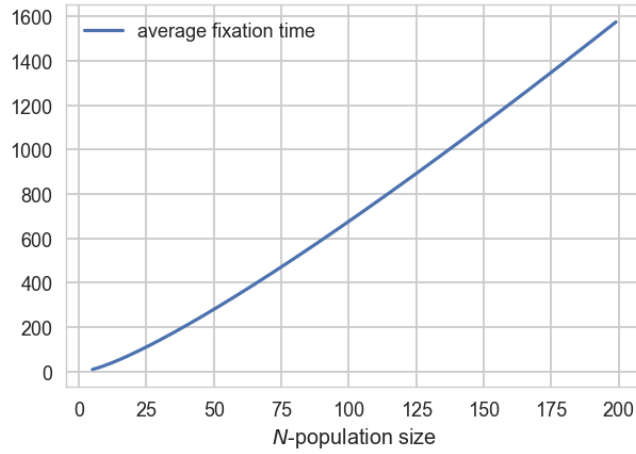


FIGURE 4.12: The average time until absorption growing like $N \log(N)$ in the coordination case.

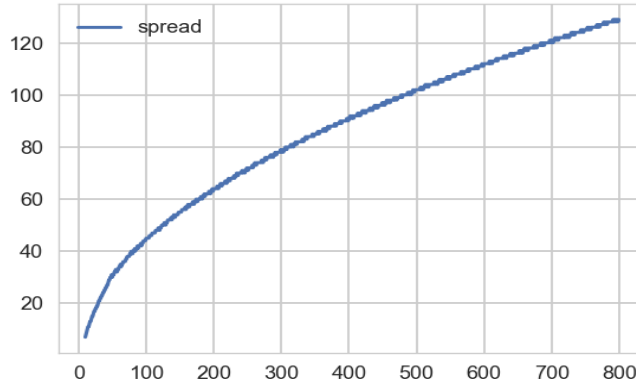


FIGURE 4.13: Length of uncertainty interval of a coordination imitation chain for different values of N . The spread was derived as the distance between k and l where k is the smallest state where $\rho_k \geq 0.001$ and l is the largest state with $\rho_l \leq 0.999$.

it was observed that it grows only logarithmic, which means that in the limit of N infinitely large it becomes insignificant. We plotted this in figure 4.13, the irregularities in the graph are due to the discrete state space but a slowing growth of the length of the interval is undeniable. This re-establishes the known fact that the replicator dynamic is the limit of our imitation chain, because only when starting within this interval the two models disagreed. All other behaviours stay the same for different N .

4.2.4 Anti-coordination or coexistence

Although we are using an anti-coordination game now we will not use the classical *stag hunt* game, because nevertheless its dynamics are equivalent to the ones given in this section, we want to avoid 0 as a payoff and need a less extreme matrix. That's why we choose the payoffs closer together out of the range $[1, 2.1]$ with the smallest

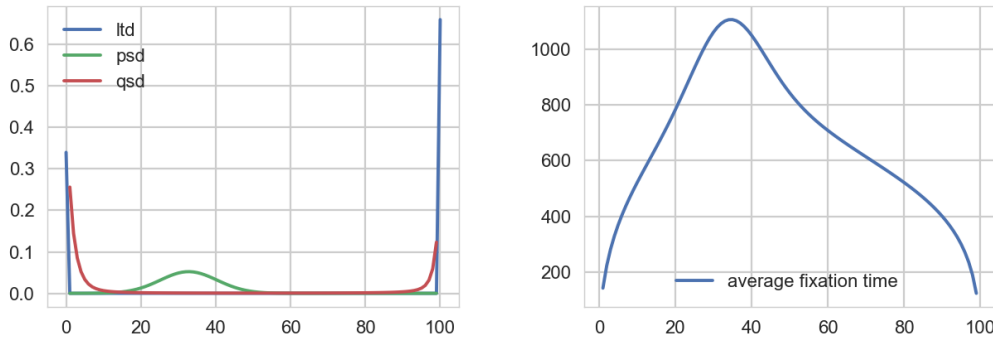


FIGURE 4.14: (Left) Long and mid term distribution and (Right) the average fixation time for a coordination imitation chain.

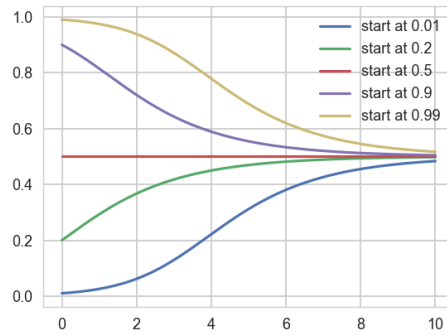


FIGURE 4.15: The replicator dynamic simulation of an anti-coordination game.

values per column on the diagonal.

$$G = \begin{pmatrix} 1.1 & 2 \\ 2.1 & 1 \end{pmatrix} \quad (4.5)$$

For this type of game the replicator dynamic has rest points at 0, N and the mixed rest point at x^* . As before we first take a look at the deterministic simulation to know what to expect, it is given in figure 4.15. We see immediately that 0 and N are not stable and all trajectories converge to x^* , which is equal to $\frac{1}{2}$. The pure populations are not stable, because of the lower payoffs of (C, C) and (D, D) compared to (C, D) and (D, C) . Now the question is, what does this mean for the stochastic model.

We define the anti-cooperation imitation chain by setting the game to G given above, setting s again to 1 and N again to 100 at least for the moment. We simulate a few paths of this chain seen in figure 4.16 and immediately see the drift to the middle of all paths, but the one started at 97, which was unlucky and became trapped at 100 quite early. We also made 10,000 steps already during this simulation and haven't been absorbed for the most part. This phenomenon is quite remarkable and in our setup exclusive to the anti-coordination imitation chains.

First let's look at the mid and long term behaviour given by the QSD, the PSD and the LTD given on the left in figure 4.17. Here the paradox of our case becomes quite clear, namely the apparent similarity between the quasi-stationary distribution

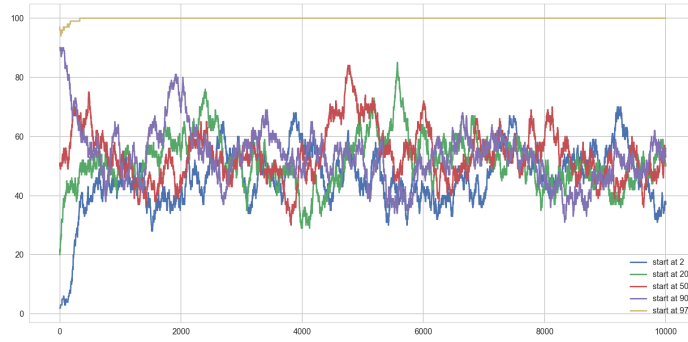


FIGURE 4.16: Simulated paths of an anti-coordination imitation chain.

and the long-term distribution. As a reminder we know the stationary distribution is our limiting distribution if we take up to infinitely many steps. So our long-term distribution should obey this trend as it does in all the cases before, where the LTD only had mass at 0 and $N = 100$, therefore reflecting the convergence to the stationary distribution. We know how much mass should ultimately get trapped at N when starting uniformly by calculating the mean of the ρ_i vector, which gives 0.6499. But now our abort condition triggered after 2,839 steps with almost all of the mass being unabsorbed and distributed over T following the QSD in shape. This paradox was also recognised by **Da Zhou, Bin Wu and Hao Ge, 2010**, where they study the *conditional stationary distribution* in the same kind of model just with added mutation. An analogous effect was mentioned in the book **An Introduction to Stochastic Processes with Applications to Biology, 2003** by **Linda J. S. Allen** in a more general birth-death chain setting. Within our model this paradox arises only in anti-coordination imitation chains with large enough values of N . We arrive at our LTD with an *uniform* starting distribution and at each step a bit of mass is shifted to the traps. This shift to the traps gets so small that almost any abort condition triggers and tells us there is no more change in the LTD. So when N is small enough the flow to the traps happens fast enough before the bulk of the mass gets pulled towards the state 50 corresponding to x^* . In figure 4.18 on the left we see the transition probabilities describing the pull of our chain and the intersection of birth and death probabilities at 50. Now the pull towards the state 100 is only dominating in the states approximately 5 to 45 and the same is true for the death pull on the states 55 to 95 towards 0. These two forces cancel each other out always shifting mass towards 50 which is why we can stay such a long time in the proximity of this state. The expected time to absorption, shown on the right in figure 4.17, of on average 970,026,786.80 mirrors this fact and is by far the largest of the different game types. We also see that $N = 100$ is a little bit stronger attraction wise than 0, because of the higher amount of mass allocated to it in the LTD. Here 0.021 is at state 0 and 0.022 is at N , because we set the payoff $Of(C, C)$ to 1.1, this becomes also more apparent later.

Now what's also interesting is the shape of the quasi-stationary distribution, compared to say the coordination case. Before our pre-absorption distribution was near the absorbing states, now it's concentrated around 50 and almost looks like a gaussian. The reason for that is again the strong pull towards the middle where we will stay for the longest time. That's why we are still in this shape prior to absorption

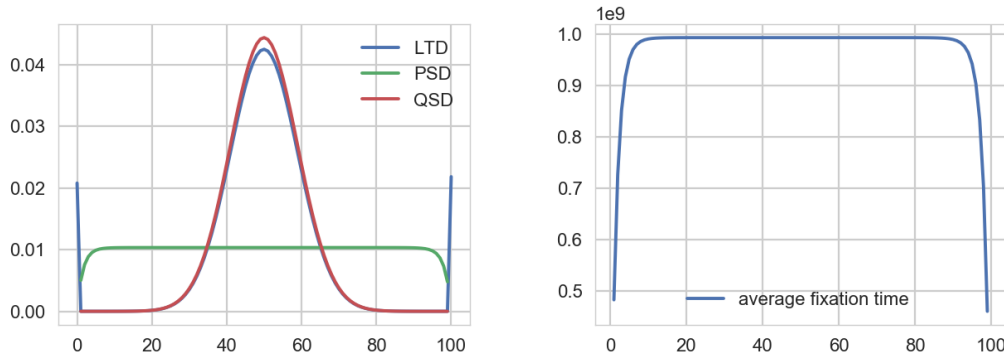


FIGURE 4.17: (Left) Long and mid term distribution of the Imitation chain with an anti-coordination game. (Right) The expected time to absorption with the highest values by far of all game types.

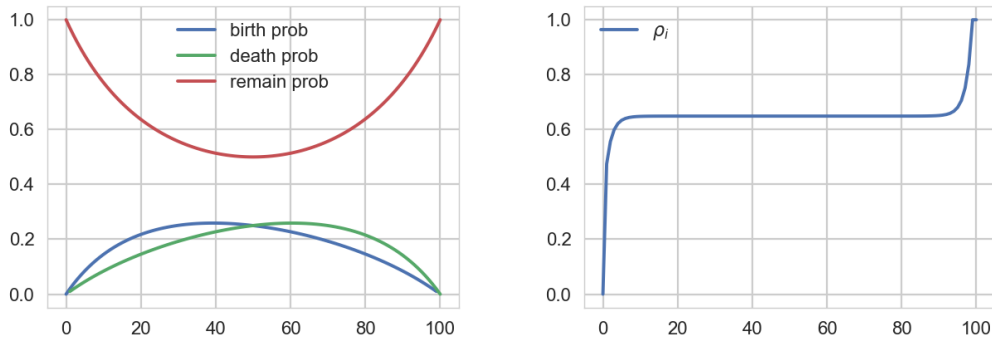


FIGURE 4.18: (Left) Transition probabilities of a anti-coordination imitation chain, with intersection at approximately 50. (Right) The probability to be absorbed at N for each state i , being almost constant from 15 to 82.

and only on the far left and far right the tails of the QSD will flow towards the traps. Meaning most paths will move around the interior states and need to have a streak of bad luck to move straight to an absorbing state and get trapped. The pseudo-stationary distribution shows our mid-term distribution which is now almost uniformly distributed with decreases at the traps. This is due to the fact that it's now possible to be in the interior states and not become absorbed for a long time. This again is verified through the high expected time until absorption in the states from 12 to at least 82. Here the fixation probability sadly is no indicator of how the PSD is shaped. If we tweak the (C, C) payoff α to 1.4 our fixation probability is almost everywhere 1, meaning fixation in N is certain yet the PSD's shape remained more or less unchanged.

The fixation probability also shows an interesting property. Starting on the fringes of the state space still means we will be mostly absorbed next to the trap we started, but now if we start in between 15 to 85 we have a nearly constant probability of around 64.89% to be absorbed in N . To reiterate starting at 80 we have almost the same probability to wander to 0 as if we would start in 20. This shows again how balanced the pulls towards extinction and fixation are in the interior states. First we get pulled towards x^* , then we stay there for a long time and after that wander

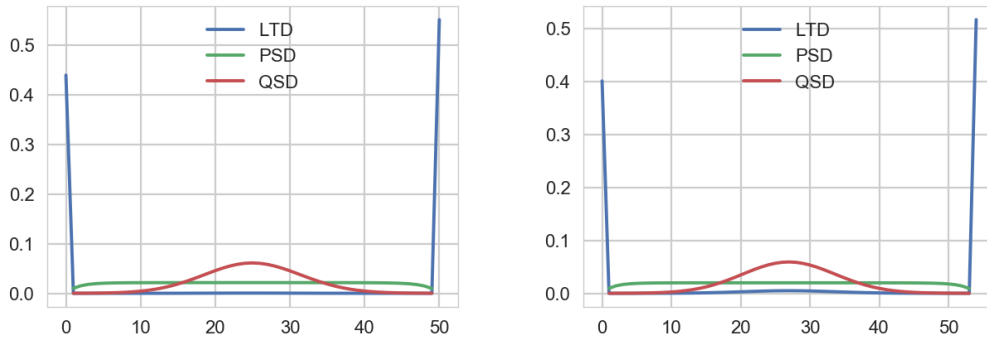


FIGURE 4.19: Long and mid term distribution of the Imitation chain with an anti-coordination game. (Left) N equal to 50 and no mass survival in the LTD. (Right) N equal to 54 where 8.4% survived around state 27.

towards a trap choosing it by chance. Again the absorption strength is stronger at N which is hard to see in the plot of the fixation probability. If we would now decrease the population size the pulls of 0 and N would stay the same, but the number of states with chance 64.89% would go down, meaning only the portion of fixation probabilities that are constant becomes smaller.

The paradox described here only arises if the game matrix is balanced enough between all four entries and the population size is large enough to give place for the mass to fluctuate around the state corresponding to x^* , without being too close to the traps. Leaving our setting constant and only changing N we first find the paradox at a population of around 54. For lower values of N our uniform starting mass gets absorbed completely yet it still takes a very long time. For N equal to 53 all of our mass is absorbed and 0.441 of it at 0 and 0.559 at N . This chain has an average fixation time of already 198,437.95. Now we repeat our simulation with N equal to 54 and only a tiny amount of mass is not absorbed, even after 1,000,000 steps which is the maximal amount we allow for a run. The reach of the maximum amount of steps is due to our strong abort condition. We even surpassed the average fixation time of 395,412.38 by a huge margin, but still no complete fixation took place. The run with $N = 54$ ended with 0.400 mass at state 0 and 0.516 at state N which leaves 0.084 to be allocated around state 27, again the middle of the state space. We show the mid and long term behaviour of these two examples in figure 4.19. The QSD and PSD are independent from N but as we see the LTD is not.

We can recapture an observation already made in the above mentioned book by **Linda J.S. Allen**, where she stated that the average time until absorption grows exponentially with the population size N . Her statement also considered population models based on birth-death chains and now we found it again in this special case for Moran models. We show the graph of the average time until absorption dependent on population size in figure 4.20 where we applied a logarithmic scale to the y axis, so one can easily verify the exponential growth. Our findings again align with **Antal and Scheuring, 2006** who state that for anti-coordination games the average fixation time grows exponentially with N . This exponential growth, surpassing the growth in the other cases, is what separates the anti-coordination case from the remaining ones and restates its differing nature regarding survival times.

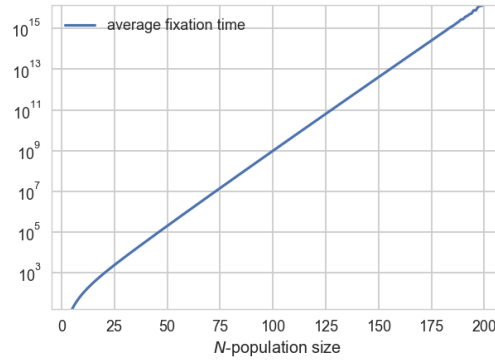


FIGURE 4.20: We plot the average time it takes to become absorbed for an anti-coordination chain for different values of N . We applied an *logarithmic* scale on the y-axis.

4.2.5 Almost neutral case

Now we look at an imitation chain based on a game that is not totally neutral, but should induce no drift in the population. We start with the following matrix G where both rows are identical, but α is different from β .

$$G = \begin{pmatrix} \alpha & \beta \\ \alpha & \beta \end{pmatrix} \quad (4.6)$$

The replicator dynamics of this type of game are the same as for the neutral case, because there are no differences in the column entries, which leads to $\dot{x} = 0$. So according to that our imitation chain should also be completely neutral, like the one in figure 4.2, where we see no particular drift and mostly long survival times. But for N again 100 and s equal to 1 we can fix α to 1 and let β increase over the range $[1, \infty)$. We then witness an increasing pull of the state $N = 100$, which we show by plotting the absorbed mass at N for each value of β in figure 4.21 on the left. As β increases so does the mass absorbed at N approaching 0.6755. One interesting thing to note is that the curve in figure 4.21 looks the same for all values of N and only the maximum value increases with decreasing N . The absorbed mass at N increases almost logarithmic and after $\beta = 100$ there is almost no more gain until the maximum is reached. So this phenomenon arises quickly, but doesn't scale with the increase of β . Now for example with $\beta = 6$ and everything else the same, the chain still looks a lot like a neutral imitation chain only with a little bit more pull towards N . This is verified by the slightly higher mass of the QSD near N , which is otherwise constant like in the neutral case. We again see the LTD on the right in figure 4.21 where the mass at N (0.6287) is significantly higher than at state 0 (0.3712) and also the PSD with a peak shifted slightly to the left. The PSD again mirrors the maximum of the expected time to fixation of 6,000, which we plot on the left in figure 4.22 and has only positive mass where the fixation probability is non-trivial. This chain has an average time to fixation of 4,350.88, which is only a little bit lower than the average fixation time of the neutral chain, which was 5,000. Also the growth of the average fixation time with increasing N is analogously to the neutral case quadratic. On the right in the same plot we see the fixation probability per state and recognise the absorption in N is always more likely, than in the neutral case where we had a line from $(0,0)$ to $(100,1)$.

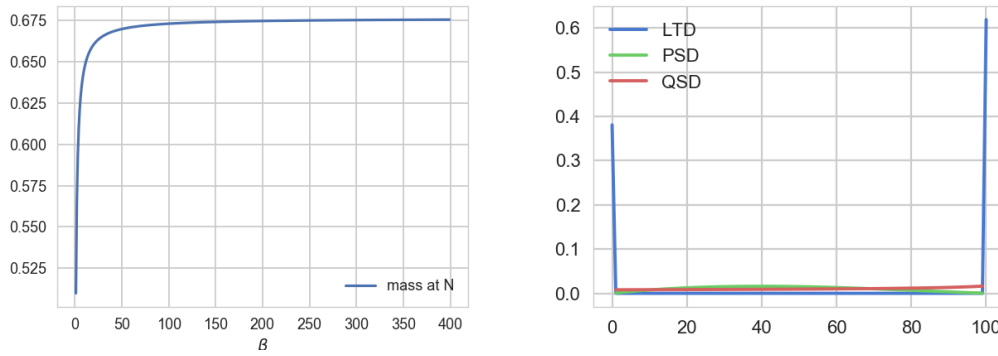


FIGURE 4.21: (Left) For $N = 100$ we plot the mass that get's absorbed at N for different games defined by β . (Right) We plot the QSD, LTD and the PSD for $\alpha = 1$ and $\beta = 6$, which results in an almost neutral behaviour.

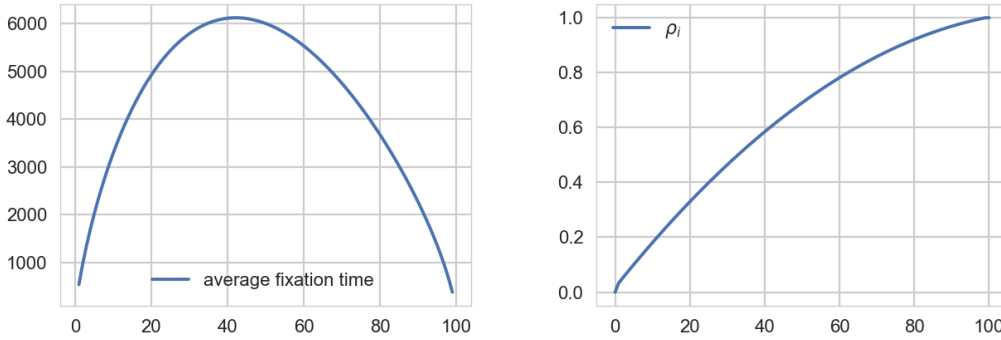


FIGURE 4.22: (Left) The expected time until absorption per state for an almost neutral imitation chain. (Right) The fixation probability for the same chain.

Now to recognize where this effect comes from, one needs to look at the model details to realize we excluded *self-play* when calculating our average payoff in (2.34). This leads to a paradoxical situation, where the higher the payoff β for D against D compared to α , the higher the resulting loss from the exclusion of self play. One could say, no one has an incentive to switch because the rows of the game are the same, but D gets a higher penalty than C on their average payoff as a result from excluding one interaction of two D players. This leads to a slight advantage of C over D , although α is smaller than β . This effect is unique to the stochastic model and isn't captured at all from the replicator equation. This leads to this case being a deviation from the deterministic model, because even for large N the effect is still significant and not evened out by a large population size. For example while keeping everything constant, except for the population size which was set to 800, we still had almost the same LTD as before. Meaning we would need to change our model to include self-play to get rid of this phenomenon and achieve again a truly neutral imitation chain. Although one could easily question the practicality of a game matrix with equal rows and different values for α and β , but the effect is nonetheless interesting and should be mentioned.

4.2.6 Cases of degeneration

We already showed what happens for nice examples of coordination and anti-coordination games. It turns out that one can choose parameter constellations that technically fall into one of the above categories, but behave and look like a dominated or neutral case. Because we set s to 1 for most of our simulations the game matrix needs to have only positive entries but in theory they are not bounded from above. The population size is also unbounded and is chosen independently from the game matrix. We already talked about N and how to choose it in 4.1 and as a result we already know that we need to choose it higher than 5, but less than 2,000 and we arrived at 100 as a suitable population size. So we only look at the game matrix for this size and its significance in determining the observable classification of the chain.

We use the neutral case of our game with every entry being 1 as a baseline. Let's start with a coordination game, so without loss of generality we set δ to 3 and set α as a variable which we add to 1, this gives us the following matrix G . For very large α the resulting process will look in almost every detail like a dominated game which is what we call degenerated.

$$G = \begin{pmatrix} 1 + \alpha & 1 \\ 1 & 3 \end{pmatrix} \quad (4.7)$$

To find out how large α needs to be we can plug in values out of the interval $[0, \infty)$ for which we calculate the *interior state* i where the probabilities for birth and death are equal, which is analogous to x^* of the replicator equation. What we recognise is that for α large enough the intersection between birth and death probabilities happens at 1, which we see in figure 4.23. We also plot x^* which approaches 0 for α large. We can compute x^* with the known formula

$$x^* = \frac{\delta - \beta}{\alpha - \beta - \gamma + \delta} \quad (4.8)$$

and we see in our plot that the state i , where birth and death probabilities are equal, is closely related to it. We now call a coordination imitation chain defined by the game G degenerated, if its x^* or the equivalent state i is at the fringes of our state space, i.e. the states 1, 2 or 3 and 97, 98 and $N - 1 = 99$ in our case. Normally it should be in the interior of the state space so between 4 and 96. Of course these numbers are not exact, but only an estimate. It follows that only α less than 75 will not completely degenerate to an dominated game and could be considered when setting model parameters, but the resulting imitation chain will still look immensely like a dominated chain, with the exception of the QSD and the PSD. Of course this is not a strict definition for the parameter range, but should instead be used as a heuristic as to what games can be considered, for which population sizes and still behave like an example of the category they technically belong. It should be noted that in theory one can just choose a larger N if the game is too unbalanced, but this could soon reach unfeasible ranges of N to work with.

We can witness the same behaviour of degeneration for *anti-coordination* games where we use the matrix

$$G = \begin{pmatrix} 1 & 1 + \beta \\ 3 & 1 \end{pmatrix} \quad (4.9)$$

and do the same as before but with the parameter β . We can recover almost the same picture only flipped upside down. We show it on the right in figure 4.23. The same

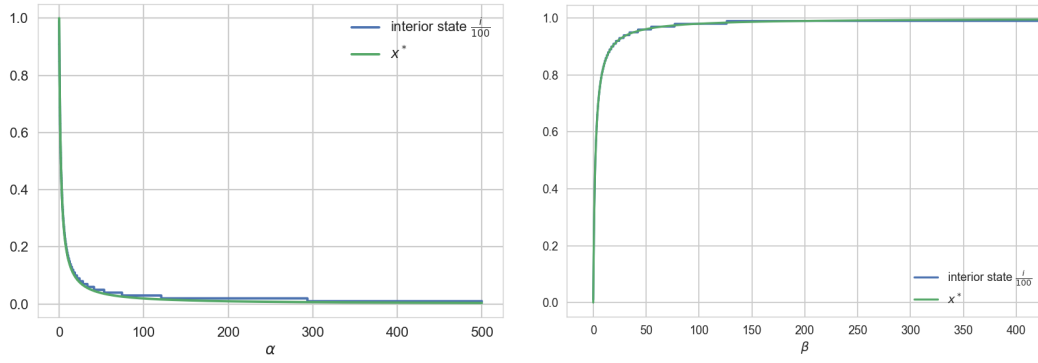


FIGURE 4.23: The interior state i where birth and death probabilities are equal together with x^* for different α or β .

heuristic as before can be applied here and we obtained nice games when all values were in the range $[1, 4]$. Obviously one can lift the lower end of the range and then set larger values for the game matrix, but we excluded this because our baseline was 1. The gist is that one can determine if a game is particularly extreme by looking at its x^* and its equivalent state i in relation to N .

In both cases of degeneration the imitation chain behaves similarly to the corresponding deterministic replicator dynamic. We saw in figure 4.23, that for a very unbalanced game x^* is getting close to 0 or 1. In the coordination game this leads to a basin of attraction of 1, which spans almost all of $[0, 1]$. In the anti-coordination case only x^* is attractive and it approaches 1 for β large. We can conclude that in both cases the replicator dynamics predict the fixation at 1 with increasing likelihood, the more unbalanced the game G becomes with increasing α or β . One should note that the probability for fixation at 0 is always at least positive in the deterministic model, but with increasing N the imitation chain would start to reflect that again. So in the limit of an infinite population size both models agree in this aspect as well.

The other extreme is if the game is not differentiating enough between its different payoffs. If this is the case almost no selection pressure will be induced, which leads to almost no pull, which in turn let's the process look like the neutral case. Here our recommendation is only to not chose values smaller then 0.1% of your baseline. The imitation chain induced by the game G below differed in no way from a neutral imitation chain even for very large values of N . Again in theory one can find N large enough that these small fitness differences have a significant impact, but without serious computing power it's almost impossible.

$$G = \begin{pmatrix} 1 & 1.001 \\ 1.002 & 1 \end{pmatrix} \quad (4.10)$$

Chapter 5

Conclusion

We witnessed how different the imitation chain and the replicator dynamics lay themselves out for different games. Balanced versions of the classical coordination or anti-coordination games produce really nice stochastic models, which incorporate the characteristic details of the dynamics. One can say that for the most part with large N the deterministic and stochastic models agree with each other. But the stochastic model often leaves more wiggle room and is therefore a somewhat more accurate representation of a realistic frequency dependent selection in small to medium size populations where random effects usually play a role.

The anti-coordination case has the most paradoxical nature where it seems like the stationary distribution is no longer relevant. But as it turns out the LTD would converge to the stationary distribution, but needs excruciatingly huge amounts of time compared to all other cases. One could say it converges so slowly that the quasi-stationary distribution is a more relevant prediction. Additionally the QSD mirrors the interior stable state of the corresponding REP dynamic and therefore recovers the connection between REP and imitation chain. This paradox only gets stronger for infinite population sizes, so in a sense the replicator equation is again a correct limit to the imitation chain.

Otherwise interesting is the connection between states where the PSD has positive mass and the states where the fixation probability is non-trivial. Here some formal investigation into the calculus behind the two would be interesting. Also the correspondence between expected time until fixation and the PSD could be studied in detail.

One should note that even for large N the payoff range to choose from to get a typical example is still quite small. It's easy to choose games where some aspect may look confusing although the others are readily classified. For example the fixation probability in the anti-coordination case is very sensible or the location of the PSD peak in the dominated case.

For further investigations one could extend the model to three strategy games, which then considers the dynamics of a population consisting of three different types of players. A first implementation was done for this project and **Harper and Fryer, 2016** already did something similar but with added mutation. In their approach the results were in many ways analogous to their two strategy imitation chain, which we could replicate in our model. This leads to the prediction that our model would again replicate their results in the three by three game case.

With more computing power and an completely optimized framework one could try to run the results again for very large N and take a look at when the stochastic imitation chain goes over into the deterministic model. Also realistic values for selection strength and the game matrix to mirror true biological settings, which would get very low, are a possibility for further research.

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