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Evolution in Finite Structured Populations with Group Interactions

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Declaration

I confirm that this thesis presented for the degree of Doctor of Philosophy in Mathematics, has been composed entirely by myself, been solely the result of my own work, and not been submitted for any other degree or professional qualification.

Abstract

The study of an evolutionary process has traditionally considered a population with a homogeneous structure where each pair of individuals is equally likely to interact with one another. Later studies have considered heterogeneous structures implemented using evolutionary graph theory, and other studies have considered group interactions of fixed size. This work builds upon these later studies by implementing a set of evolutionary dynamics that can be used to study more complex evolutionary processes consisting of a population with a heterogeneous structure where individuals interact in groups of varying size.

This research begins by analytically studying simple evolutionary processes using a set of standard evolutionary dynamics. Results are derived that identify the structures for which an evolutionary process is identical to a Moran process, which has a homogeneous population structure, for each of the evolutionary dynamics. These results form a basis for the work that follows by providing a better understanding of evolutionary dynamics.

Before considering more complex evolutionary processes, a class of multiplayer games called social dilemmas are defined for variable group sizes. The two main types of social dilemmas are identified, namely public goods dilemmas and commons dilemmas, and examples of each type of dilemma are given whose characteristics are visually illustrated.

More complex evolutionary processes are then studied based on the framework of Broom-Rychtář that provides the mathematical tools to model group interactions in mobile individuals. First, the evolutionary dynamics that can be used within this framework are developed. The updated version of the framework is then used to demonstrate how it can applied to study various kinds of behaviour in an evolutionary setting.

The first application is the territorial raider model. It considers territorial behaviour where each individual has their own territory that overlaps with those of other individuals. Interactions take place between groups of individuals when they meet in the overlapping parts of their territories. Two kinds of social dilemmas are studied in this model: a multiplayer hawk-dove game and a multiplayer public goods game. It is shown that the temperature, which measures how often an individual is likely to be replaced, plays an important role in determining the success of a given strategy.

A generalized version of the territorial raider model is also considered where subpopulations rather than individuals share the same territory. A multiplayer public goods game is used to study the evolution of cooperation, which is a suboptimal strategy at the individual level but an optimal strategy at the group level. The structure and dynamics are shown to be critical in the evolution of cooperation where an extension of the temperature, called the subpopulation temperature, dictates the relative success of cooperators.

Finally, a model where individual move base upon their previous interactions is considered called the Markov movement model. A multiplayer public goods game is used to study the evolution of cooperation. It is shown that cooperators can benefit by staying with one another provided that there is a movement cost that slows down their competitors, the defectors. In this case, the dynamics play a less critical role in the evolution of cooperation.

Chapter 1

Introduction

Population evolution is a fascinating subject that has been studied both theoretically and practically. In simple terms, evolution is the process though which the genetic makeup of a population changes over time. To explain how evolution works, Charles Darwin proposed the idea of *natural selection* in his 1859 book *The Origin of Species*. Natural selection acts on individuals and states that they are more likely to pass on their genetic makeup through their offspring if it gives them a survival and reproductive advantage. This is because an individual with a survival and reproductive advantage is more likely to produce more offspring than one who does not. Instead, the genetic makeup of individuals with a survival and reproductive disadvantage is likely to eventually vanish. *Mutation* also plays an important role in the evolutionary process. Through mutation the genetic makeup that is passed on to an offspring can change. The mutated genetic makeup may or may not give the offspring a survival and reproductive advantage but through natural selection this mutation will either spread or die out. On the other hand, the mutation could be neutral, that is, it is neutral to natural selection because it is neither beneficial nor disadvantageous. In this case *neutral drift* comes into play which means that the change in this mutated genetic makeup in a population is random. The population in question could be a humans, animals or even cells, though, the mechanism of evolution can also be applied to non-biological phenomena like language evolution.

The study of population evolution through *evolutionary game theory* has proven to be a popular approach. It is a powerful mathematical modelling tool that has shown its versatility in terms of modelling different kinds of interactions between individuals. Whilst a lot of the work on evolutionary game theory focuses on interactions between pairs of individuals, considering the interactions between multiple individuals is now more common presenting room for further development in this area.

This chapter introduces the basics of evolutionary game theory. The starting point is game theory itself followed by bridging the connection to evolution giving rise to evolutionary game theory. Various developments to evolutionary game theory over the years are then highlighted, like the Moran process and evolutionary graph theory. These developments in the context of multiplayer models are then considered. Finally, the comprehensive evolutionary game theory framework of Broom-Rychář is introduced and this chapter ends by outlining the work contained in this thesis.

1.1 Classical Game Theory

Game theory is a mathematical theory used to study the interaction between individuals that involve strategic decisions. It was developed by John von Neumann and Oskar Morgenstern [63], and has been widely applied in various fields of study. We start by defining a game before looking at at how it is applied to population evolution.

In the games that will be considered, called *symmetric normal form* games, interactions take place between a finite number of individuals. The actions that individuals take against one another is determined by their strategy. A *strategy* is a plan of action for all possible scenarios an individual can find themselves in. A strategy is *pure* if there is only one specific action for all possible scenarios. *Mixed* strategies on the other hand combine pure strategies such that each pure strategy is played with a given probability. Note that one can consider an infinite population composed of different proportions using pure strategies or every individual using a mixed strategy composed of those pure strategies. The former is considered here. The outcome of an interaction is determined by the *payoff function* that represents the motivation of the players to play a strategy. In symmetric games all players have the same set of pure strategies and payoff function.

In general, for two player symmetric games with N strategies, labelled $S_1, \ldots, S_N$, the payoffs can be represented using a *payoff matrix* as follows

$$\begin{array}{c|cccc} & S_1 & S_2 & \cdots & S_N \\ \hline S_1 & E(1,1) & E(1,2) & \cdots & E(1,N) \\ S_2 & E(2,1) & E(2,2) & \cdots & E(2,N) \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ S_N & E(N,1) & E(N,2) & \cdots & E(N,N) \end{array} \tag{1.1}$$

where each entry $E(i,j)$ is the payoff to an individual using strategy S_i against an opponent using strategy S_j. Much of the theory that follows with regards to matrix games will involve multiple strategies, however, for simplicity, the examples given have two strategies A and B

with payoff matrix

$$\begin{array}{c|cc} & A & B \\ \hline A & a & b \\ B & c & d \end{array} \tag{1.2}$$

The entries a, b, c, d give the payoffs where, for example, b is the payoff to an individual using strategy A with opponent using strategy B.

Games are analysed in terms of the best possible strategy an individual should take against their opponent. A *best response* to a particular strategy is one that gives the highest possible payoff to all the other set of strategies. A *Nash equilibrium* [62] is where every individual is using a strategy that is a best response. In this case, no individual can improve their payoff by using another strategy. A Nash equilibrium strategy is one that is a best response to itself, in general, strategy i is a Nash equilibrium if $E(i,i) \geq E(j,i)$ for all j. For example, for the game defined by payoff matrix (1.2), strategy A is a Nash equilibrium if $a \geq c$ and a strict Nash equilibrium if $a > c$. Similarly, strategy B is a Nash equilibrium if $d \geq b$ and a strict Nash equilibrium if $d > b$.

1.2 Evolutionary Game Theory

One of the first published works in evolutionary game theory was by Hamilton [34]. The application of game theory to population evolution was later considered in more detail by John Maynard Smith and George Price [56]. Classical game theory considers isolated interactions between players where the strategy used by each player remains fixed therefore, assuming that players behave rationally, we analyse what is the best strategy for each individual to play by finding the Nash equilibria. Evolutionary game theory considers multiple isolated interactions over time in a constantly changing population where the players can replicate, i.e. make copies of themselves. In this case, the objective is find the evolutionary equilibria, which are points where the strategic composition of the population remains constant.

In evolutionary game theory the payoff a player receives is assumed to contribute to their *fitness*, which in turn determines how likely an individual is to replicate itself. The forces of evolution come into play in the replication stage. In particular, a player with a higher fitness is more likely to be selected to replicate itself thereby increasing the number of players in the population playing that strategy. However, a mutation during the replication process may result in the replicated player playing a different strategy. When studying evolutionary games, it is assumed that individuals have either *constant* or *frequency-dependent* fitness. In the latter case, the fitness of the individuals depends upon the frequencies of the strategies in the population.

Overall, the number of individuals in the population playing a more successful strategy should increase.

1.2.1 Evolutionarily Stable Strategy (ESS)

One of the traditional approaches to analysing evolutionary games is the Evolutionarily Stable Strategy (ESS) [56]. An ESS is a strategy that, if adopted by the population, can prevent invasion from any alternative strategy used by a small fraction of the population. The ESS considers a snapshot in time where the invading strategy is already introduced into the population through mutation and does not consider the replication process. We are interested in finding the condition that will oppose the invading strategy from being selected. In particular, this is the case when individuals using the invading strategy have a lower fitness than the residents of the population. This means that the invading strategy will die out in the subsequent generations of the population.

For an infinite population with two-player interactions where every individual is equally likely to meet each other, the condition is given as follows. Suppose that $1-\epsilon$ proportion of individuals are using strategy i and ϵ proportion of individuals are using some other strategy $j \neq i$. The fitness of individuals using strategy i is given by $(1-\epsilon)E(i,i)+\epsilon E(i,j)$ and that of the individuals using strategy $j \neq i$ is $(1-\epsilon)E(j,i)+\epsilon E(j,j)$. For the population to prevent invasion from the individuals using strategy $j \neq i$ we require that

$$(1-\epsilon)E(i,i)+\epsilon E(i,j) > (1-\epsilon)E(j,i)+\epsilon E(j,j).$$

As $\epsilon \to 0$, we can ignore the terms with ϵ, which give $E(i,i) > E(j,i)$. However, if $E(i,i) = E(j,i)$ then the terms with ϵ should satisfy $E(i,j) > E(j,j)$. This means that strategy i is evolutionarily stable against strategy j whenever

$$E(i,i) > E(j,i) \quad \text{or} \quad E(i,i) = E(j,i) \text{ and } E(i,j) > E(j,j).$$

Furthermore, if this is true for all strategies $j \neq i$, strategy i is an ESS. For example, for the two strategy game defined by payoff matrix (1.2), strategy A is an ESS if

$$a > c \quad \text{or} \quad a = c \text{ and } b > d.$$

1.2.2 The Replicator Equation

The other traditional approach to analysing evolutionary games involves defining the replication process using a deterministic equation and solving that equation to find the evolutionary equilibria of the population. The *replicator equation* [38, 39, 40, 101] is defined as follows

$$\dot{x}_i = x_i[F_i - \phi] \tag{1.3}$$

where x_i is the frequency of individuals using strategy i, F_i is the fitness of individuals using strategy i and ϕ is the average fitness of the population. The replicator equation says that the frequency of individuals using a strategy will increase if their fitness is higher than the average fitness of the population and will decrease if it is lower.

We can find the evolutionary equilibria for the two strategy payoff matrix (1.2), by solving equation (1.3). Assuming the frequency of individuals playing strategy A is x and B is $1-x$, we have that

$$F_A = xa + (1-x)b \quad \text{and} \quad F_B = xc + (1-x)d.$$

The average fitness of the population is given by

$$\phi = xF_A + (1-x)F_B.$$

The change in frequency of type A individuals is then given by

$$\begin{aligned}\dot{x}_A &= x\left[F_A - \phi\right] \\ &= x\left[F_A - xF_A + (1-x)F_B\right] \\ &= x\left[(1-x)F_A - (1-x)F_B\right] \\ &= x(1-x)\left[F_A - F_B\right] \\ &= x(1-x)\left[x(a-b-c+d) + b - d\right]\end{aligned}$$

The equilibrium points x^* are found by solving $\dot{x}_A = 0$, giving the following equilibrium points

$$x^* = 1, \quad x^* = 0, \quad x^* = \frac{d-b}{a-b-c+d}.$$

Whether these equilibrium points are stable or not depends upon the payoff values. We have the following cases:

1. $x^* = 1$ stable: in this case we have that $a > c$ and $b > d$. Regardless of the starting frequency x of type A individuals, we always end up at the equilibrium point where there are only type A individuals. This is because strategy A is a strict Nash equilibrium strategy and therefore dominates strategy B.

2. $x^* = 0$ stable: in this case we have that $c > a$ and $d > b$, which is the exact opposite of the previous case.

3. $x^* = 0$ and $x^* = 1$ are both stable: in this case we have that $a > c$ and $d > b$. This means that both A and B are best responses to themselves. The equilibrium point we converge to depends upon the starting frequency x. In particular, if $x > \frac{d-b}{a-b-c+d}$ then the population converges to $x^* = 1$, and $x^* = 0$ otherwise.

4. $x^* = \frac{d-b}{a-b-c+d}$ is stable: in this case $a < c$ and $d < b$. This means that A is a best response to B and vice versa. Both types can stably coexist with each other and will converge to this equilibrium.

1.3 Evolutionary Game Theory in a Finite Population

Finding the ESS and using the replicator equation to find the equilibrium points are based on models that assume that the population is infinite. While this gives us an idea about how successful a given strategy is, in reality populations are finite and we therefore have to consider analysing strategies in such conditions. In finite populations capturing relevant biological phenomena, like genetic drift, requires that stochastic dynamics are used. A classical model of evolution in a finite population with stochastic dynamics is the *Moran process* [58, 59].

The Moran process considers a population of size N where there are n type A individuals and $N - n$ type B individuals. Type A individuals have fitness $F_A(n) = r$ and type B individuals have fitness $F_B(n) = 1$ for all n i.e. there is constant fitness where r can be thought of as the relative fitness of type A with respect to type B. Note here that the fitness does not depend on n, that is, it is not frequency dependent. The individuals are homogeneous in every other respect and, in particular, are equally likely to meet each other. The Moran process uses stochastic dynamics with the property that the population size remains constant, that is, the population size is always N. This means that for every birth there is a death in the population. These replacement events are assumed to be asynchronous, which means that there is only one birth and one death per replacement event. An individual is chosen to replicate proportional to its fitness, in particular, for type A and B individuals the probability of being selected for birth are respectively given by

$$b_A(n) = \frac{F_A(n)}{nF_A(n) + (N-n)F_B(n)}, \quad b_B(n) = \frac{F_B(n)}{nF_A(n) + (N-n)F_B(n)}. \tag{1.4}$$

An individual's offspring then randomly replaces another individual in the population with probability $\frac{1}{N-1}$. Note that the birth event affects the death event because the individual that gives birth is excluded, that is, there is simple random sampling without replacement. This means that the individual that gives birth is excluded before selecting an individual for death from the population. The order of the birth and death events therefore matters, and the Moran process uses birth-death with selection on birth (BD-B) dynamics.

It is assumed that there are no mutations in the population. This implies that one of the types will eventually fixate in the population, which means that only one of the types, A or B, will persist. Note that this does not mean that mutation is ignored, rather, we start by considering a population of only type B individuals and a mutation takes place that introduces a type A

individual into the population. It is at this point that the following question is asked, 'what is the probability of type A fixating?'. More specifically, the probability of 1 type A individual fixating in a population of $N-1$ type B individuals is called the *fixation probability* of type A, denoted ρ_A. In other words, this is the probability that all individuals in the population have this 1 type A individual introduced into the population as their ancestor. To calculate the fixation probabilities, we need to define the state transition probabilities $P_{n,k}$ of transitioning from a state where there are n type A individuals to a state where there are k type A individuals. These are defined as follows

$$P_{n,k} = \begin{cases} nb_A(n) \times \frac{N-n}{N-1} & k = n+1 \\ (N-n)b_B(n) \times \frac{n}{N-1} & k = n-1 \\ 1 - P_{n,n+1} - P_{n,n-1} & k = n \end{cases} \tag{1.5}$$

The evolution of the population is therefore described as a discrete time absorbing Markov chain with $N+1$ states. The solution to the fixation probability is given by [41] as follows

$$\rho_A = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \frac{P_{k,k-1}}{P_{k,k+1}}}. \tag{1.6}$$

Substituting in the transition probabilities gives

$$\rho_A = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \frac{1}{r}} = \begin{cases} \dfrac{1-\frac{1}{r}}{1-\frac{1}{r^N}} & r \neq 1, \\ \dfrac{1}{N} & r = 1. \end{cases} \tag{1.7}$$

This solution to ρ_A is referred to as the *Moran probability.* Ideally, we should observe that in a finite population the success of type A is subject to *random drift* because of the stochastic evolutionary dynamics and, therefore, there is no guarantee that type A will fixate. In the case where $r = 1$ the fixation probability of type A is $\rho_A = 1/N$ and there is said to be *neutral drift.* Here, the type A mutant has an equal chance of fixating to any other of the $N-1$ type B individuals and selection neither favours type A or B individuals. On the other hand, selection favours the type A mutant when $r > 1$ since $\rho_A > 1/N$ and favours the type B individuals when $r < 1$ since $\rho_A < 1/N$. Note that the fixation probability is not the only measure for evolutionary success and the fixation time [12, 27] can be looked at as well.

1.3.1 Games in finite populations

The Moran process is extended to the case where fitness is frequency dependent as in [69, 99]. The individuals are assumed to be playing a game whose payoff matrix is given by equation (1.2) and, therefore, all that changes from the constant fitness case is the fitness of the individuals. In particular, the fitness of the individuals needs to calculated with respect to equation (1.2) so that the state transition probabilities can be plugged into equation (1.6). Then, under certain assumptions, a rule stating when selection favours type A individuals fixating is obtained.

The fitness of a type A individual in the state where there are n type A individuals is given by

$$F_A(n) = 1 - w + w\left[\frac{a(n-1) + b(N-n)}{N-1}\right]. \tag{1.8}$$

The terms inside the square brackets gives the average payoff to a type A individual when it is equally likely to interact with all members of the population, that is, the probability of meeting a type A (B) individual is $\frac{n-1}{N-1}$ ($\frac{N-n}{N-1}$), which gives a payoff of a (b). The background fitness is 1. The intensity of selection is controlled by $w \in [0, 1]$. With $w = 1$, selection with respect to this game is strong as it determines a substantial part of the fitness with the background fitness being negligible. With $w \to 0$, selection is weak with respect to this game as the fitness is dominated by the background fitness and the game contributing only a small portion. With $w = 0$, there is neutral drift. Similarly, we obtain the fitness of a type B individual as follows

$$F_B(n) = 1 - w + w\left[\frac{cn + d(N-n-1)}{N-1}\right] \tag{1.9}$$

where the probability of meeting a type A (B) individual is $\frac{n}{N-1}$ ($\frac{N-n-1}{N-1}$), which gives a payoff of c (d). Using these fitness values we can calculate the state transition probabilities and plug them into equation (1.6).

After plugging in the appropriate state transition probabilities, the following Taylor expansion of equation (1.6) is obtained for $w \to 0$

$$\rho_A \approx \frac{1}{N}\frac{1}{1 - (\alpha N - \beta)w/6} \tag{1.10}$$

where $\alpha = a + 2b - c - 2d$ and $\beta = 2a + b + c - 4d$. We know that selection favours the type A individuals if $1/N < \rho_A$, which is the same as saying that $\beta < \alpha N$. Plugging in the values of α and β gives

$$c(N+1) + d(2N-4) < a(N-2) + b(2N-1). \tag{1.11}$$

Assuming that N is large, we only need to consider the terms multiplied by N and, therefore, the following is obtained

$$\begin{aligned} c + 2d &< a + 2b \Rightarrow \\ 2d - 2b &< a - c \Rightarrow \\ 3d - 3b &< a - c + d - b \Rightarrow \end{aligned}$$

$$\frac{d-b}{a-b-c+d} < \frac{1}{3}. \tag{1.12}$$

This is known as the *rule of 1/3* [99] and states that selection favours type A fixating if the internal equilibrium point is less than 1/3. Note that it was previously shown that that $\frac{d-b}{a-b-c+d}$ is an internal equilibrium point using the replicator equation.

1.4 Evolutionary Graph Theory

Evolutionary graph theory was introduced by [52] and used graphs to describe the structure of the population. In the Moran process as we have seen that the population is homogeneous such that the offspring of an individual can replace any individual in the population. However, in reality populations are generally structured in the sense that certain individuals are more likely to interact with one another than others, for example scientific collaboration networks seem to be scale-free [64]. Representing the individuals as nodes on a graph, as done in [52], is one way of describing the structure such that only individuals who are connected to one another can interact with/ replace one another, see figure 1.1.

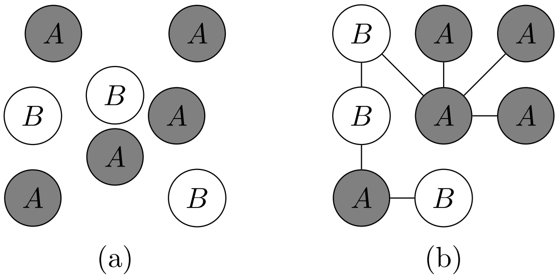


Figure 1.1: The figures shows two populations with type A and B individuals. Figure (a) represents an unstructured population where all individuals can interact with one another. Figure (b) shows a structured population represented using a graph. Each node represents an individual such that only connected individuals can interact with one another.

A graph represented by an $N \times N$ weighted adjacency matrix $\mathbf{W} = (w_{ij})$ is used to define the structure of a population. Each vertex represents an individual such that there exists an edge an edge (i, j) when $w_{ij} > 0$ that gives the probability that the offspring of individual i can replace individual j. The BD-B dynamics used in the Moran process can be adapted to be used on an evolutionary graph such that an individual i will be selected to reproduce proportional to its fitness as before but its offspring will replace individual j with probability w_{ij}. The *temperature* then measures how often an individual is likely to be replaced and is given by

$$T_j = \sum_{i=1}^{N} w_{ij}. \tag{1.13}$$

Like for the Moran process, it is possible to calculate the fixation probability of a type A mutant in a population of type B individuals for an evolutionary graph, in some cases the exact formula has been given [15] otherwise it can be calculated numerically. There are several important results with regards to this for the constant fitness case. One of these is the *isothermal theorem* [52] that states if the evolutionary graph is *isothermal*, which means that every individual has the same temperature, then the fixation probability of a type A mutant ρ_A is equal to the Moran probability. This is an important result because it helps identify those structures that have no effect on the selection of individuals.

A more general way of describing the structure of the population is using weights that are not probabilities. In this case, individual i would replace individual j proportional to $F_i w_{ij}$ where F_i is the fitness of individual i and $w_{ij} \geq 0$. Once again for the constant fitness case, the fixation probability of a type A mutant in a population of type B individuals can be calculated. In this case, the *circulation theorem* [52] states that if the evolutionary graph is a *circulation*, which means that the incoming weights and outgoing weights for all individuals are the same, that is,

$$\sum_{j=1}^{N} w_{kj} = \sum_{j=1}^{N} w_{jk} \quad \forall k = 1, \ldots, N, \tag{1.14}$$

then ρ_A is equal to the Moran probability. This result is more general and includes isothermal graphs as well. In addition to showing what kind of graphs have no effect on the selection of individuals, certain graphs can be shown to have an amplifying or suppressing effect on the selection of individuals. For example a star graph [52], where all vertices are connected to one central vertex, amplifies the effect of selection such that the fixation probability of a type A mutant in a population of type B individuals is greater (less) than the Moran probability if $r > 1$ ($r < 1$).

There has been a lot of interest in evolutionary graph theory where different evolutionary dynamics have been studied. In [15] obtained analytical results for the fixation probability of a mutant type on a line graph and compared it to that of a circle graph. It was found that that average fixation probability of a fitter mutant type was larger on a line graph than a circle graph. In [54, 55] it was shown that for directed degree-correlated small-world networks the global connectivity plays an important role in the fixation probability of a mutant type for three different update rules. [103] also studied directed graphs and found that there is correlation between the vertex in-degree variation and the difference between the fixation probabilities for a given graph and a complete graph. The implicit assumptions made when calculating the fixation probability was investigated by [53] and it was shown that, given the heterogeneity of the population, mutations were more likely to appear in certain locations, for example, in a star graph where all vertices are connected to one central hub a mutant is more likely to appear in the hub for death birth dynamics.

1.4.1 Games on Graphs

In this section frequency-dependent fitness is considered in the context of evolutionary graph theory. As opposed to traditional evolutionary game theory that mainly considers infinite well-mixed populations, the use of graphs to model population structure on standard games enables finite inhomogeneous populations to be studied [32, 70, 88]. This follows earlier work considering finite and/or spatial populations such as [67, 68] that studied the prisoner's dilemma on an $n \times n$ square lattice of patches such that each patch is occupied by one individual and games are played between immediate neighbours. Other games in this kind of setting were studied in [46]. To motivate the idea of games on graphs, a public goods game that requires its players to cooperate in order to reach the optimal outcome is studied. In particular, [65] outlined 5 different mechanisms for cooperation to evolve of which network reciprocity will be focused on here. This idea of network reciprocity was studied in [70] where a two-player public goods game was studied on evolutionary graphs with degree k, that is, each vertex is connected to k other vertices such that each edge has weight $1/k$.

The two-player public goods game used in [70] has payoff matrix

$$\begin{array}{c|cc} & A & B \\ \hline A & b-c & -c \\ B & b & 0 \end{array} . \tag{1.15}$$

Here, type A individuals are cooperators because they are willing to pay a cost c so that they can provide a public good to the individual they are interacting with. On the other hand, type B players are called defectors because they do not pay a cost to provide a public good but receive one if they are present with a cooperator. The evolutionary graph is used to determine the payoff an individual receives such that two individuals who are connected to each other on the evolutionary graph will play a game with one another. Note that it is possible to define another interaction graph instead of using the evolutionary graph as demonstrated in [73]. The payoff to a cooperator connected to k individuals, of which i are cooperators, is given by $bi - ck$. The payoff to a defector connected to j cooperators is given by bj. The fitnesses of cooperators and defectors are respectively given by

$$F_A(k,i) = R + w - w(bi - ck), \quad F_B(j) = R + w - wbj$$

where R is the background fitness and w controls of the intensity of selection. For small w there is weak selection, which means that there are other factors other than this game that determines their overall fitness, which is captured by the background fitness R. The background fitness also ensures that the fitness does not go negative because the fitnesses are used in the dynamics, which are stochastic so negative fitnesses would not make sense.

For the weak selection limit and large population size, it was shown for BD-B dynamics that selection favours defection because $\rho_A < 1/N < \rho_B$. To see why this is the case, consider a circular graph where each vertex is connected to two other vertices such that it forms a closed chain. Consider a sequence of cooperators within this circular graph. A cooperator at the end of the sequence interacts with a cooperator who is inside the sequence and a defector at the border of this sequence giving a payoff of $b - 2c$. The defector at the border of the sequence has payoff b and, therefore, a higher fitness. With BD-B dynamics, this defector is more likely to be selected for reproduction than the cooperator at the end of the sequence. This leads to the sequence of cooperators shrinking as the defectors at the border of the sequence will get more chances to replace the cooperator at the end of the sequence with their offspring. On the other hand, death-birth with selection on birth (DB-B) dynamics can be used. In this case, an individual randomly dies and is replaced by the offspring of one of its k neighbours proportional to their fitness. With DB-B dynamics, selection favours cooperators, that is, $\rho_B < 1/N < \rho_A$, if

$$b/c > k. \tag{1.16}$$

Once again we consider what happens at the border of a sequence of cooperators in a circular graph for the DB-B dynamics. Note that the payoffs remain the same as the interactions are the same between the individuals. A cooperator at the end of the sequence, randomly chosen for death, is more likely to be replaced by its neighbouring cooperator inside the sequence, who has payoff $2b - 2c$, than its neighbouring defector at the border, who has payoff b, whenever $b/c > k$, where $k = 2$ in this case. This is because $2b - 2c > b$ whenever $b/c > 2$. The probability of cooperators reducing is therefore lower. A defector at the border who is randomly chosen for death is more likely to be replaced by its neighbouring cooperator who has payoff $b - 2c > 0$, since $b/c > 2$, than its neighbouring defector who has payoff 0. The probability of cooperators increasing is therefore higher.

Evolutionary graph theory with games has been studied quite extensively. [71] derived the replicator equation for evolutionary graphs using various evolutionary dynamics. [8] studied the average time to fixation for a Moran process and found that, independent of the payoff matrix elements and population size, the fixation time for two strategies is identical. [100] used an alternative method to predict the fixation probabilities for the cooperation game on graphs. For games on regular graphs [72] derived the ESS conditions. [12] gave the exact fixation probabilities for a general two player game on certain non-directed graphs, and [32] considered the star graph where they calculated the exact fixation probability for various evolutionary dynamics and games. A [93] lists a set of open problems in evolutionary graph theory that are related to game theoretic extensions together with various other developments like evolutionary graphs that change over time.

1.5 Multiplayer Games

The games we have considered up to this point are based on interactions between two players. However, many interactions in reality include interactions between multiple individuals. In particular, many multiplayer interactions cannot be obtained from aggregating the corresponding pairwise interactions. Consider two types A and B and suppose that a type A individual is interacting with a and b other type A and type B individuals, respectively, in a group. The payoff to this individual can be obtained by aggregating the pairwise interactions between the individuals in this group if the payoff function is linear in a and b. However, non-linear payoff functions are more common in biology [9]. For example, cooperative hunters share the prey evenly amongst themselves regardless of the effort they put in, some examples include Harris' hawks [10], lions [75, 97] and African wild dogs [21].

Determining the payoffs for multiplayer games involves complexities that are not present in 2-player games. Multi-player games were introduced into biology in [76] and the theory developed by [11], see also [19]. The games considered in [11] are *symmetric*. This means that the payoff an individual receives depends upon the strategy it uses and the combination of strategies used by its opponents rather than each opponent's strategy. To elaborate, consider 3 players playing a multiplayer game where players 1, 2, 3 use strategies A, A, B or A, B, A. For symmetric games, player 1 would receive the same payoff regardless of whether the first or the second set of strategies is used, however, for asymmetric games the two payoffs could be different. The *order* of the players matters in asymmetric games and examples of biological interactions of this kind include hunting in lioness packs [98] where the position taken by each lioness during the hunt matters. Since the ordering does not matter, a *power notation* can be used when writing the payoffs to account for identical strategies. For example, the payoff to a type A individual playing against n type A and k type B individuals is written $E[A; A^n, B^k]$. The multiplayer games considered in this thesis will not consider the order of the players. For a comparison between multiplayer payoffs and pairwise payoffs see Figure 1.2.

For multiplayer games the group sampling also needs to be determined. In [11] a population of infinite size is considered where groups of fixed size m are randomly chosen to play a game. This simplifies the analysis of the multiplayer games. The complete randomness in which the groups are picked implies that here symmetric and asymmetric games are essentially the same

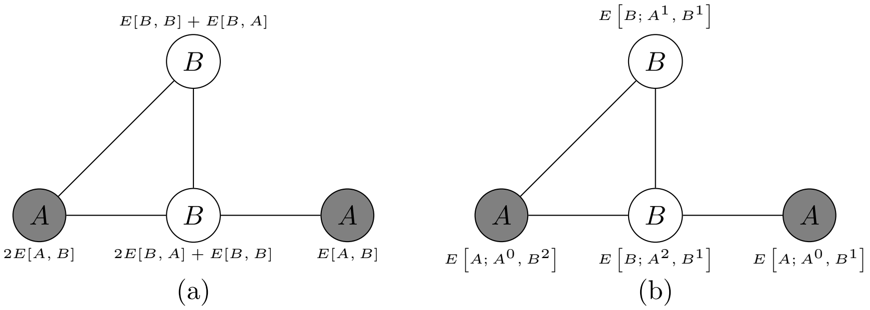


Figure 1.2: This figure shows two graphs where each node represents a type A or B individual and only connected individuals can interact with one another. In figure (a), the payoffs are obtained by aggregating the pairwise interactions between the individuals such that $E[A, B]$ is the payoff to a type A individual interacting with a type B individual. In figure (b), the payoffs are given by a multiplayer payoff function in which the ordering of the players does not matter, that is, $E[A; A^i, B^j]$ is the payoff to a type A individual interacting with i other type A individuals and j other type B individuals.

[29]. With these assumptions the ESS of m-player games can be defined [11, 19, 76], as well as the replicator equation [85]. In particular, the ESS for an m-player game can be naturally extended from the a two-player game as follows. Strategy A in an m-player game is *evolutionarily stable* against strategy B if there exists $\epsilon_B \in (0, 1]$ such that for all $\epsilon \in (0, \epsilon_B]$

$$\sum_{k=0}^{m-1}\binom{m-1}{k}(1-\epsilon)^k\epsilon^{m-1-k}E[A;A^k,B^{m-1-k}] > \sum_{k=0}^{m-1}\binom{m-1}{k}(1-\epsilon)^k\epsilon^{m-1-k}E[B;A^k,B^{m-1-k}] \tag{1.17}$$

such that this is derived using the fact that the population is infinite and groups are formed with complete randomness so that the probability of a group forming in contests with two strategies follows a binomial distribution. Now, A is called an ESS if, for every $B \neq A$, there exists $\epsilon_B > 0$ such that equation (1.17) holds for all $\epsilon \in (0, \epsilon_B]$, for more details see [17] Chapter 9. In finite populations, [29, 48] adapted the Moran process for m-player games with two strategies and extended the 1/3 law for multiple players, which was further studied by [50].

A substantial part of the literature considers mutliplayer games between a fixed group size of m individuals, for example, in [9] groups of size m form in an infinite and well mixed population, [74] considers a finite population, [81, 83] considers a spatially structured population with groups of fixed size and [102] considers a specific structure, the cycle, where an unbroken sequence of m players play a game. One advantage of doing this is that group structure can be easily incorporated using regular graphs [80]. However, group heterogeneity plays an important role, for example, [86, 90] showed that group heterogeneity between individuals helps the evolution of cooperation, similarly, cooperation was shown to dominate in scale-free networks where the few highly connected individuals are also directly interconnected [87]. In [91] a multiplayer public goods game was studied on a complex network. In the multiplayer public goods game each cooperator pays a contribution c towards a public good and defectors contribute nothing. The total contribution that is received is multiplied by a synergy factor r and evenly shared between all players. Each individual i plays $k_i + 1$ games, where k_i is the degree of player i on the complex network, such that 1 game is played with its neighbours and another game with each of its k_i neighbours in their neighbourhood. It was shown that with heterogeneous groups selection favoured cooperation.

Group formation is important when there are heterogeneous group size and has to be accounted for. In [91], the individuals that can interact with each other are connected to each other. However, there are many ways in which these groups can be formed where the method used, as described in the previous paragraph, is just one of the possibilities. One solution to resolve this ambiguity is to use bi-partite graphs to preserve the pairwise connections and the group structure [30, 31]. With these bi-partite graphs one set of nodes represents the individuals and another the groups. Individuals can interact in a group if they are connected to the same group node, which also implies that they are connected to each other on a graph. For these kinds of bi-partite graph, it was shown that the actual group structure plays an important role in the evolution of cooperation in a multiplayer public goods game. In particular, [82] showed that the driving force behind the evolution of cooperation was the degree of overlap between the groups.

There are various other ways group structure has been modelled in multiplayers games. In [104] a hierarchical structure was considered where individuals are part of different groups at multiple levels such that groups at higher levels are larger than those at a lower level. Another way to allow groups to form is to allow individuals to be mobile and there are several ways in which one can model this. For example, [20] considered the random movement of individuals in a continuous two-dimensional plane such that the group structure is determined by a random geometric graph with constant radius, which means that individuals that are within a certain radius of each other are connected to each other and, therefore, interact in a group. With mobile agents the group structure is always changing. Other ways in which this can be achieved is by updating the group structure depending upon the payoffs individuals receive [105]. The idea behind this kind of mechanism is to strengthen beneficial ties between individuals, which helps cooperation evolve in a multiplayer public goods game. There are many more examples in which group structure can be accounted for, in particular, [84] gives several different examples. The material in this thesis is predominantly based on multiplayer interactions between individuals.

Notation	*Description*
N	Population size
$I_1, \ldots, I_N$	Individuals in population
M	Number of places in habitat
$P_1, \ldots, P_M$	Places in habitat
$\mathbf{X}(t)$	Matrix representing population distribution at time t
$X_{n,m}(t)$	Indicates presence of I_n in P_m at time t
$\mathbf{x}$	Current distribution of $\mathbf{X}(t)$
$x_{n,m}$	Indicates presence of I_n in P_m for current distribution
$\mathbf{x}_{<t}$	Entire history of the system
$p_{n,m,t}(\mathbf{x}_{<t})$	Probability of I_n being in P_m at time t given $\mathbf{x}_{<t}$
$\mathcal{P}_n$	Home range or territory of I_n
$R(n, \mathbf{x}, t, \mathbf{x}_{<t})$	Reward function
R_n	Mean reward

Table 1.1: Notation used in the framework of Broom-Rychtar [16].

The models used are constructed using the comprehensive mutliplayer evolutionary game theory framework of Broom-Rychtář [16].

1.6 The Framework of Broom-Rychtář

The framework of Broom-Rychtář [16] forms the basis for the work done in this thesis. The motivation behind this framework is to incorporate group interactions that take place in real life, for example, in African wild dogs [28] and roadrunners [43]. The framework is based on the premise that there are N individuals distributed over M places and group interactions take place whenever two or more individuals are present in the same place at the same time. Varying degrees of complexity can be achieved depending upon the exact assumptions made about the movement of individuals, for example, the movement of the individuals can be defined in such a way that resembles a metapopulation [51]. The framework consists of several building blocks that are described below. The notation used is summarised in Table 1.1.

1.6.1 Structure

The structure of a population is given by the number of places, the number of individuals and the probability of these individuals being present in these places.

Population Distribution

The location of every individual in the population at time t is given by the $N \times M$ binary matrix $\mathbf{X}(t) = (X_{n,m}(t))$ such that

$$X_{n,m}(t) = \begin{cases} 1 & \text{if } I_n \text{ is in } P_m \text{ at time } t \\ 0 & \text{otherwise.} \end{cases} \tag{1.18}$$

The current distribution of the population is $\mathbf{x} = (x_{n,m})$ and the entire history of the population distributions is $\mathbf{x}_{<t} = (\mathbf{x}_1, \mathbf{x}_2, \ldots, \mathbf{x}_{t-1})$. In the most general case, the current distribution of the population is conditional on the entire history of the population distributions which is denoted as

$$\mathbb{P}(\mathbf{X}(t) = \mathbf{x})(\mathbf{x}_{<t}) = \mathbb{P}(\mathbf{X}(t) = \mathbf{x} | \mathbf{X}(1) = \mathbf{x}_1, \ldots, \mathbf{X}(t-1) = \mathbf{x}_{t-1}). \tag{1.19}$$

There is a unique distribution of the values of $\mathbf{X}(t)$ because at any time t an individual has to be present at exactly one place which means that every system must satisfy the property

$$\sum_{\mathbf{x}} \mathbb{P}(\mathbf{X}(t) = \mathbf{x})(\mathbf{x}_{<t}) = 1 \quad \forall\ t, \mathbf{x}_{<t}. \tag{1.20}$$

Focal Individual

In addition to being able to describe the population as a whole, the characteristics of a particular individual in a population need to be described as well. This individual is referred to as the focal individual. The presence of the focal individual I_n in place P_m at time t conditional on the history $\mathbf{x}_{<t}$ is given by the probability

$$\mathbb{P}(X_{n,m}(t) = 1)(\mathbf{x}_{<t}) = p_{n,m,t}(\mathbf{x}_{<t}). \tag{1.21}$$

The focal individual can be present at one place only at any given time therefore every system should satisfy the property

$$\sum_{m} p_{n,m,t}(\mathbf{x}_{<t}) = 1 \quad \forall\ n, t, \mathbf{x}_{<t}. \tag{1.22}$$

The subset of all the places the focal individual can visit is called its *home range* or *territory* and is defined as follows

$$\mathcal{P}_n = \{P_m : p_{n,m,t}(\mathbf{x}_{<t}) > 0\} \tag{1.23}$$

History Dependency

Depending upon the movement behaviour being modelled, varying levels of dependency on the historical distributions can be considered. Examples of history dependency include the following

- *Dependence on entire history:* This is an extreme case such that the current distribution depends upon all historical population distributions. It is also the most general case and was introduced earlier as follows

$$\mathbb{P}(\mathbf{X}(t)=\mathbf{x})(\mathbf{x}_{<t})=\mathbb{P}(\mathbf{X}(t)=\mathbf{x}|\mathbf{X}(1)=\mathbf{x}_1,\ldots,\mathbf{X}(t-1)=\mathbf{x}_{t-1}). \tag{1.24}$$

- *Markov:* This is an intermediate case where the current distribution depends upon the previous historical population distribution only. The population distribution simplifies to

$$\mathbb{P}(\mathbf{X}(t)=\mathbf{x})(\mathbf{x}_{<t})=\mathbb{P}(\mathbf{X}(t)=\mathbf{x}|\mathbf{X}(t-1)=\mathbf{x}_{t-1}) \tag{1.25}$$

- *History independent:* This is the simplest case of all where the the current distribution is independent of all historical population distributions, and the population distribution is given by

$$\mathbb{P}(\mathbf{X}(t)=\mathbf{x})(\mathbf{x}_{<t})=\mathbb{P}(\mathbf{X}(t)=\mathbf{x}) \tag{1.26}$$

Time homogeneous structure

In general, the movement of individuals can depend upon time to take into account, for example, seasonal movement patterns. With time homogeneity, the movement of individuals does not change with time, and, therefore, the population distribution that is independent of time satisfies the following

$$\mathbb{P}(\mathbf{X}(t)=\mathbf{x})(\mathbf{x}_{<t})=\mathbb{P}(\mathbf{X}(s)=\mathbf{x})(\mathbf{x}_{<s}) \quad \forall\ s,t\geq 1. \tag{1.27}$$

Row independent structure

Row indpendence is the assumption that individuals move independently of what others are doing at time t. For any I_{n_1}, I_{n_2} in such a structure who are moving to P_{m_1}, P_{m_2} respectively, the following holds

$$\mathbb{P}(X_{n_1,m_1}(t)=1\ \&\ X_{n_2,m_2}(t)=1)(\mathbf{x}_{<t})=p_{n_1,m_2,t}(\mathbf{x}_{<t})p_{n_1,m_2,t}(\mathbf{x}_{<t}). \tag{1.28}$$

Independent and fully independent structures

An *independent* structure is history independent and row independent. The subset of independent structures that are also time homogeneous are known as *fully independent* structures. The fully independent structures are the simplest to work with.

1.6.2 Fitness

The fitness of individuals will be determined by the game played. The *reward* the focal individual receives for playing a game is determined by the reward function

$$R(n, \mathbf{x}, t, \mathbf{x}_{<t}). \tag{1.29}$$

The *mean reward* is the average reward over all possible population distributions at time t conditional on the historical distributions that is

$$R_n = \sum_{\mathbf{x}} \mathbb{P}(\mathbf{X}(t) = \mathbf{x})(\mathbf{x}_{<t}) R(n, \mathbf{x}, t, \mathbf{x}_{<t}). \tag{1.30}$$

In general, the mean reward is the preferred way of calculating the fitness because it is more natural.

1.7 Outline

An outline of the work contained in the following chapters in given. All the work is new and where a paper has been published, the details are provided.

In chapter 2, evolutionary graphs are identified where a fixed fitness evolutionary process is identical to the Moran process for different types of dynamics. The work of [52] identified such evolutionary graphs for the Link and BD-B dynamics in the form of the circulation and isothermal theorems. This is extended to a whole set of standard dynamics used in the literature. Even though this work focuses on the fixed fitness case, it provides a better understanding of evolutionary dynamics in general, especially in the context of evolutionary graphs. The work in this chapter was published in *Royal Society Proceedings A* article [79]. For this paper I developed the original concept in discussion with my supervisor, M. Broom, and carried out the majority of the analysis and writing.

In chapter 3, social dilemmas with variable group sizes are mathematically defined. Social dilemmas are essentially mutliplayer games where the optimal strategy for an individual is not the best for the group. In the literature, such multiplayer interactions between individuals have considered groups of fixed size. However, the framework of Broom-Rychtář is suited to groups of variable size and, hence, this work is a logical precursor to work involving this framework. This work has not been published, though, at the time of writing, the material in this chapter is a subset of a yet to be completed article.

In chapter 4, the framework of Broom-Rychtář is developed further to allow the consideration of a dynamic evolutionary process. A bulk of the work involved defining the evolutionary dynamics and describing how they can be derived based on the assumptions in the framework.

This was influenced by the work in chapter 2, whose focus is predominantly on the dynamics. The notation used was also changed from the original framework to allow for a more coherent description of the complete framework. The framework of Broom-Rychtář is then used to model territorial behaviour in what is called the territorial-raider model. This work is the first instance in which a dynamic evolutionary process is illustrated within the framework. The success of a mutation in a population of 3 and 4 individuals with different territories is considered for two types of multiplayer interactions based on social dilemmas. Here, the temperature of the individuals, or how often individuals are replaced, plays a key role in determining the success of a mutation. This work was published in the *Journal of Mathematical Biology* article [14]. For this paper I helped construct the dynamics used in the model and carried out part of the analysis.

In chapter 5, the territorial-raider model of the previous chapter is generalized to allow a subpopulation to occupy a territory rather than just a lone individual. This generalization increases the frequency of interactions between individuals and, therefore, may help or hinder a mutation. As in the territorial raider model, the subpopulation temperature, or how often one subpopulation replaces another, plays a key role in predicting the success of a mutation. This work also considers a full set of dynamics as opposed to just the BD-B dynamics in the territorial raider model. This work was published in the *Journal of Theoretical Biology* article [77]. For this paper I helped develop the original concept through joint discussions with my supervisor, M. Broom, and carried out the majority of the analysis and writing.

In chapter 6, the framework is used to model movement behaviour that is characterized by Markov history dependence known as the Markov movement model. Individuals would make a choice of where to go next depending upon whether their current group interaction was beneficial or not. The group interactions are characterized by a social dilemma that involves the production of a public good. A beneficial interaction would therefore involve cooperators who contribute towards the production of this public good as opposed to defectors who do not. Given that movement is Markov, several new variables are introduced to deal with this. In particular, the movement cost and exploration time play important roles in helping cooperative behaviour spread. This work had been accepted by the journal *Discrete and Continuous Dynamical Systems Series B (DCDS-B)* article [78]. For this paper I helped develop the original concept through discussions with the other authors, M. Broom and J. Rychtář, and carried out the majority of the analysis and writing.

In chapter 7, the final chapter, different variations of the dynamics that can be used with the framework are discussed. To illustrate how these variations differ from one another the territorial raider model of chapter 4 is used. The dynamics used shown in this chapter resulted from the investigations that went into the development of the dynamics for the framework. The main aim is to demonstrate the flexibility of the dynamics used within the framework. This work has not been published but forms a basis for a lot of the work in the previous chapters and is therefore included to give a complete picture of the work in this thesis.

Chapter 2

When is an evolutionary process equivalent to the Moran process?

2.1 Introduction

This chapter considers a model of population evolution based on the evolutionary graph theory framework of [52], which was a development of the classical Moran population model [58]. The model population has a finite size that is fixed at all times and is allowed to evolve through replacement events that occur at successive discrete time points. The replacement events are stochastically determined by the fitness of the individuals and the structure of the population. The individuals are assumed to have fixed fitness, i.e. there are no game-theoretic interactions, rather, two types of individuals are considered whose fitness are given relative to each other. The structure is given by a weighted digraph where each node represents an individual with the directed edges indicating where an individual's offspring can be placed. For the replacement events, several different dynamics are considered that depend upon whether birth or death is the first event and whether selection, i.e. fitness, acts on the first or second event. In particular the single most important property of such a process is the fixation probability, the probability that a randomly placed mutant individual of one type will eventually completely replace the population of the other type.

The objective of this chapter is to expand on the central theme of the classic paper [52] that identified the circumstances in which the dynamics and structure of the population interact in such a way that the fixation probability is equivalent to that of the Moran model, that is, it behaves just as if the population was homogeneous. The reason for doing this is to be able to identify population structures that neither amplify or suppress the effect of selection. Two important results, the circulation theorem and the isothermal theorem, were developed that addressed this question (see also [94] for related work). In this chapter, six different dynamics are considered of which two were originally considered in [52]. The circulation theorem and isothermal theorem are expanded by showing that they apply to four of these dynamics, including the two original ones. For the two remaining dynamics, a proposition is given to classify the population structures that are equivalent to a homogeneous population. All the results given in this chapter apply to graphs with general weights.

2.2 The Model

The population model used in this chapter is of [52] as described in Section 1.4 (pg. 31), which generalises the model of [58] by incorporating a replacement structure. The notation used is summarised in Table 2.1. The main assumptions of the model are as follows.

The population has a constant size $N \in \mathbb{Z}$, $N \geq 2$, consisting of individuals $I_1, \ldots, I_N$. Every individual is either of type A or B.

This implies that there are 2^N different states of the population given by the combination of type A and B individuals. Each state is represented by a set S such that $n \in S$ if an individual I_n is of type A. It is easier to revert to using the number of type A individuals, $|S|$, if the population is homogeneous. The states $\emptyset$ and $\mathcal{N} = \{1, 2, \ldots, N\}$ have only type B and A individuals respectively.

Individuals have a constant fitness that may depend upon their type.

The fitness of individuals in state S is thus given by the vector $\mathbf{F}(S) = (F_n(S))_{n=1,2,\ldots,N}$ where

$$F_n(S) = \begin{cases} 1 & n \notin S, \\ r \in (0, \infty) & n \in S, \end{cases}$$

is the fitness of I_n. Here the fitness r of a type A individual is given relative to the fitness of a type B individual assumed to be 1.

During a stochastic replacement event (that happens in an instant) an exact copy of an individual I_i replaces an individual I_j.

This information is summarised by the $N \times N$ weighted adjacency matrix $\mathbf{W} = (w_{ij})$, which is called the *replacement matrix*, such that I_i can replace I_j if and only if $w_{ij} > 0$. Note that $w_{ii} > 0$ is allowed and therefore I_i can replace itself.

The replacement events are stochastic which means that there is a probability $\mathfrak{r}_{ij} = \mathfrak{r}_{ij}(\mathbf{F}(S), \mathbf{W})$ associated with (a copy of) I_i replacing I_j. There are several potential *evolutionary dynamics on graphs* that govern how the probability is determined. There three main types of dynamics

Notation	*Definition*	*Description*
N	$\in \mathbb{Z}^+ \setminus \{0,1\}$	Population size.
A, B		The two types of individuals in population.
I_n		Individual n.
S	$= \{n : I_n \text{ of type } A\}$	State of the population.
$\mathcal{N}$	$= \{1, 2, \dots, N\}$	State in which all I_n of type A.
r	$\in (0, \infty)$	Fitness of a type A individual.
$F_n(S)$	$\in \{1, r\}$	Fitness of I_n in state S.
w_{ij}	$\in [0, \infty)$	Edge weight such that $w_{ij} > 0$ if and only if $(i,j) \in E$.
$\mathbf{W}$	$= (w_{ij})$	*Replacement matrix:* $N \times N$ weighted adjacency matrix.
T_n^+	$= \sum_{j=1}^{N} w_{nj}$	*Out temperature:* Sum of all outgoing weights.
T_n^-	$= \sum_{i=1}^{N} w_{in}$	*In temperature*: Sum of all incoming weights.
b_i	$\in [0, 1]$	Probability I_i chosen for birth.
d_{ij}	$\in [0, 1]$	Probability a copy of I_i replaces I_j, given that I_i chosen for birth.
d_j	$\in [0, 1]$	Probability I_j chosen for death.
b_{ij}	$\in [0, 1]$	Probability a copy of I_i replaces I_j, given that I_j chosen for death.
$\mathfrak{r}_{ij}$	$\in [0, 1]$	Probability a copy of I_i replaces I_j.
$P_{SS'}$	$\in [0, 1]$	State transition probability.
$\mathbf{S}$	$= (P_{SS'})$	State transition matrix.
$\mathcal{E}_{*,\mathbf{W},r}$		Stochastic process using $*$ dynamics, $\mathbf{W}$ and r.
ρ_S^A	$\in [0, 1]$	Fixation probability of type A individual from initial state S.
W		Set of all strongly connected replacement matrices.
W_C	$\{\mathbf{W} : T_n^+ = T_n^- \ \forall n\}$	Replacement matrices that are circulations.
W_I	$\{\mathbf{W} : T_i^+ = T_j^- \ \forall i, j\}$	Replacement matrices that are isothermal.
W_R	$\{\mathbf{W} : T_n^+ = 1 \ \forall n\}$	Right stochastic replacement matrices.
W_L	$\{\mathbf{W} : T_n^- = 1 \ \forall n\}$	Left stochastic replacement matrices.
C_N		Set of $\mathbf{W}$ that are cycles of length N.
f_R	$(w_{ij}) \mapsto (w_{ij} / \sum_n w_{in})$	Map from W to W_R.
f_L	$(w_{ij}) \mapsto (w_{ij} / \sum_n w_{nj})$	Map from W to W_L.
f'	$(w_{ij}) \mapsto (w_{ij} / \sum_{n,k} w_{nk})$	Map from W to W.
M_*		Set of $\mathbf{W}$ where $\mathcal{E}_{*,\mathbf{W},r}$ is ρ-equivalent to a Moran process.

Table 2.1: Notation used in this chapter.

that are summarised below, see also [93]. The convention that I_i is chosen for birth and I_j is chosen for death is used.

1. *Birth-Death* (BD): I_i is chosen first then I_j. In particular, $i \in V$ is chosen with probability b_i and then $(i,j) \in E_i$ is chosen with probability d_{ij}, where E_i are all edges starting in vertex i. d_{ij} is used to signify that there is 'replacement by death'. Finally, $\mathfrak{r}_{ij} = b_i d_{ij}$.

2. *Death-Birth* (DB): I_j is chosen first then I_i. In particular, $j \in V$ is chosen with probability d_j and then $(i,j) \in E_j$ is chosen with probability b_{ij}, where E_j are all edges ending in vertex j. b_{ij} is used to signify that there is 'replacement by birth'. Finally, $\mathfrak{r}_{ij} = d_j b_{ij}$.

3. *Link* (L): I_i and I_j are chosen simultaneously. In this case $(i,j) \in E$ is simply chosen with probability $\mathfrak{r}_{ij}$.

For each type of these dynamics, the natural selection can, through the fitness parameter, influence either the choice at birth (resulting in adding "B") or at death (adding "D"). It yields 6 kinds of evolutionary dynamics on graphs summarized in Table 2.2. These dynamics have been extensively studied, in particular, see [54] for a detailed comparison of them. Of these, the BDB and LB dynamics were used in [52].

2.2.1 The fixation probability

The fixation probability, $\rho_S^A = \rho_S^A(*, \mathbf{W}, r)$, is the probability that the population with initial state S is absorbed in $\mathcal{N}$ where $*$ is the dynamics being used.

Given that the replacement events are random, the transitions between the states of the population are described by a stochastic process, which is denoted $\mathcal{E}$. The properties of $\mathcal{E}$ can be investigated once the state transition probabilities of moving from state S to S', $P_{SS'} = P_{SS'}(*, \mathbf{W}, r)$, are calculated using the replacement probabilities as follows:

$$P_{SS'} = \begin{cases} \displaystyle\sum_{i \notin S} \mathfrak{r}_{ij}(\mathbf{F}(S), \mathbf{W}) & \text{if } S' = S \setminus \{j\} \text{ for some } j \in S, \\ \displaystyle\sum_{i \in S} \mathfrak{r}_{ij}(\mathbf{F}(S), \mathbf{W}) & \text{if } S' = S \cup \{j\} \text{ for some } j \notin S, \\ \displaystyle\sum_{\substack{i,j \in S \\ \vee i,j \notin S}} \mathfrak{r}_{ij}(\mathbf{F}(S), \mathbf{W}) & \text{if } S' = S. \end{cases}$$

The transition probabilities, $P_{SS'}$, satisfy the Markov property because they only depend upon the state S, that is, the probability of transitioning from the present state to another state is independent of any past and future state of the population. The stochastic process $\mathcal{E}_{*,\mathbf{W},r}$ with state transition matrix $\mathbf{S} = \mathbf{S}(*, \mathbf{W}, r) = (P_{SS'})_{S,S' \subset \{1,2,\ldots,N\}}$ is therefore a Markov chain. The Markov chain $\mathcal{E}_{*,\mathbf{W},r}$ is part of the class of evolutionary Markov chains described in [5].

The absorbing states of $\mathcal{E}_{*,\mathbf{W},r}$ are $\emptyset, \mathcal{N}$, which means that if the population is in either one of these states then it remains there indefinitely. This property of $\mathcal{E}_{*,\mathbf{W},r}$ can be used to measure the success of a type A individual by calculating the probability that it fixates, that is, everyone in the population is of type A. The fixation probability is then given by solving

$$\rho_S^A = \sum_{S' \subset \{1,2,\ldots,N\}} P_{SS'} \rho_{S'}^A \tag{2.1}$$

with boundary conditions $\rho_{\emptyset}^A = 0$ and $\rho_{\mathcal{N}}^A = 1$.

As demonstrated in [54], LB and LD dynamics may differ in time scale but they yield the same fixation probabilities when fitness is constant (which is the case here). Thus, for purposes in this chapter the dynamics are the same. They will be considered together and denoted by L.

2.2.2 The Moran Process

The Moran process [58] can be reconstructed as $\mathcal{E}_{\mathrm{BDB},\mathbf{W_H},r}$ for a constant replacement matrix

$$\mathbf{W_H} = (1/N)_{i,j}. \tag{2.2}$$

For any $r \in (0, \infty)$ and any $S \subset \{1, \ldots, N\}$, the fixation probability for this process, or *Moran probability*, is given by

$$\rho_S^A = \begin{cases} \dfrac{1 - r^{-|S|}}{1 - r^{-N}} & \text{if } r \neq 1, \\ |S|/N & \text{if } r = 1. \end{cases}$$

The objective is to characterize graphs (and evolutionary dynamics) that yield the same fixation probabilities as the homogeneous matrix $\mathbf{W_H}$ given in (2.2). Note that for this matrix all of the transition probabilities $\mathfrak{t}_{ij}$ take the same value independent of i, j or the dynamics, and consequently the fixation probability under each of the dynamics is the same.

2.2.3 Classes of Graphs/ Matrices

The set of all *admissible* replacement matrices is defined as follows

$$W = \{\mathbf{W} : \text{for every } i, j, \text{ there is } n \text{ such that } (\mathbf{W}^n)_{i,j} > 0\}.$$

This definition means that $\mathbf{W}$ is strongly connected as for any pair of vertices i and j, there is a path (of length n) going from i to j. Unless specified otherwise, only admissible replacement matrices will be considered.

As in [52], for any $\mathbf{W}$ (admissible or not) the *in temperature* of I_n, T_n^-, and the *out temperature* of I_n, T_n^+, is defined by

$$T_n^- = \sum_{j=1}^{N} w_{jn} \quad \text{and} \quad T_n^+ = \sum_{j=1}^{N} w_{nj}.$$

$\mathbf{W}$ is called a *circulation* if $T_n^+ = T_n^-$, for all $n \in V$ and it is called *isothermal* if $T_i^+ = T_j^-$, for all $i, j \in V$. $\mathbf{W}$ is called *right* stochastic if $T_n^+ = 1$, for all $n \in V$ and it is called *left* stochastic if $T_n^- = 1$, for all $n \in V$. The sets of all circulations, isothermal matrices, right stochastic matrices, and left stochastic matrices, respectively are denoted by W_C, W_I, W_R, and W_L respectively.

The set C_N denotes the sets of matrices representing *cycles* of length N, more specifically, when $(w_{ij}) \in C_N$ then $w_{ii} = 1/2$ for $i = 1, 2, \dots N$, $w_{i_1 i_2} = \cdots = w_{i_n i_{n+1}} = \cdots = w_{i_{N-1} i_N} = w_{i_N i_1} = 1/2$ for some permutation $i_1, i_2, \dots, i_N$ of the sequence $1, 2, \dots, N$, and $w_{ij} = 0$ otherwise.

The maps $f_R : W \to W_R$, $f_L : W \to W_L$, and $f' : W \to W$ are respectively defined by

$$f_R\left((w_{ij})\right) = \left(\frac{w_{ij}}{\sum_n w_{in}}\right), \quad f_L\left((w_{ij})\right) = \left(\frac{w_{ij}}{\sum_n w_{nj}}\right), \quad \text{and} \quad f'\left((w_{ij})\right) = \left(\frac{w_{ij}}{\sum_{n,k} w_{nk}}\right).$$

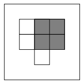
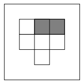
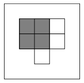
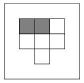
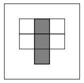
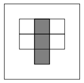
Note that f_R preserves right stochastic matrices and f_L preserves left stochastic matrices. Moreover, $f_R(\mathbf{W}) = f_L(\mathbf{W})$ for all $\mathbf{W} \in W_I$. Also, since f' simply involves multiplying $\mathbf{W}$ by the constant $1/\sum_{n,k} w_{nk}$, it implies that $\mathbf{W} \in W_\mathrm{C} \Leftrightarrow f'(\mathbf{W}) \in W_\mathrm{C}$.

When the dynamics $*$, matrices $\mathbf{W_1}$ and $\mathbf{W_2}$, and fitness r are given, it will be said that an evolutionary Markov chain $\mathcal{E}_{*,\mathbf{W_1},r}$ is *ρ-equivalent* to $\mathcal{E}_{*,\mathbf{W_2},r}$ if for every $S \subset \{1, \dots, N\}$, $\rho_S^A(*, \mathbf{W_1}, r) = \rho_S^A(*, \mathbf{W_2}, r)$, in which case it will be written $\mathbf{W_1} \sim_{*,r} \mathbf{W_2}$.

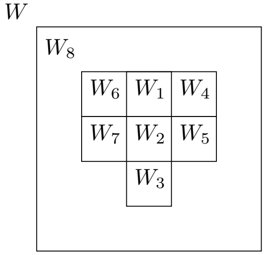
This chapter is specifically interested in finding matrices equivalent to the Moran process. For a dynamics $*$, the following is defined

$$M_* = \{\mathbf{W} : \mathbf{W} \sim_{*,r} \mathbf{W_H} \text{ for all } r > 0\}.$$

Table 2.2: List of dynamics used in this chapter together with their definition of M_*.

Process	$\mathbb{P}(I_i \text{ replaces } I_j)$	Order chosen	$\mathbb{P}$(Chosen first)	$\mathbb{P}$(Chosen second)	Definition of M_*	Illustration of M_*
BDB [7, 15, 52, 70, 71, 95, 103]	$\mathfrak{r}_{ij} = b_i d_{ij}$	I_i then I_j	$b_i = \dfrac{F_i(S)}{\sum\limits_n F_n(S)}$	$d_{ij} = \dfrac{w_{ij}}{\sum\limits_n w_{in}}$	$M_{\text{BDB}} = \{\mathbf{W} : f_R(\mathbf{W}) \in W_C\}$ $= f_R^{-1}(W_C)$	
BDD [54]	$\mathfrak{r}_{ij} = b_i d_{ij}$	I_i then I_j	$b_i = \dfrac{1}{N}$	$d_{ij} = \dfrac{w_{ij}/F_j(S)}{\sum\limits_n w_{in}/F_n(S)}$	$M_{\text{BDD}} = \{\mathbf{W} : f_R(\mathbf{W}) \in \{\mathbf{W_H}\} \cup C_N\}$ $= f_R^{-1}(\{\mathbf{W_H}\} \cup C_N)$	
DBD [6, 7, 60, 95]	$\mathfrak{r}_{ij} = d_i b_{ij}$	I_j then I_i	$d_j = \dfrac{1/F_j(S)}{\sum\limits_n 1/F_n(S)}$	$b_{ij} = \dfrac{w_{ij}}{\sum\limits_n w_{nj}}$	$M_{\text{DBD}} = \{\mathbf{W} : f_L(\mathbf{W}) \in W_C\}$ $= f_L^{-1}(W_C)$	
DBB [61, 67, 70, 71, 86]	$\mathfrak{r}_{ij} = d_i b_{ij}$	I_j then I_i	$d_j = \dfrac{1}{N}$	$b_{ij} = \dfrac{w_{ij}F_i(S)}{\sum\limits_n w_{nj}F_n(S)}$	$M_{\text{DBB}} = \{\mathbf{W} : f_L(\mathbf{W}) \in \{\mathbf{W_H}\} \cup C_N\}$ $= f_L^{-1}(\{\mathbf{W_H}\} \cup C_N)$	
LB [7, 52, 95]	$\mathfrak{r}_{ij} = \dfrac{w_{ij}F_i(S)}{\sum\limits_{n,k} w_{nk}F_n(S)}$	Simultaneous	N/A	N/A	$M_{\text{LB}} = \{\mathbf{W} : f'(\mathbf{W}) \in W_C\}$ $= f'^{-1}(W_C) = W_C$	
LD [55]	$\mathfrak{r}_{ij} = \dfrac{w_{ij}/F_j(S)}{\sum\limits_{n,k} w_{nk}/F_k(S)}$	Simultaneous	N/A	N/A	$M_{\text{LD}} = \{\mathbf{W} : f'(\mathbf{W}) \in W_C\}$ $= f'^{-1}(W_C) = W_C$	

Key for Illustration of M_*:



$$
\begin{aligned}
W_1 &= W_I \cap f_R^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
&= W_I \cap f_L^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
W_2 &= W_I \setminus f_R^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
&= W_I \setminus f_L^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
W_3 &= W_C \setminus W_I \\
W_4 &= \big(f_R^{-1}(W_C) \setminus W_C\big) \cap f_R^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
W_5 &= \big(f_R^{-1}(W_C) \setminus W_C\big) \setminus f_R^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
W_6 &= \big(f_L^{-1}(W_C) \setminus W_C\big) \cap f_L^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
W_7 &= \big(f_L^{-1}(W_C) \setminus W_C\big) \setminus f_L^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
W_8 &= W \setminus \textstyle\bigcup_{i=1}^{7} W_i
\end{aligned}
$$

The key on the left gives the definition of partitions $W_1, W_2, \ldots, W_8$ of W. The partitions W_i that make up M_* are highlighted for each of the dynamics in the last column. The partition of W where $\mathcal{E}$ is ρ-equivalent to a Moran process regardless of the standard dynamics being used is given by $M_{\text{L}} \cap M_{\text{BDB}} \cap M_{\text{BDD}} \cap M_{\text{DBD}} \cap M_{\text{DBB}} \equiv M_{\text{BDD}} \cap M_{\text{DBB}} \equiv W_1$.

2.3 Results

The map f_R preserves the equivalence classes of BDB and BDD dynamics, f_L preserves the equivalence classes of DBB and DBD dynamics and f' preserves the equivalence classes for link dynamics. Specifically, as one can see from the proofs in Section 2.5, for any $\mathbf{W}$ and any $r > 0$

$$\begin{aligned} \mathbf{W} &\sim_{\mathrm{BDB},r} f_R(\mathbf{W}), \qquad (2.3)\\ \mathbf{W} &\sim_{\mathrm{BDD},r} f_R(\mathbf{W}),\\ \mathbf{W} &\sim_{\mathrm{DBD},r} f_L(\mathbf{W}),\\ \mathbf{W} &\sim_{\mathrm{DBB},r} f_L(\mathbf{W}),\\ \mathbf{W} &\sim_{\mathrm{L},r} f'(\mathbf{W}). \end{aligned}$$

The following results are thus obtained, which completely specify the graphs which are equivalent to the homogeneous matrix $\mathbf{W_H}$ for each of the evolutionary dynamics considered here.

Proposition 1 (Link). *$M_L = W_C$. More precisely, the following statements are equivalent:*

(a) $\mathbf{W}$ is a circulation.

(b) For all $r > 0$, $\mathbf{W} \sim_{L,r} \mathbf{W_H}$.

(c) There is $r > 0$ such that $\mathbf{W} \sim_{L,r} \mathbf{W_H}$.

Note that $W_C = f'^{-1}(W_C) = \{\mathbf{W} : f'(\mathbf{W}) \in W_C\}$ and thus, similarly to Proposition 2 below, Proposition 1 can be written as $M_L = f'^{-1}(W_C)$.

Proposition 2 (BDB and DBD). *$M_{BDB} = f_R^{-1}(W_C)$ and $M_{DBD} = f_L^{-1}(W_C)$. More precisely, the following statements are equivalent:*

(a) $f_R(\mathbf{W})$ is a circulation.

(b) For all $r > 0$, $\mathbf{W} \sim_{BDB,r} \mathbf{W_H}$.

(c) There is $r > 0$ such that $\mathbf{W} \sim_{BDB,r} \mathbf{W_H}$

The equivalent conditions for DBD are similar to the above for BDB but f_R is replaced by f_L.

Proposition 3 (BDD and DBB). *$M_{BDD} = f_R^{-1}(\{\mathbf{W_H}\} \cup C_N)$ and $M_{DBB} = f_L^{-1}(\{\mathbf{W_H}\} \cup C_N)$. More precisely, the following statements are equivalent:*

(a) $f_R(\mathbf{W}) = \mathbf{W_H}$ or $f_R(\mathbf{W}) \in C_N$.

(b) For all $r > 0$, $\mathbf{W} \sim_{BDD,r} \mathbf{W_H}$.

The equivalent conditions for DBB are similar to the above for BDD but f_R is replaced by f_L.

In particular, $M_{\text{BDD}} \subset M_{\text{BDB}}$ and $M_{\text{DBB}} \subset M_{\text{DBD}}$. The sets M_* are illustrated in Table 2.2.

Note that unlike in Propositions 1 and 2, Proposition 3 does not contain “any r implies all r”. In fact, when $r = 1$, there is no selection and thus the dynamics BDB and BDD are the same (and also the dynamics DBB and DBD are the same). Consequently, by Proposition 2,

$$\mathbf{W} \sim_{\text{BDD},1} \mathbf{W_H} \Leftrightarrow f_R(\mathbf{W}) \in W_C \Leftrightarrow \mathbf{W} \in M_{\text{BDB}},$$
$$\mathbf{W} \sim_{\text{DBB},1} \mathbf{W_H} \Leftrightarrow f_L(\mathbf{W}) \in W_C \Leftrightarrow \mathbf{W} \in M_{\text{DBD}}.$$

2.3.1 Results here in the context of known results

For the LB dynamics, Proposition 1 was stated and proved in [52] as the Circulation theorem. For the LD dynamics, Proposition 1 follows from the Circulation theorem and the result of [54] that the fixation probabilities for LB and LD are the same.

As shown in Section 2.5.1, BDB is the same as the LB dynamics for right stochastic matrices (in particular, for BDB dynamics, Proposition 2 can be seen as the Isothermal theorem from [52]). Proposition 2 thus follows from Proposition 1 thanks to (2.3). The natural symmetries between f_R and f_L and BDB and DBD dynamics allow us to extend the Isothermal theorem to DBD dynamics as well (see also [42]).

Overall, Propositions 1 and 2 and the occurrence of W_C within them are consistent with the claim made in [52] that the circulation criterion completely classifies all replacement matrices where $\mathcal{E}_{*,\mathbf{W},r}$ is ρ-equivalent to a Moran process. Figure 2.1 shows two graphs with the same number of edges, but one is a circulation and the other is not, i.e. a circulation graph can be constructed by changing the edge weights.

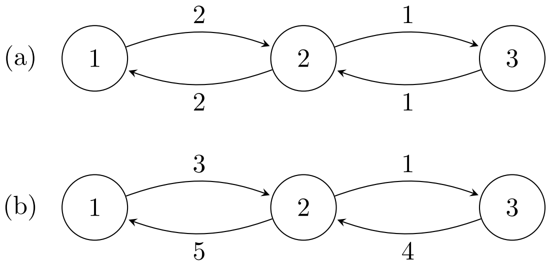


Figure 2.1: Two graphs are shown that have the same number of edges but different weights. Figure (a) is a circulation since the in temperature and out temperature is the same for each vertex, i.e. $T_1^+ = T_1^- = 4$, $T_2^+ = T_2^- = 3$ and $T_3^+ = T_3^- = 2$. Figure (b) shows that by changing the edge weights the graph is no longer a circulation. It suffices to check that only one edge does not satisfy the circulation criterion, i.e. $T_1^+ = 3 \neq T_1^- = 5$.

The most important new result is Proposition 3. It shows that the BDD and DBB dynamics require very strict conditions to yield the Moran process. Either the population structure is homogeneous, or it is a directed cycle. This latter structure is an interesting theoretical example, but is unlikely to apply to real populations, meaning that the homogeneous population is practically the only way to get the Moran process for a realistic population.

2.3.2 The importance of self-loops in BDD and DBB dynamics

Proposition 3 by definition requires that $w_{ii} > 0 \ \forall i = 1, 2, \ldots, N$. Without such self-loops, $\mathcal{E}_{\mathrm{BDD},\mathbf{W},r}, \mathcal{E}_{\mathrm{DBB},\mathbf{W},r}$ cannot ever be ρ-equivalent to the Moran process. The ability of an individual to replace itself therefore plays an important role in the replacement structure of the population and cannot be discounted. For BD dynamics, when increasing the diagonal weights of $\mathbf{W}$, the fixation probability decreases for BDB and increases for BDD. For DB dynamics, the increase in fixation probability DBB is greater than that for DBD. For LB dynamics, the fixation probability remains the same.

With BDD and DBB evolutionary dynamics on graphs one may encounter the following problems if there are no self-loops. For DBB dynamics, a type A individual with almost infinite fitness still has a fixation probability bounded away from 1 because even type A individuals can be randomly picked for death and replaced by type B individuals [17, page 245]. With self-loops, however, a type A individual will almost always be replaced by itself (or another type A individual) and therefore has a fixation probability approaching 1. Similarly, for BDD dynamics, a type A individual with almost zero fitness does not have near probability 0 of fixating as type A individuals can be randomly picked for birth and replace type B individuals [17, page 245]. With self-loops, such an individual will almost always pick itself (or another type A) to replace and therefore its fixation probability is near 0. Thus the inclusion of self-loops removes some problematic features of the BDD and DBB dynamics, and makes them more attractive dynamics to use in models.

2.4 Discussion

This fixation probability depends upon the fitnesses of the two types of individuals, but can also be heavily influenced by the population structure as given by the weights, and by the evolutionary dynamics used. These effects are commonly observed, although in some circumstances evolution proceeds as if on a well-mixed population as from the original work of [58], dependent only upon the fitnesses of the two types, and some important results in this regard were already given in [52]. The aim of this chapter was to provide a generalised set of conditions for when this would be the case.

By defining what is meant by fixation-equivalence to the Moran process, a general result was provided which, independent of the specific dynamics used, helps identify graphs that do not affect the fixation probability. With respect to each of the standard dynamics, sets of evolutionary graphs were classified that have the same fixation probability as the Moran process (or well mixed population). These sets include graphs that are circulations and therefore generalises the work of [52].

An important new result shows that the set of weights for which fixation equivalence to the Moran process is obtained for the BDD and DBB dynamics is very restricted, and so that for most populations with any structure this equivalence will not hold for these dynamics. Note also that the inclusion of non-zero self weights w_{ii} eliminates some problematic features of these two dynamics (i.e. that individuals with 0 fitness could fixate or those with infinite fitness could be eliminated) and so improves the applicability of these dynamics.

Presenting evolutionary dynamics on graphs in the way done here allows one to incorporate a variety of dynamics in their analysis, both of standard type and other definitions. This improves the understanding of dynamics on graphs in general. Note that the list of dynamics in Table 2.2 is not exhaustive. For example, [71] used imitation dynamics, which is a class of DBB dynamics with an additional requirement $w_{ii} > 0 \ \forall i$, and [106] consolidates the BDB and DBD dynamics such that one is chosen with a given probability.

In general the inclusion of non-zero self weights, in contrast to many earlier evolutionary graph theory works, allows for a greater flexibility of modelling. Note that this is consistent with the original work of [58], which allowed self-replacement as an integral part of the process. For well-mixed populations it does not matter much whether this possibility is included or not (at least for sufficiently large populations with intermediate fitness values), and it is likely that it has often been excluded for reasons of convenience because of this without the ramifications being fully considered in many later works. It is thus important to consider whether to include such self weights when modelling spatial structure using evolutionary graph theory.

2.5 Proofs

2.5.1 BDB is the same as LB for right stochastic matrices

For BDB dynamics we have $\mathfrak{r}_{ij} = b_i d_{ij}$. By definition $\sum_{ij} b_i d_{ij} = 1$, we can therefore write this as $\mathfrak{r}_{ij} = b_i d_{ij} \Big/ \sum_{n,k} b_n d_{n,k}$. Substituting $b_i = F_i \Big/ \sum_{m=1}^{N} F_m$ gives

$$\mathfrak{r}_{ij} = \frac{d_{ij} F_i \Big/ \sum_{m=1}^{N} F_m}{\sum_{n,k} \left(d_{nk} F_n \Big/ \sum_{m=1}^{N} F_m \right)} = \frac{d_{ij} F_i}{\sum_{n,k} d_{nk} F_n}.$$

If $\mathbf{W}$ is right stochastic, i.e. $\sum_{n=1}^{N} w_{in} = 1$ for all $i = 1, 2, \dots N$, for BDB dynamics we have that $d_{ij} = w_{ij} \Big/ \sum_{n=1}^{N} w_{in} = w_{ij}$ giving $\mathfrak{r}_{ij} = w_{ij} F_i \Big/ \sum_{n,k} w_{nk} F_n$ which is the LB dynamics as required. We also have that DBD is the same as LD for left stochastic matrices. The explanation follows the same procedure as above.

2.5.2 Lemma 1 (Forward Bias)

The key Lemma 1 stated below is used in the proofs of all propositions and it relies heavily on the notion of *forward bias* of state S which is then given by the ratio of the probabilities of a forward transition to a backward transition from S. A forward and backward transition from S occurs when the number of type A individuals increase and decrease by one respectively, which happen with probability

$$P_S^+ = \sum_{n \notin S} P_{S, S \cup \{n\}} \quad \text{and} \quad P_S^- = \sum_{n \in S} P_{S, S \setminus \{n\}}.$$

Lemma 1 (Constant Forward Bias)**.** *Let $\mathcal{E}$ be an evolutionary process on states $S \subset \{1, 2, \dots, N\}$ with transition probabilities $P_{S,S'}$ that satisfy*

- *$P_{S,S'} > 0$ only if S and S' differ in at most one element*
- *for every $S \neq \emptyset, \{1, \dots, N\}$, there are S^+ and S^- such that $|S^+| = |S|+1$ and $|S^-| = |S|-1$ and $P_{S,S^+} > 0, P_{S,S^-} > 0$.*

Then, the following are equivalent

a) There is a constant $c > 0$ such that for all $S \subset \{1, 2, \dots, N\}$

$$\rho_S^A = \begin{cases} \dfrac{1 - c^{-|S|}}{1 - c^{-N}} & \text{if } c \neq 1, \\ |S|/N & \text{if } c = 1 \end{cases}$$

b) $\mathcal{E}$ has constant forward bias, that is, there is a constant d such that for all $S \subset \{1, 2, \dots, N\}$

$$P_S^+ / P_S^- = d.$$

Moreover, if either (a) or (b) hold, then $c = d$.

Note that a similar result is given in [4, 52] where the forward bias is explicitly defined as

$$r \sum_{a \in S} \sum_{b \notin S} w_{ab} \Bigg/ \sum_{a \in S} \sum_{b \notin S} w_{ba} \ ,$$

which is what one gets when using Link dynamics, or BDB dynamics if $\mathbf{W} \in W_R$. Note that in Lemma 1 the forward bias is defined independent of the dynamics and therefore applies to all dynamics that satisfy the assumptions.

Proof. “(a) $\Rightarrow$ (b)”: Take any $S \subset \{1, 2, \ldots, N\}$. It is known that

$$\rho_S^A = \sum_{S'} P_{S,S'}\rho_{S'}^A = P_{S,S}\rho_S^A + \sum_{n \notin S}\left(P_{S,S\cup\{n\}}\rho_{S\cup\{n\}}^A\right) + \sum_{n\in S}\left(P_{S,S\setminus\{n\}}\rho_{S\setminus\{n\}}^A\right)$$

and using $P_{S,S} = 1 - P_S^+ - P_S^-$ gives

$$0 = \sum_{n\notin S}\left(P_{S,S\cup\{n\}}\left(\rho_{S\cup\{n\}}^A - \rho_S^A\right)\right) + \sum_{n\in S}\left(P_{S,S\setminus\{n\}}\left(\rho_{S\setminus\{n\}}^A - \rho_S^A\right)\right). \tag{2.4}$$

For $c \neq 1$, equation (2.4) simplifies to

$$\begin{aligned} 0 &= \frac{1 - c^{-|S|-1} - 1 + c^{-|S|}}{1 - c^{-N}}P_S^+ + \frac{1 - c^{-|S|+1} - 1 + c^{-|S|}}{1 - c^{-N}}P_S^- \Rightarrow \\ P_S^+/P_S^- &= \frac{c^{-|S|} - c^{-|S|+1}}{c^{-|S|-1} - c^{-|S|}} = \frac{1-c}{c^{-1}-1} = c. \end{aligned}$$

For $c = 1$, equation (2.4) simplifies to

$$0 = (|S| + 1 - |S|)P_S^+ + (|S| - 1 - |S|)P_S^- \Rightarrow \quad P_S^+/P_S^- = 1.$$

“(b) $\Leftarrow$ (a)”: The state transition matrix $\mathbf{S} = (P_{S,S'})$ can be scaled to give $\mathbf{S}' = (P'_{S,S'})$ such that $P'_{S,S} = 0$ and $P'_{S,S'} = P_{S,S'}/(1 - P_{S,S}) = P_{S,S'}/(P_S^+ + P_S^-)$ where S is a non-absorbing state. The fixation probability ρ_S^A will be the same whether $\mathbf{S}'$ or $\mathbf{S}$ is used. This is because equation (2.1) can be rearranged as follows

$$\begin{aligned} \rho_S^A &= \sum_{S'} P_{SS'}\rho_{S'}^A \Rightarrow \quad \rho_S^A = P_{SS}\rho_S^A + \sum_{S':S'\neq S} P_{SS'}\rho_{S'}^A \Rightarrow \\ \rho_S^A(1 - P_{SS}) &= \sum_{S':S'\neq S} P_{SS'}\rho_{S'}^A \Rightarrow \quad \rho_S^A = \sum_{S':S'\neq S}\frac{P_{SS'}}{P_S^+ + P_S^-}\rho_{S'}^A. \end{aligned}$$

Let $\{\mathcal{S}_0, \mathcal{S}_1, \ldots, \mathcal{S}_N\}$ be a partition of the states S such that $S \in \mathcal{S}_i$ if $|S| = i$. The probability $P_{i,j}(S)$ of transitioning from state $S \in \mathcal{S}_i$ to *lumped state* $\mathcal{S}_j$ with respect to $\mathbf{S}'$ is

$$P_{i,j}(S) = \begin{cases} 0 & j \neq i \pm 1, \\ 1/(d+1) & j = i - 1, \\ d/(d+1) & j = i + 1 \end{cases} \quad \text{for } i = 1, 2, \ldots, N-1. \tag{2.5}$$

This can be easily verified, for example, take $j = i - 1$ then

$$P_{i,i-1}(S) = \sum_{S'\in\mathcal{S}_{i-1}} P'_{S,S'} = \sum_{S'\in\mathcal{S}_{i-1}}\frac{P_{S,S'}}{P_S^+ + P_S^-} = \frac{P_S^-}{P_S^+ + P_S^-} = \frac{1}{1+d}$$

since the forward bias is equal to d. Equation (2.5) satisfies the necessary and sufficient condition for the Markov chain with state transition matrix $\mathbf{S}'$ to be lumpable with respect to the partition $\{\mathcal{S}_0, \mathcal{S}_1, \ldots, \mathcal{S}_N\}$ (Theorem 6.3.2 page 124, [44]). Let $\hat{\mathbf{S}} = (P_{i,j})$ be the state transition matrix for this lumped Markov chain then the probability $P_{i,j}$ of transitioning from lumped states $\mathcal{S}_i$ to $\mathcal{S}_j$ is given by

$$P_{i,j} = P_{i,j}(S).$$

The state transition matrix $\hat{\mathbf{S}}$ describes a random walk with absorbing barriers and therefore the probability ρ_i^A of type A individuals fixating when the population starts in lumped state $\mathcal{S}_i$ is calculated using the methods in [41] to give

$$\rho_i^A = 1 + \sum_{j=1}^{i-1} \prod_{k=1}^{j} \frac{P_{k,k-1}}{P_{k,k+1}} \Bigg/ 1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \frac{P_{k,k-1}}{P_{k,k+1}} .$$

In this case,

$$\rho_i^A = \begin{cases} \dfrac{1-d^{-i}}{1-d^{-N}} & d \neq 1, \\ i/N & d = 1 \end{cases}$$

since $P_{k,k-1}/P_{k,k+1} = 1/r$ for $k = 1, 2, \ldots, N-1$. By definition, $\rho_S^A = \rho_i^A$ where $i = |S|$ as required. □

2.5.3 Proposition 1 (Link)

The following statements are equivalent:

(a) $\mathbf{W}$ is a circulation.

(b) For all $r > 0$, $\mathbf{W} \sim_{\mathrm{L},r} \mathbf{W_H}$.

(c) There is $r > 0$ such that $\mathbf{W} \sim_{\mathrm{L},r} \mathbf{W_H}$.

(d) For all $r > 0$ and for all $S \subset \{1, 2, \ldots, N\}$, the forward bias of $\mathcal{E}_{\mathrm{L},\mathbf{W},r}$ is r, i.e.

$$P_S^+ / P_S^- = r.$$

(e) There is $r > 0$ such that for all $a \in \{1, 2, \ldots, N\}$, the forward bias of the one element set $S = \{a\}$ is r, i.e.

$$\frac{\sum_{b \neq a} P_{\{a\},\{a,b\}}}{P_{a,\emptyset}} = r.$$

Proof. For LB dynamics the forward bias is given by

$$\frac{P_S^+}{P_S^-} = \frac{\displaystyle\sum_{a \in S} \sum_{b \notin S} \frac{w_{ab} F_a}{\sum_{n,k} w_{nk} F_n}}{\displaystyle\sum_{a \in S} \sum_{b \notin S} \frac{w_{ba} F_b}{\sum_{n,k} w_{nk} F_n}} = \frac{r \displaystyle\sum_{a \in S} \sum_{b \notin S} w_{ab}}{\displaystyle\sum_{a \in S} \sum_{b \notin S} w_{ba}}.$$

For LD dynamics the forward bias is given by

$$\frac{P_S^+}{P_S^-} = \frac{\displaystyle\sum_{a\in S}\sum_{b\notin S}\frac{w_{ab}/F_b}{\sum_{n,k} w_{nk}/F_k}}{\displaystyle\sum_{a\in S}\sum_{b\notin S}\frac{w_{ba}/F_a}{\sum_{n,k} w_{nk}/F_k}} = \frac{r\displaystyle\sum_{a\in S}\sum_{b\notin S} w_{ab}}{\displaystyle\sum_{a\in S}\sum_{b\notin S} w_{ba}}.$$

"(a) ⇒ (d)": **W** is a circulation i.e. $T_n^+ = T_n^-$ for all $n \in \{1, \dots, N\}$ and thus

$$\begin{aligned}
&\sum_{a\in S}\sum_{b\notin S} w_{ab} = \sum_{a\in S}\left(\sum_n w_{an} - \sum_{k\in S} w_{ak}\right) = \sum_{a\in S}\left(T_a^+ - \sum_{k\in S} w_{ak}\right) \Rightarrow\\
&\sum_{a\in S}\sum_{b\notin S} w_{ab} = \sum_{a\in S}\left(T_a^- - \sum_{k\in S} w_{ka}\right) = \sum_{a\in S}\left(\sum_n w_{na} - \sum_{k\in S} w_{ka}\right) \Rightarrow\\
&\sum_{a\in S}\sum_{b\notin S} w_{ab} = \sum_{a\in S}\sum_{b\notin S} w_{ba}.
\end{aligned}$$

Note that $\sum_{a\in S}\sum_{b\notin S} w_{ab} \neq 0$ because **W** is admissible and represents a strongly connected graph. Thus, the forward bias for both LB and LD is equal to r.

"(d)⇒(e)" is trivial as (d) is much stronger than (e).

"(e)⇒(a)" Let a and r is fixed. By above calculations of the forward bias, we have

$$\sum_{b\notin S=\{a\}} w_{ab} = \sum_{b\notin S=\{a\}} w_{ba} \Rightarrow \quad -w_{aa} + \sum_{i=1}^N w_{ai} = -w_{aa} + \sum_{i=1}^N w_{ia} \Rightarrow \quad \sum_{i=1}^N w_{ai} = \sum_{i=1}^N w_{ia}$$

therefore **W** is a circulation.

"(d)⇒(b)" follows from Lemma 1.

"(b)⇒(c)" is trivial.

"(c)⇒(e)" follows from Lemma 1. □

2.5.4 Proposition 2 (BDB and DBD)

More precisely, the following statements are equivalent:

(a) $f_R(\mathbf{W})$ is a circulation.

(b) For all $r > 0$, $\mathbf{W} \sim_{\mathrm{BDB},r} \mathbf{W_H}$.

(c) There is $r > 0$ such that $\mathbf{W} \sim_{\mathrm{BDB},r} \mathbf{W_H}$

(d) For all $r > 0$ and for all $S \subset \{1, 2, \dots, N\}$, the forward bias of $\mathcal{E}_{\mathrm{BDB},\mathbf{W},r}$ is r, i.e.

$$P_S^+ / P_S^- = r.$$

(e) There is $r > 0$ such that for all $a \in \{1, 2, \ldots, N\}$, the forward bias of $\mathcal{E}_{\mathrm{BDB},\mathbf{W},r}$ of the one element set $S = \{a\}$ is r, i.e.

$$\frac{\displaystyle\sum_{b \neq a} P_{\{a\},\{a,b\}}}{P_{a,\emptyset}} = r.$$

Proof. Let $\mathbf{U} = (u_{ij}) = f_R(\mathbf{W}) = (w_{ij}/\sum_n w_{in})$ then for BDB dynamics the forward bias of $\mathcal{E}_{BDB,\mathbf{W},r}$ is given by

$$\frac{P_S^+}{P_S^-} = \frac{\displaystyle\sum_{a\in S}\sum_{b\notin S} \frac{F_a}{\displaystyle\sum_n F_n} \frac{w_{ab}}{\displaystyle\sum_n w_{an}}}{\displaystyle\sum_{a\in S}\sum_{b\notin S} \frac{F_b}{\displaystyle\sum_n F_n} \frac{w_{ba}}{\displaystyle\sum_n w_{bn}}} = \frac{r\displaystyle\sum_{a\in S}\sum_{b\notin S} u_{ab}}{\displaystyle\sum_{b\notin S}\sum_{a\in S} u_{ba}}$$

and therefore the forward bias of $\mathcal{E}_{\mathrm{BDB},\mathbf{W},r}$ is the same as forward bias of $\mathcal{E}_{\mathrm{BDB},\mathbf{U},r}$.

Similarly, with almost identical working as above, when $\mathbf{V} = f_L(\mathbf{W})$, the forward bias of $\mathcal{E}_{\mathrm{DBD},\mathbf{W},r}$ is the same as forward bias of $\mathcal{E}_{\mathrm{DBD},\mathbf{V},r}$ and is given by

$$\frac{P_S^+}{P_S^-} = \frac{\displaystyle\sum_{a\in S}\sum_{b\notin S} \frac{1/F_b}{\displaystyle\sum_n 1/F_n} \frac{w_{ab}}{\displaystyle\sum_n w_{nb}}}{\displaystyle\sum_{a\in S}\sum_{b\notin S} \frac{1/F_a}{\displaystyle\sum_n 1/F_n} \frac{w_{ba}}{\displaystyle\sum_n w_{na}}} = \frac{\displaystyle\sum_{a\in S}\sum_{b\notin S} v_{ab}}{\displaystyle\frac{1}{r}\sum_{a\in S}\sum_{b\notin S} v_{ba}}.$$

and the proof of the Proposition for DBD closely follows the one for BDB given below with $\mathbf{U}$ and f_R appropriately replaced by $\mathbf{V}$ and f_L.

"(a)⇒ (d)": If $\mathbf{U} = f_R(\mathbf{W}) \in W_{\mathrm{C}}$, i.e. if $\mathbf{U}$ is doubly stochastic, then the forward bias (for $S \neq \emptyset, \mathcal{N}$) is equal to

$$\frac{P_S^+}{P_S^-} = \frac{r\displaystyle\sum_{a\in S}\left(\sum_n (u_{an}) - \sum_{k\in S}(u_{ak})\right)}{\displaystyle\sum_{a\in S}\left(\sum_n (u_{na}) - \sum_{k\in S}(u_{ka})\right)} = \frac{r\left(|S| - \displaystyle\sum_{a\in S}\sum_{k\in S} u_{ak}\right)}{|S| - \displaystyle\sum_{a\in S}\sum_{k\in S} u_{ka}} = r$$

"(d)⇒(e)" is trivial as (d) is stronger than (e).

"(e)⇒(a)" Let a and r is fixed. By above calculations of the forward bias, we have

$$\sum_{a\in S}\sum_{b\notin S} u_{ab} = \sum_{a\in S}\sum_{b\notin S} u_{ba}.$$

Consider the states $S = \{a\}$ in which there is only one individual of type A then

$$\sum_{b\notin S} u_{ab} = \sum_{b\notin S} u_{ba} \Rightarrow \quad -u_{aa} + \sum_{i=1}^{N} u_{ai} = -u_{aa} + \sum_{i=1}^{N} u_{ia} \Rightarrow \quad 1 = \sum_{i=1}^{N} u_{ia}$$

is true for all $a = 1, 2, \ldots, N$ and therefore $\mathbf{U}$ is doubly stochastic and thus $f_R(\mathbf{W})$ is a circulation.

"(d)⇒(b)" follows from Lemma 1.

"(b)⇒(c)" is trivial.

"(c)⇒(e)" follows from Lemma 1. □

2.5.5 Proposition 3 (BDD and DBB)

The following statements are equivalent:

(a) $f_R(\mathbf{W}) = \mathbf{W_H}$ or $f_R(\mathbf{W}) \in C_N$.

(b) For all $r > 0$, $\mathbf{W} \sim_{\mathrm{BDD},r} \mathbf{W_H}$.

Proof. The replacement probabilities $\mathfrak{r}_{ij}(\mathbf{F}(S), \mathbf{W})$ for BDD dynamics can be rewritten as $\mathfrak{r}_{ij}(\mathbf{F}(S), \mathbf{U})$ where $\mathbf{U} = (u_{ij}) = f_R(\mathbf{W}) = (w_{ij}/\sum_n w_{in})$ by multiplying the numerator and denominator with $\sum_n w_{in}$ as follows

$$\mathfrak{r}_{ij}(\mathbf{F}(S), \mathbf{W}) = \frac{1}{N}\frac{w_{ij}/F_j(S)}{\sum_n w_{in}/F_n(S)} = \frac{1}{N}\frac{w_{ij}/\left(F_j(S)\sum_n w_{in}\right)}{\sum_n w_{in}/\left(F_n(S)\sum_n w_{in}\right)} \Rightarrow$$
$$\frac{u_{ij}/F_j(S)}{\sum_n u_{in}/F_n(S)} = \mathfrak{r}_{ij}(\mathbf{F}(S), \mathbf{U})$$

and therefore we have that $\mathbf{W} \sim_{\mathrm{BDD},r} \mathbf{U}$, for all $r > 0$. The forward bias using $\mathbf{U}$ for state S is given by

$$\frac{P_S^+}{P_S^-} = \frac{\displaystyle\sum_{a\in S}\sum_{b\notin S}\frac{1}{N}\frac{u_{ab}/F_b}{\displaystyle\sum_n u_{an}/F_n}}{\displaystyle\sum_{a\in S}\sum_{b\notin S}\frac{1}{N}\frac{u_{ba}/F_a}{\displaystyle\sum_n u_{bn}/F_n}} = \frac{\displaystyle\sum_{a\in S}\sum_{b\notin S}\frac{u_{ab}}{\displaystyle\sum_n u_{an}/F_n}}{\displaystyle\frac{1}{r}\sum_{a\in S}\sum_{b\notin S}\frac{u_{ba}}{\displaystyle\sum_n u_{bn}/F_n}}. \tag{2.6}$$

Similarly, let $\mathbf{V} = (v_{ij}) = f_L(\mathbf{W}) = (w_{ij}/\sum_n w_{nj})$. Then for DBB dynamics we have

$$b_{ij} = \frac{w_{ij}F_i}{\sum_n w_{nj}F_n} = \frac{w_{ij}F_i/\sum_n w_{nj}}{\sum_n w_{nj}F_n/\sum_n w_{nj}} = \frac{v_{ij}F_i}{\sum_n v_{nj}F_n}$$

and therefore the forward bias when using $\mathbf{V}$ is given by

$$\frac{P_S^+}{P_S^-} = \frac{\displaystyle\sum_{a\in S}\sum_{b\notin S}\frac{1}{N}\frac{v_{ab}F_a}{\displaystyle\sum_n v_{nb}F_n}}{\displaystyle\sum_{a\in S}\sum_{b\notin S}\frac{1}{N}\frac{v_{ba}F_b}{\displaystyle\sum_n v_{na}F_n}} = \frac{\displaystyle r\sum_{a\in S}\sum_{b\notin S}\frac{v_{ab}}{\displaystyle\sum_n v_{nb}F_n}}{\displaystyle\sum_{a\in S}\sum_{b\notin S}\frac{v_{ba}}{\displaystyle\sum_n v_{na}F_n}}.$$

The proof of the Proposition for DBB closely follows the one for BDD given below with $\mathbf{U}$ and f_R appropriately replaced by $\mathbf{V}$ and f_L.

If $\mathbf{U} \in C_N$, then $\mathbf{U} \sim_{\mathbf{BDD},r} \mathbf{W_H}$

If $\mathbf{U} \in C_N$ then there are only two nonzero elements in each row. In particular, in row i of $\mathbf{U}$ we have that $u_{ii}, u_{ik_i} = 1/2$ for some $k_i \neq i$. In the numerator of equation (2.6) for $a \in S$, $b \notin S$ and $k_a \neq a$ we have that for all S

$$\frac{u_{ab}}{\sum\limits_n u_{an}/F_n(S)} = \frac{u_{ab}}{u_{aa}/F_a(S) + u_{ak_a}/F_{k_a}(S)} = \begin{cases} 0 & \text{if } b \neq k_a, \\ \frac{1/2}{1/2r+1/2} & \text{if } b = k_a. \end{cases}$$

Similarly, in the denominator of equation (2.6) for $a \in S$, $b \notin S$ and $k_b \neq b$ we have that for all S

$$\frac{u_{ba}}{\sum\limits_n u_{bn}/F_n(S)} = \frac{u_{ba}}{u_{bb}/F_b(S) + u_{bk_b}/F_{k_b}(S)} = \begin{cases} 0 & \text{if } a \neq k_b, \\ \frac{1/2}{1/2+1/2r} & \text{if } a = k_b. \end{cases}$$

This means that equation (2.6) for all S can be written as

$$\frac{x/2}{1/2r+1/2} \Big/ \frac{1}{r}\frac{y/2}{1/2+1/2r} = rx/y$$

where x (y) is the number of nonzero u_{ab} (u_{ba}) terms in the numerator (denominator). If we partition the vertices of the graph of $\mathbf{U}$ into any two sets V_1, V_2 then the number of edges $e(i,j)$ and $e(j,i)$ for $i \in V_1$ and $j \in V_2$ are by definition the same because it is a cycle. This means that for $a \in S$ and $b \notin S$ the number of nonzero u_{ab}, u_{ba} terms in the numerator and denominator respectively are the same hence $x = y$ and $rx/y = r$ as required. As per Lemma 1, $\mathcal{E}_{\mathrm{BDD},\mathbf{U},r}$ is ρ-equivalent to the Moran process.

If $\mathbf{U} \sim_{\mathbf{BDD},r} \mathbf{W_H}$ for all $r > 0$, then $\mathbf{U} = \mathbf{W_H}$ or $\mathbf{U} \in C_N$

By Lemma 1, the forward bias (2.6) is equal to r for all $S \subset \{1, \dots, N\}$ giving

$$\sum_{a \in S}\sum_{b \notin S} \frac{u_{ab}}{\sum\limits_n u_{an}/F_n} = \sum_{a \in S}\sum_{b \notin S} \frac{u_{ba}}{\sum\limits_n u_{bn}/F_n} \Rightarrow$$

$$\sum_{a \in S} \frac{\sum\limits_{b \notin S} u_{ab}}{\sum\limits_{j \notin S} u_{aj} + \frac{1}{r}\sum\limits_{i \in S} u_{ai}} = \sum_{b \notin S} \frac{\sum\limits_{a \in S} u_{ba}}{\sum\limits_{j \notin S} u_{bj} + \frac{1}{r}\sum\limits_{i \in S} u_{bi}}. \tag{2.7}$$

Note that if $r = 1$, (2.7) holds for all $\mathbf{U} \in W_C$. From now, we will consider $r \neq 1$ only. For clarity, the remainder of this section of the proof is broken down into the following six steps.

Step 1: Derivation of general state dependent row-sum equation

Let $U(a,S) = \sum_{i \in S} u_{ai}$, i.e. $1 - U(a,S) = \sum_{j \notin S} u_{aj}$. Equation (2.7) thus becomes

$$\sum_{a \in S} \frac{1 - U(a,S)}{1 - U(a,S) + U(a,S)/r} = \sum_{b \notin S} \frac{U(b,S)}{1 - U(b,S) + U(b,S)/r} \Rightarrow$$

$$\sum_{a \in S} \frac{1}{1 + U(a,S)(1/r-1)} = \sum_{n=1}^{N} \frac{U(n,S)}{1 + U(n,S)(1/r-1)}. \tag{2.8}$$

Equation (2.8) can be written as a Taylor series as follows

$$\sum_{a \in S} \sum_{k=0}^{\infty} (-1)^k (1/r-1)^k \left[U(a,S)\right]^k = \sum_{n=1}^{N} U(n,S) \sum_{k=0}^{\infty} (-1)^k (1/r-1)^k \left[U(n,S)\right]^k \Rightarrow$$

$$\sum_{a \in S} \sum_{k=0}^{\infty} (1-1/r)^k \left[U(a,S)\right]^k = \sum_{n=1}^{N} \sum_{k=0}^{\infty} (1-1/r)^k \left[U(n,S)\right]^{k+1} \tag{2.9}$$

For equation (2.9) to hold for all r the coefficients of $(1-1/r)^k$ should be same, that is, for all k

$$\sum_{a \in S} \left[U(a,S)\right]^k = \sum_{n=1}^{N} \left[U(n,S)\right]^{k+1}. \tag{2.10}$$

Step 2: The diagonal of U consists of non-zero elements

Consider the state $S = \{a\}$ then equation (2.10) gives

$$u_{aa}^k = \sum_{n=1}^{N} u_{na}^{k+1}. \tag{2.11}$$

If $u_{aa} = 0$ or 1 then (2.11) implies that all off-diagonal terms in column n are zero which is a contradiction with $\mathbf{W}$ (and thus also $\mathbf{U} = f_R(\mathbf{W})$) being strongly connected, which means that $0 < u_{aa} < 1$.

Step 3: The n^{th} column of U contains m_n nonzero elements, all equal to $1/m_n$

Since $0 < u_{aa} < 1$, we can divide equation (2.11) by u_{aa}^k giving

$$1 = \sum_{n=1}^{N} u_{na} \left(\frac{u_{na}}{u_{aa}}\right)^k. \tag{2.12}$$

We have that

$$\lim_{k \to \infty} \left(\frac{u_{na}}{u_{aa}}\right)^k = \begin{cases} \infty & u_{na} > u_{aa}, \\ 1 & u_{na} = u_{aa}, \\ 0 & u_{na} < u_{aa}, \end{cases}$$

and therefore (2.12) implies that $0 \leq u_{na} \leq u_{aa}$. There must be $n \neq a$ such that $u_{na} = u_{aa}$ as otherwise, by (2.12), we would have $u_{aa} = 1$. Let $\mathcal{C}_a = \{i : u_{ia} = u_{aa}\}$. (2.12) becomes

$$1 = \left(\sum_{i \in C_a} u_{aa}\right) + \left(\sum_{j \notin C_a} \frac{u_{ja}^{k+1}}{u_{aa}^k}\right) = |C_a| u_{aa} + \left(\sum_{j \notin C_a} \frac{u_{ja}^{k+1}}{u_{aa}^k}\right). \tag{2.13}$$

As $k \to \infty$, (2.13) implies that $u_{aa} = 1/|\mathcal{C}_a|$. Thus, again by (2.13), $u_{ja} = 0$ for all $j \notin \mathcal{C}_a$. This means that in column n of $\mathbf{U}$ there should be $m_n = |C_n|$ with $2 \leq m_n \leq N$ nonzero elements, including u_{nn}, that are all equal to $1/m_n$.

Step 4: m_n is the same for all n

Considering state $S = \{i, j\}$ and using $u_{aa} = 1/m_a$, (2.10) can be written as follows

$$(u_{ii} + u_{ij})^k + (u_{ji} + u_{jj})^k = \alpha \frac{1}{m_i^{k+1}} + \beta \frac{1}{m_j^{k+1}} + \gamma \left(\frac{1}{m_i} + \frac{1}{m_j} \right)^{k+1} \tag{2.14}$$

where α, β, γ are the number of rows where $1/m_i$ is adjacent to 0, 0 is adjacent to $1/m_j$, and $1/m_i$ is adjacent to $1/m_j$ in columns i and j respectively. More precisely, α is the cardinality of the set $K^i_{ij} = \{n : u_{ni} = 1/m_i, u_{nj} = 0\}$, β is the cardinality of the set $K^j_{ij} = \{n : u_{ni} = 0, u_{nj} = 1/m_j\}$ and γ is the cardinality of the set $K^{ij}_{ij} = \{n : u_{ni} = 1/m_i, u_{nj} = 1/m_j\}$.

Since $\mathcal{C}_i = K^i_{ij} \cup K^{ij}_{ij}$ and $\mathcal{C}_j = K^j_{ij} \cup K^{ij}_{ij}$, we have that $m_i = \alpha + \gamma$ and $m_j = \beta + \gamma$. Since $K^i_{ij}, K^j_{ij}, K^{ij}_{ij}$ are disjoint, we have $\alpha + \beta + \gamma \le N$. Now, consider the different possibilities we can have on the left-hand side of equation (2.14).

Case 1:

$u_{ii} = 1/m_i,\ u_{ij} = 0$ in row i and $u_{ji} = 1/m_i,\ u_{jj} = 1/m_j$ in row j. Thus $\alpha, \gamma \ge 1$ and therefore equation (2.14) gives

$$\frac{1}{m_i^k} + \left(\frac{m_i + m_j}{m_i m_j} \right)^k = \frac{\alpha}{m_i^{k+1}} + \frac{\beta}{m_j^{k+1}} + \gamma \left(\frac{m_i + m_j}{m_i m_j} \right)^{k+1} \Rightarrow$$

$$\frac{1}{(\alpha+\gamma)^k} + \left(\frac{\alpha+\beta+2\gamma}{(\alpha+\gamma)(\beta+\gamma)} \right)^k = \frac{\alpha}{(\alpha+\gamma)^{k+1}} + \frac{\beta}{(\beta+\gamma)^{k+1}} + \gamma \left(\frac{\alpha+\beta+2\gamma}{(\alpha+\gamma)(\beta+\gamma)} \right)^{k+1} \Rightarrow$$

$$\frac{(\beta+\gamma)^k + (\alpha+\beta+2\gamma)^k}{[(\alpha+\gamma)(\beta+\gamma)]^k} = \frac{\alpha(\beta+\gamma)^{k+1} + \beta(\alpha+\gamma)^{k+1} + \gamma(\alpha+\beta+2\gamma)^{k+1}}{[(\alpha+\gamma)(\beta+\gamma)]^{k+1}} \Rightarrow$$

$$(\beta+\gamma)^k + (\alpha+\beta+2\gamma)^k = \frac{\alpha(\beta+\gamma)^{k+1} + \beta(\alpha+\gamma)^{k+1} + \gamma(\alpha+\beta+2\gamma)^{k+1}}{(\alpha+\gamma)(\beta+\gamma)} \Rightarrow$$

$$(\beta+\gamma)^k + (\alpha+\beta+2\gamma)^k = \frac{\alpha(\beta+\gamma)^k}{\alpha+\gamma} + \frac{\beta(\alpha+\gamma)^k}{\beta+\gamma} + \frac{(\alpha\gamma+\beta\gamma+2\gamma^2)(\alpha+\beta+2\gamma)^k}{\alpha\beta+\alpha\gamma+\beta\gamma+\gamma^2} \Rightarrow$$

$$\frac{\gamma(\beta+\gamma)^k}{\alpha+\gamma} = \frac{\beta(\alpha+\gamma)^k}{\beta+\gamma} + \frac{(\gamma^2-\alpha\beta)(\alpha+\beta+2\gamma)^k}{\alpha\beta+\alpha\gamma+\beta\gamma+\gamma^2}.$$

As $k \to \infty$, we get $(\beta+\gamma)^k \neq (\alpha+\gamma)^k \pm (\alpha+\beta+2\gamma)^k$ since $\alpha+\beta+2\gamma > \beta+\gamma,\ \alpha+\gamma$ hence we want $\gamma^2 = \alpha\beta$ to get rid off $(\alpha+\beta+2\gamma)^k$. This implies that $\beta+\gamma = \alpha+\gamma \Rightarrow\ \alpha = \beta \Rightarrow\ \alpha = \beta = \gamma$ giving $m_i = m_j$.

Case 2:

$u_{ii} = 1/m_i,\ u_{ij} = 1/m_j$ in row i and $u_{ji} = 0,\ u_{jj} = 1/m_j$ in row j. This case is symmetrical to Case 1 and therefore we get that $\alpha = \beta = \gamma$ giving $m_i = m_j$.

Case 3:

$u_{ii} = 1/m_i,\ u_{ij} = 1/m_j$ in row i and $u_{ji} = 1/m_i,\ u_{jj} = 1/m_j$ in row j. Thus $\gamma \ge 2$ and therefore equation (2.14) gives

$$2\left(\frac{m_i + m_j}{m_i m_j} \right)^k = \frac{\alpha}{m_i^{k+1}} + \frac{\beta}{m_j^{k+1}} + \gamma \left(\frac{m_i + m_j}{m_i m_j} \right)^{k+1} \Rightarrow$$

$$\begin{aligned}
2\left(\frac{\alpha+\beta+2\gamma}{(\alpha+\gamma)(\beta+\gamma)}\right)^k &= \frac{\alpha(\beta+\gamma)^{k+1}+\beta(\alpha+\gamma)^{k+1}+\gamma(\alpha+\beta+2\gamma)^{k+1}}{[(\alpha+\gamma)(\beta+\gamma)]^{k+1}} \Rightarrow \\
2\left(\alpha+\beta+2\gamma\right)^k &= \frac{\alpha(\beta+\gamma)^{k+1}+\beta(\alpha+\gamma)^{k+1}+\gamma(\alpha+\beta+2\gamma)^{k+1}}{(\alpha+\gamma)(\beta+\gamma)} \Rightarrow \\
2\left(\alpha+\beta+2\gamma\right)^k &= \frac{\alpha(\beta+\gamma)^k}{\alpha+\gamma}+\frac{\beta(\alpha+\gamma)^k}{\beta+\gamma}+\frac{(\alpha\gamma+\beta\gamma+2\gamma^2)(\alpha+\beta+2\gamma)^k}{\alpha\beta+\alpha\gamma+\beta\gamma+\gamma^2} \Rightarrow \\
\frac{(2\alpha\beta+\alpha\gamma+\beta\gamma)(\alpha+\beta+2\gamma)^k}{\alpha\beta+\alpha\gamma+\beta\gamma+\gamma^2} &= \frac{\alpha(\beta+\gamma)^k}{\alpha+\gamma}+\frac{\beta(\alpha+\gamma)^k}{\beta+\gamma}.
\end{aligned}$$

As $k \to \infty$, we get $(\alpha+\beta+2\gamma)^k \neq (\beta+\gamma)^k+(\alpha+\gamma)^k$ since $\alpha+\beta+2\gamma > \beta+\gamma,\ \alpha+\gamma$ hence we want $2\alpha\beta+\alpha\gamma+\beta\gamma = 0 \Rightarrow \alpha, \beta = 0$ giving $m_i = m_j$.

Case 4:

$u_{ii} = 1/m_i,\ u_{ij} = 0$ in row i and $u_{ji} = 0,\ u_{jj} = 1/m_j$ in row j. Thus $\alpha, \beta \geq 1$ and therefore equation (2.14) gives

$$\begin{aligned}
1/m_i^k + 1/m_j^k &= \frac{\alpha}{m_i^{k+1}}+\frac{\beta}{m_j^{k+1}}+\gamma\left(\frac{m_i+m_j}{m_i m_j}\right)^{k+1} \Rightarrow \\
\frac{1}{(\alpha+\gamma)^k}+\frac{1}{(\beta+\gamma)^k} &= \frac{\alpha}{(\alpha+\gamma)^{k+1}}+\frac{\beta}{(\beta+\gamma)^{k+1}}+\gamma\left(\frac{\gamma+\beta+2\gamma}{(\alpha+\gamma)(\beta+\gamma)}\right)^{k+1} \Rightarrow \\
\frac{(\beta+\gamma)^k+(\alpha+\gamma)^k}{[(\alpha+\gamma)(\beta+\gamma)]^k} &= \frac{\alpha(\beta+\gamma)^{k+1}+\beta(\alpha+\gamma)^{k+1}+\gamma(\alpha+\beta+2\gamma)^{k+1}}{[(\alpha+\gamma)(\beta+\gamma)]^{k+1}} \Rightarrow \\
(\beta+\gamma)^k+(\alpha+\gamma)^k &= \frac{\alpha(\beta+\gamma)^{k+1}+\beta(\alpha+\gamma)^{k+1}+\gamma(\alpha+\beta+2\gamma)^{k+1}}{(\alpha+\gamma)(\beta+\gamma)} \Rightarrow \\
(\beta+\gamma)^k+(\alpha+\gamma)^k &= \frac{\alpha(\beta+\gamma)^k}{\alpha+\gamma}+\frac{\beta(\alpha+\gamma)^k}{\beta+\gamma}+\frac{\gamma(\alpha+\beta+2\gamma)^{k+1}}{\alpha\beta+\alpha\gamma+\beta\gamma+\gamma^2}.
\end{aligned}$$

As $k \to \infty$, we get $0 \neq (\alpha+\beta+2\gamma)^k$ since $\alpha, \beta \geq 1$ hence we require that $\gamma = 0$ to get an equality.

Conclusion from all the cases above

We see that $m_i \neq m_j$ is potentially possible only in Case 4. However, $\mathbf{U}$ is strongly connected. If one connects i and j by a path $i = i_0, i_1, i_2, \ldots i_n = j$, then one has $m_{i_k} = m_{i_{k+1}}$ as i_k and i_{k+1} must fall into Case 1, Case 2 or Case 3 above. Thus $m_i = m_j$. This implies that every column of $\mathbf{U}$ has $2 \leq m \leq N$ nonzero elements, including u_{nn}, that are all equal to $1/m$. This is also true for every row of $\mathbf{U}$ because it is right stochastic by definition.

Step 5: There exists state S such that $\mathcal{C}_a = \mathcal{C}_{a'}$ for all $a, a' \in S$

We can define the state $\mathcal{R}_x = \{n : u_{xn} = u_{xx}\}$ then, by definition, $x \in \mathcal{R}_x$ and $|\mathcal{R}_x| = m$ since there are m nonzero elements in row x of $\mathbf{U}$. Consider the state $S = \mathcal{R}_x \setminus \{y\}$ for $y \in \mathcal{R}_x \setminus \{x\}$. For this S (as well as any other state), we have that

$$\left.\begin{array}{ll} \text{if } n \in S \text{ then} & 1/m \\ \text{if } n \notin S \text{ then} & 0 \end{array}\right\} \leq U(n,S) \leq \frac{\min(m,|S|)}{m}.$$

We can therefore write equation (2.10) in the form

$$\sum_{i=1}^{\min(m,|S|)} \lambda_S(i) \left(\frac{i}{m}\right)^k = \sum_{i=0}^{\min(m,|S|)} \lambda'_S(i) \left(\frac{i}{m}\right)^{k+1} \tag{2.15}$$

where $\lambda_S(i)$ is the number of $U(n,S)$ terms equal to i/m for $n \in S$ and $\lambda'_S(i)$ is the number of $U(n,S)$ terms equal to i/m for $n \in \mathcal{N}$, which means that $\lambda'_S(i) \geq \lambda_S(i)$ for $i \neq 0$. The ratio of the left-hand side and right-hand side of equation (2.15) should always be equal to one. Therefore, as $k \to \infty$, we require that

$$\lambda_S(i_{\max}) = \lambda'_S(i_{\max}) \frac{i_{\max}}{m}$$

where $i_{\max}$ is the largest i such that $\lambda_S(i) > 0$.

We have that $i_{\max} = m-1$ in equation (2.15) because $|S| = m-1$ so $U(x,S) = (m-1)/m$. This means that for state S, as $k \to \infty$, we require that

$$\lambda_S(m-1) = \lambda'_S(m-1) \frac{m-1}{m}.$$

Since $\lambda_S(m-1)$ is an integer, $\lambda'_S(m-1)$ has to be a multiple of m and the only possible value that satisfies this criteria is $\lambda'_S(m-1) = m$ hence $\lambda_S(m-1) = m-1$.

Since $\lambda'_S(m-1) = m$ there exist m rows $j_1, j_2, \ldots, j_m$ such that $U(j_n, S) = (m-1)/m$, that is, $u_{j_n a} = 1/m \ \forall a \in S$. This means that $\mathcal{C}_a = \{j_1, j_2, \ldots, j_m\} \ \forall a \in S$ hence $\mathcal{C}_a = \mathcal{C}_{a'}$ for all $a, a' \in S$.

Step 6: $m = 2$ **or** $m = N$

By contradiction, assume that $2 < m < N$. We can consider another state $S' = \mathcal{R}_x \setminus \{z\}$ such that $z \in \mathcal{R}_x \setminus \{x, y\}$. We then have that $i_{\max} = m-1$ in equation (2.15) because $|S'| = m-1$ so $U(x,S') = (m-1)/m$. As before, this means that $\mathcal{C}_a = \mathcal{C}_{a'}$ for all $a, a' \in S'$. Since $x \in S, S'$ and $\mathcal{R}_x = S \cup S'$ we have that $\mathcal{C}_a = \mathcal{C}_{a'}$ for all $a, a' \in \mathcal{R}_x$. For $2 < m < N$ this implies that vertices $i \in \mathcal{R}_x$ are disconnected from $j \in \mathcal{N} \setminus \mathcal{R}_x$ and we therefore have disconnected graphs, a contradiction. $\square$

Chapter 3

Social Dilemmas with Variable Group Size

3.1 Introduction

This chapter defines and classifies different multiplayer games that are social dilemmas. In social dilemmas the group as a whole faces faces a dilemma because, collectively, unselfish behaviour, i.e. cooperating, would benefit the entire group but, individually, selfish behaviour, i.e. defecting, would leave the individual better off. A model of population evolution is not used to classify these games and, instead, the payoff for variable group sizes are calculated and compared to one another. Therefore, the structure of the population and dynamics (i.e. births and deaths) are not required. For a focal individual in a group, changing the group composition, by adding or removing a cooperator or defector, may or may not be beneficial in terms of the payoff received. By looking at this behaviour, we get a better understanding of the social dilemma being studied.

In a social dilemma, there are several different interpretations of cooperative behaviour [45]. The one we want to focus on in this chapter is the one considered in [83] that is a slight variation of the *individual-centered* interpretation of [45] where the effect of cooperation is measured through the change in payoff of individuals rather than the group. In particular, this interpretation compares the payoff an individual receives when interacting in groups of the same size and is therefore quite restrictive. The objective of this chapter is to extend this interpretation to interactions in groups of variable size. Overall this will give us a more general idea of what is meant by cooperative behaviour.

In chapter 2, the model considered worked with fixed fitness but the models considered later have multiplayer game-theoretic interactions. Therefore, this chapter provides a preview of these kinds of multiplayer interactions before they are considered in the context of a population evolution model.

3.2 Conditions for Cooperation

The social dilemmas considered involve two strategies called cooperate (C) and defect (D). The games considered are *symmetric* [11], which means that only the combination of strategies matters rather than the strategy used by each individual player. In particular, the payoff to a cooperator (defector) in a group with c other cooperators and d other defectors is written as $R_C(c,d)$ ($R_D(c,d)$). When the type of the focal individual does not need to be specified, $R_*(c,d)$ will be used instead.

The cooperate and defect strategies depend upon the exact interpretation of cooperation used, which imposes conditions on the payoffs received by a focal individual. In particular, the conditions restrict how the payoffs to a focal individual should change when the group it is present in changes. The change in payoff for three different scenarios are considered: the composition of the group changes but its size remains the same; the number of defectors in the group changes; and the number of cooperators in the group changes.

3.2.1 Conditions for groups of fixed size

For groups of fixed size where the composition of the group changes, the conditions that specify the change in payoff to a focal individual are given by [83] and is based on the premise that the focal individual, regardless of its own strategy, prefers group members who cooperate. For groups of size $m+1$, this condition is given by

$$R_*(c, m-c) \leq R_*(c', m-c') \quad \text{for } 0 \leq c < c' \leq m, \tag{3.1}$$

which states that the payoff to a focal individual may increase if defectors are replaced by cooperators in a group of fixed size. To ensure that cooperation has a chance to evolve, the following additional condition is imposed by [83]

$$R_C(m,0) > R_D(0,m). \tag{3.2}$$

This condition says that a cooperator in a group of cooperators strictly has a higher payoff that a defector in a group of defectors, i.e. the best possible situation for cooperators yields a higher reward than the worst possible situation for defectors. However, this additional condition is not required for cooperation.

An equivalent way of expressing condition (3.1) without m and, therefore, more suitable when talking about groups of variable size is the following

$$R_*(c,d) \leq R_*(c+1,d-1) \quad c \geq 0, d > 0. \tag{3.3}$$

Note here that the group size remains the same because adding a cooperator is compensated for by removing a defector. This equation can then be rewritten in either one of the following ways

$$R_*(c-1,d) \leq R_*(c,d-1) \quad c > 0, d > 0 \tag{3.4}$$

or

$$R_*(c,d+1) \leq R_*(c+1,d) \quad c,d \geq 0. \tag{3.5}$$

This says that a focal individual, regardless of its type, prefers replacing a defector in the group by a cooperator for groups of the same size. As will be seen later, both (3.4) and (3.5) are used when making comparisons with $R_*(c,d)$.

3.2.2 Conditions for changing the number of defectors

In the context of variable groups sizes, the conditions for cooperation when the number of defectors changes has not been specified before and will therefore be specified here as follows. A focal individual, regardless of its type, prefers not to add a defector to the group. This can be written as

$$R_*(c,d+1) \leq R_*(c,d) \quad c,d \geq 0 \tag{3.6}$$

or, by induction,

$$R_*(c,d) \leq R_*(c,d-1) \quad c \geq 0, d > 0. \tag{3.7}$$

Combining equations (3.6) and (3.7) gives the following condition

$$R_*(c,d+1) \leq R_*(c,d) \leq R_*(c,d-1) \quad c \geq 0, d > 0. \tag{3.8}$$

This is the condition required for cooperation when the number of defectors changes. This condition is specified in this way in order to be able to clearly differentiate between defectors and cooperators. In particular, a defector cannot benefit a focal individual but, as is specified later, a cooperator can. In general, if a defector could benefit a focal individual, there would be no pure defectors or cooperators, rather each individual's behaviour would be determined by a continuum of strategies with both cooperative and defective elements. So whether an individual is a defector or not is relative to the behaviour of others. This is not what is wanted here, hence, the condition used clearly separates defectors from cooperators.

$R_*(\ldots)$	$\leq$	$R_*(\ldots)$	$\leq$	$R_*(\ldots)$	$\leq$	$R_*(\ldots)$	$\leq$	$R_*(\ldots)$
$c, d+1$		c, d		$c-1, d$		$c, d-1$		$c+1, d$
$c, d+1$		c, d		$c-1, d$		$c+1, d$		$c, d-1$
$c-1, d$		$c, d+1$		c, d		$c, d-1$		$c+1, d$
$c, d+1$		$c-1, d$		c, d		$c, d-1$		$c+1, d$
$c-1, d$		$c, d+1$		c, d		$c+1, d$		$c, d-1$
$c, d+1$		$c-1, d$		c, d		$c+1, d$		$c, d-1$
$c, d+1$		$c-1, d$		$c+1, d$		c, d		$c, d-1$
$c-1, d$		$c, d+1$		$c+1, d$		c, d		$c, d-1$
$c, d+1$		c, d		$c+1, d$		$c-1, d$		$c, d-1$
$c, d+1$		$c+1, d$		c, d		$c-1, d$		$c, d-1$
$c, d+1$		$c+1, d$		$c-1, d$		c, d		$c, d-1$

Table 3.1: Possible payoff rankings for a cooperation game.

3.2.3 Conditions for changing the number of cooperators

The conditions required for cooperation when the number of cooperators changes are left open. This means that, for the interpretation of cooperation used here, a focal individual may or may not prefer adding a cooperator to the group. This interpretation of cooperation is more general and allows many more cooperative strategies to be considered. For example, suppose that cooperators provide a shared resource such that adding another cooperator increases the shared resource. If the amount provided by each additional cooperator diminishes, a point will be reached where adding another cooperator results in a fall in the share that each individual receives. In this case, cooperators provide a benefit to the focal individual up to a certain point. If cooperators always benefited the focal individual, this kind of behaviour would be excluded. Therefore, conditions given by equations (3.4), (3.5) and (3.8) are all that is required for the interpretation of cooperation used here.

3.2.4 Combining the conditions

By combining the conditions given by equations (3.4), (3.5) and (3.8), the payoffs where there is one more cooperator ($c+1, d$), one more defector ($c, d+1$), one less cooperator ($c-1, d$) and one less defector ($c, d-1$) can be ranked with respect to the group (c, d) for a focal individual, regardless of its type. All the possible payoff rankings are given in Table 3.1.

3.3 Types of Social Dilemmas

There are two broad categories of social dilemmas that identified in [47] that are described here in relation to the conditions identified above.

3.3.1 Public Goods Dilemmas

This dilemma involves the *production* of a public good that can be enjoyed by all group members whether or not they have contributed towards its production. This means that public goods are *non-excludable* and, in additions to this, they may also be *non-rival* whereby its consumption by one individual does not diminish its availability to another individual. A *pure* public good is both entirely non-exludable and non-rival, however, in general public goods have a varying degree of both non-excludability and non-rivalry. For public goods dilemmas, the cooperators are assumed to always contribute towards the production of the public good and defectors do not.

For the public goods dilemmas considered here, the payoffs are of the form

$$R_C(c,d) = p_C(c) \cdot u_C(c,d) \cdot V - k_C(c) \cdot K \tag{3.9}$$

$$R_D(c,d) = p_D(c) \cdot u_D(c,d) \cdot V \tag{3.10}$$

where $p_*(c)$ is the production function that determines how much of a public good V is produced when a focal individual is present with c other cooperators, $u_*(c,d)$ is the share of the public good a focal individual gets when present with c (d) other cooperators (defectors), $k_C(c)$ is the cost function that determines the share of the cost K paid by a focal cooperator present with c other cooperators. The public good $V > 0$ and cost $K > 0$ are used as universal parameters for the different public goods games. Note that since the defectors do not contribute to the production of a good, the defector production function will be set to $p_D(c) = p_C(c-1)$. Also, for the same reason, the defectors do not have a cost function.

In [47], several different forms of production functions are identified. Let $\Delta p_C(c) = p_C(c) - p_C(c-1)$ then the production function can take the following forms:

- Convex (accelerating or increasing returns to scale):

$$\Delta p_C(c+1) > \Delta p_C(c) > 0 \ \forall c.$$

- Linear (constant returns to scale):

$$\Delta p_C(c+1) = \Delta p_C(c) \ \forall c.$$

- Concave (decelerating or decreasing returns to scale):

$$0 < \Delta p_C(c+1) < \Delta p_C(c) \ \forall c.$$

- Step function: In this case no public good is produced if the number of cooperators is below some threshold L, for example, $p_C(c) = \mathbf{1}_{c+1\geq L}$ where

$$\mathbf{1}_{c+1\geq L} = \begin{cases} 1 & c+1 \geq L, \\ 0 & c+1 < L. \end{cases}$$

The public good sharing function $u_*(c,d)$ can be interpreted in two different ways. First, they can be constant such that $u_C(c,d) = u_D(c,d) = x > 0$. This implies that the public good is pure, i.e. non-excludable and non-rivalrous, and all group members get the same amount of the public good. Second, it is some non-constant function that represents a public good exhibiting excludability or rivalry (or both). The cost function $k_C(c)$ behaves in the same way.

In Table 3.1, all the inequalities can appear within a public goods dilemma. For the inequalities where $R_*(c-1,d) \leq R_*(c+1,d)$, this seems consistent because cooperators contribute towards the production of a public good. The inequalities where $R_*(c-1,d) \geq R_*(c+1,d)$ may at first seem inconsistent, however, they do appear in public goods dilemmas particularly when the production function is decelerating. In this case, adding another cooperator may not increase the payoff to the focal individual.

Examples of Public Goods Dilemmas

The public goods dilemmas considered are summarized in Table 3.2. An explanation of each one is given in what follows.

Prisoner's Dilemma [33] The public good is non-excludable but rivalrous such that it is shared equally amongst all group members and grows linearly with the number of cooperators. The cost is not shared amongst the cooperators in the group who each pay K. The payoffs are given by

$$R_C(c,d) = \frac{c+1}{c+d+1}V - K, \tag{3.11}$$

$$R_D(c,d) = \frac{c}{c+d+1}V. \tag{3.12}$$

In Figure 3.1, the vector field for the prisoner's dilemma is shown. The way in which the vector field is constructed is explained in Section 3.4 (pg. 81). Each vector gives the direction in which an increase in payoff to the focal individual can be achieved. Given that the x-axis (y-axis) indicates the number of cooperators (defectors) present with the focal individual, a vector pointing to the right (left) indicates that the payoff can be increased by adding (removing) a cooperator and a vector pointing downwards indicates that an increase in payoff can be achieved by removing a defector. Note that there are no vectors pointing upwards as adding a defector

	$p_C(c)$	$u_C(c,d)$	$u_D(c,d)$	$k_C(c)$
Prisoner's Dilemma	$c+1$	$\frac{1}{c+d+1}$	$\frac{1}{c+d+1}$	1
Prisoner's Dilemma with variable production function	$\sum_{k=0}^{c} \omega^k$	$\frac{1}{c+d+1}$	$\frac{1}{c+d+1}$	1
Stag Hunt	$(c+1)\mathbf{1}_{c+1\geq L}$	$\frac{1}{c+d+1}$	$\frac{1}{c+d+1}$	1
Fixed Stag Hunt	$\mathbf{1}_{c+1\geq L}$	$\frac{1}{c+d+1}$	$\frac{1}{c+d+1}$	1
Charitable Prisoner's Dilemma	$c+1$	$\begin{cases} \frac{c}{c+1}\frac{1}{c+d} & c>0 \\ 0 & c=0 \end{cases}$	$\begin{cases} \frac{1}{c+d} & c>0 \\ 0 & c=0 \end{cases}$	1
Volunteer's Dilemma	1	1	1	1
Threshold Volunteer's Dilemma	$\mathbf{1}_{c+1\geq L}$	1	1	1
Snowdrift	1	1	1	$\frac{1}{c+1}$
Threshold Snowdrift	$\mathbf{1}_{c+1\geq L}$	1	1	$\frac{\mathbf{1}_{c+1<L}}{L} + \frac{\mathbf{1}_{c+1\geq L}}{c+1}$

Table 3.2: Summary of public goods dilemmas used in this chapter. In each case $P_D(c) = P_C(c-1)$.

cannot increase the payoff. A vector pointing diagonally right (left) and downwards indicates that a payoff can be increased by either adding (removing) a cooperator and removing a defector. However, if it biased more the the right (left) than downwards, adding (removing) a cooperator is more effective than removing a defector.

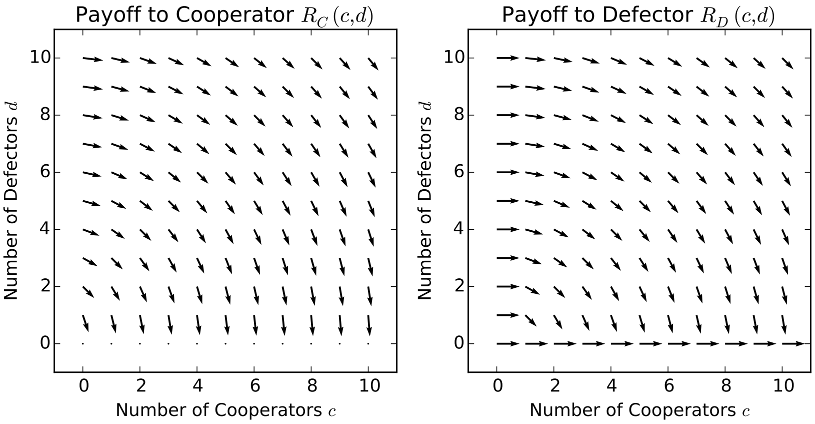


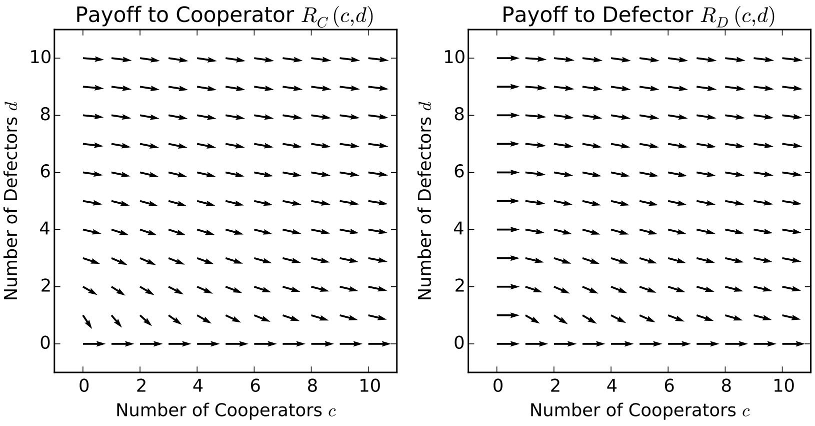
Figure 3.1: Vector field for prisoner's dilemma where $V = 5/2,\ K = 4/3$. The construction of the vector fields is explained in Section 3.4 (pg. 81). The direction of each vector indicates the change in group composition required to increase the payoff to a focal individual. For example, a vector pointing diagonally right indicates that an increase in payoff can be achieved by adding a cooperator or removing a defector. If the vector has more rightward bias, adding a cooperator is more effective that removing a defector, and, if the vector has more downward bias, the opposite is true.

Prisoner's dilemma with variable production function [9] Similar to the Prisoner's Dilemma but the public good can grow at a varying rate with respect to the number of cooperators. The payoffs are given by

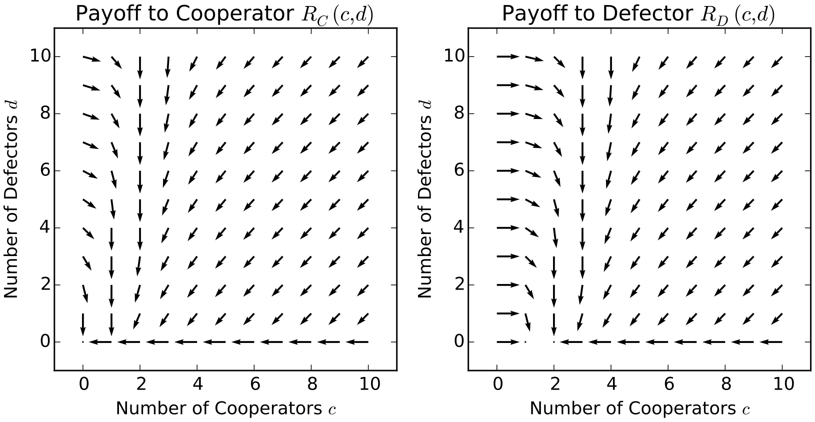
$$R_C(c,d) = -K + \frac{V}{c+d+1}\sum_{n=0}^{c}\omega^n \quad \omega > 0 \tag{3.13}$$

$$R_D(c,d) = \frac{V}{c+d+1}\sum_{n=0}^{c-1}\omega^n \quad \omega > 0 \tag{3.14}$$

The production function is convex for $\omega > 1$, concave for $\omega < 1$, and linear for $\omega = 1$ (this gives the original prisoner's dilemma).



(a) Accelerating production function $\omega = 1.5$.



(b) Decelerating production function $\omega = 0.5$.

Figure 3.2: Vector field for prisoner's dilemma with variable production function where $V = 5/2,\ K = 4/3$.

Stag Hunt [74] This is a prisoner's dilemma where the production function is a step function such that at least $L > 1$ cooperators are required for the public good to be produced. The cooperators always pay a cost K whether the threshold is met or not. The payoffs are given by

$$R_C(c,d) = \begin{cases} \frac{c+1}{c+d+1}V - K & c+1 \geq L \\ -c & c+1 < L \end{cases} \tag{3.15}$$

$$R_D(c,d) = \begin{cases} \frac{c}{c+d+1}V & c \geq L \\ 0 & c < L \end{cases} \tag{3.16}$$

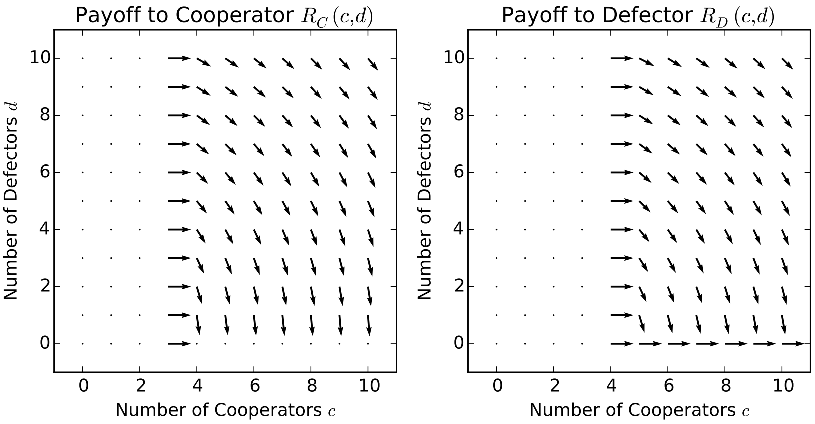


Figure 3.3: Vector field for stag hunt with threshold $L = 5$ where $V = 5/2,\ K = 4/3$.

Fixed Stag Hunt[74] Similar to the stag hunt but the public good is of a fixed size, i.e. it does not grow with the number of cooperators. The payoffs are given by

$$R_C(c,d) = \begin{cases} \frac{V}{c+d+1} - K & c+1 \geq L \\ -c & c+1 < L \end{cases} \tag{3.17}$$

$$R_D(c,d) = \begin{cases} \frac{V}{c+d+1} & c \geq L \\ 0 & c < L \end{cases} \tag{3.18}$$

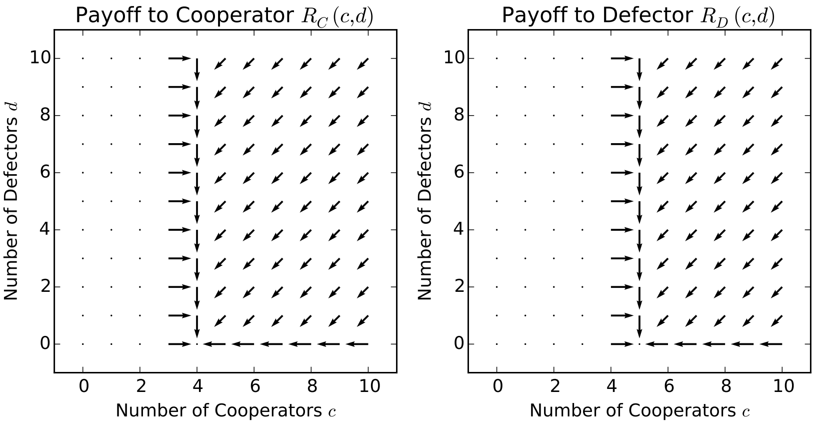


Figure 3.4: Vector field for fixed stag hunt with threshold $L = 5$ where $V = 5/2,\ K = 4/3$.

Charitable Prisoner's Dilemma [14] This is an extension of the prisoner's dilemma where the public good is now excludable so that a cooperator cannot consume its own contribution to the public good. In other words, the cooperators behave charitably by giving away their contribution to the other members of the group. Furthermore, it is assumed that a cooperator will still pay the cost K when alone but not receive the public good. The payoffs are then given by

$$R_C(c,d) = \begin{cases} \frac{c}{c+d}V - K & c > 0 \\ -K & c = 0 \end{cases} \tag{3.19}$$

$$R_D(c,d) = \begin{cases} \frac{c}{c+d}V & c > 0 \\ 0 & c = 0 \end{cases} \tag{3.20}$$

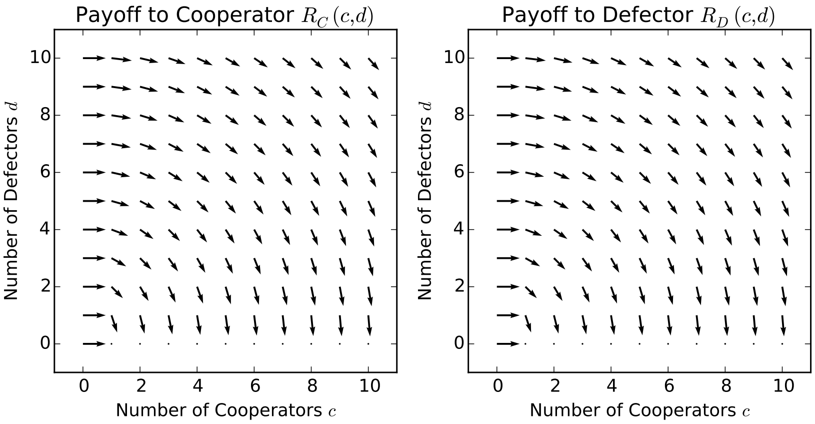


Figure 3.5: Vector field for charitable prisoner's dilemma where $V = 5/2,\ K = 4/3$.

Volunteer's Dilemma [22] The public good is pure and of fixed size; it is provided if at least one cooperator pays a cost K, which all cooperators do. The payoffs are given by

$$R_C(c,d) = V - K \tag{3.21}$$

$$R_D(c,d) = \begin{cases} V & c > 0 \\ 0 & c = 0 \end{cases} \tag{3.22}$$

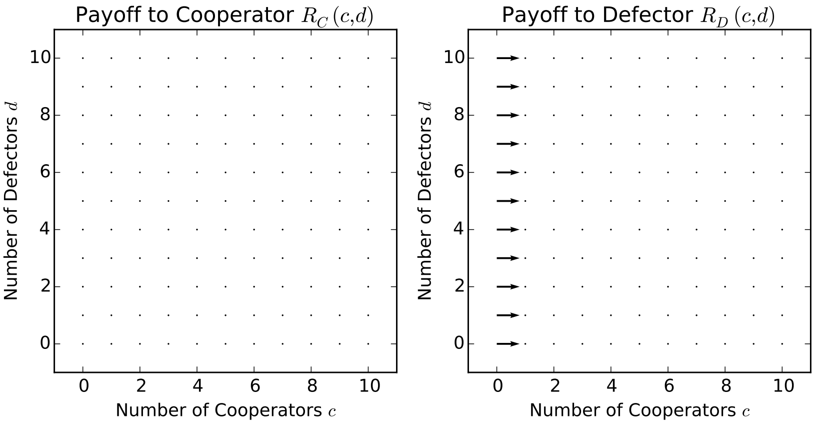


Figure 3.6: Vector field for volunteer's dilemma where $V = 5/2,\ K = 4/3$.

Threshold Volunteer's Dilemma [9] Volunteer's dilemma with threshold production function such that $L > 1$ cooperators are required to provide the public good. The cooperators always pay cost K regardless of whether the threshold is met or not. The payoffs are given by

$$R_C(c,d) = \begin{cases} V - K & c + 1 \geq L \\ -K & c + 1 < L \end{cases} \tag{3.23}$$

$$R_D(c,d) = \begin{cases} V & c \geq L \\ 0 & c < L \end{cases} \tag{3.24}$$

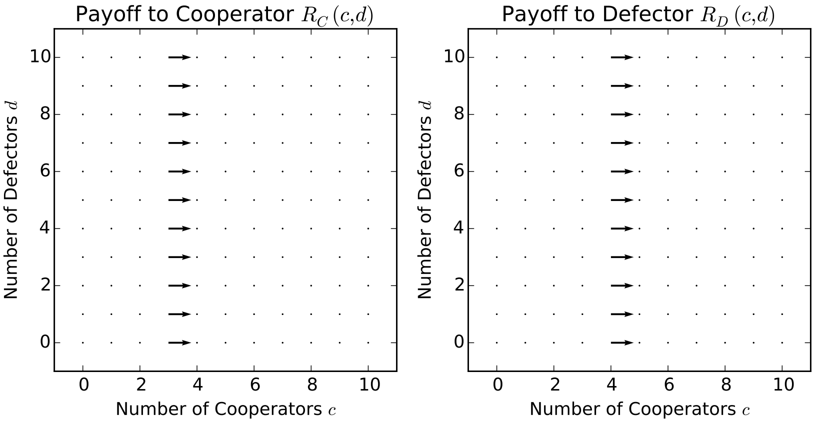


Figure 3.7: Vector field for threshold volunteer's dilemma with $L = 5$ where $V = 5/2,\ K = 4/3$.

Snowdrift [9] Volunteer's dilemma where the cost is shared equally between all cooperators in the group. The payoffs are given by

$$R_C(c,d) = V - \frac{K}{c+1} \tag{3.25}$$

$$R_D(c,d) = \begin{cases} V & c > 0 \\ 0 & c = 0 \end{cases} \tag{3.26}$$

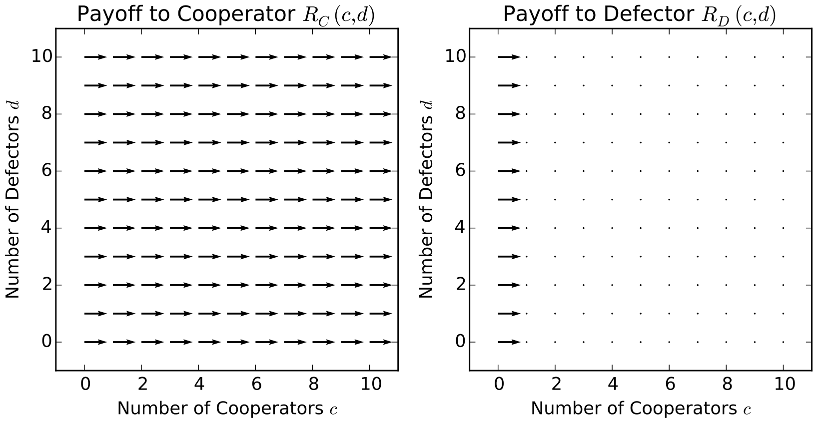


Figure 3.8: Vector field for snowdrift where $V = 5/2,\ K = 4/3$.

Threshold Snowdrift [96] Snowdrift game with a threshold production function such that at least $L > 1$ cooperators are required to produce the public good. The cost is shared equally between the cooperators if the threshold is met, otherwise, each cooperator pays K/L. The payoffs are given by

$$R_C(c,d) = \begin{cases} V - \frac{K}{c+1} & c+1 \geq L \\ -\frac{K}{L} & c+1 < L \end{cases} \tag{3.27}$$

$$R_D(c,d) = \begin{cases} V & c \geq L \\ 0 & c < L \end{cases} \tag{3.28}$$

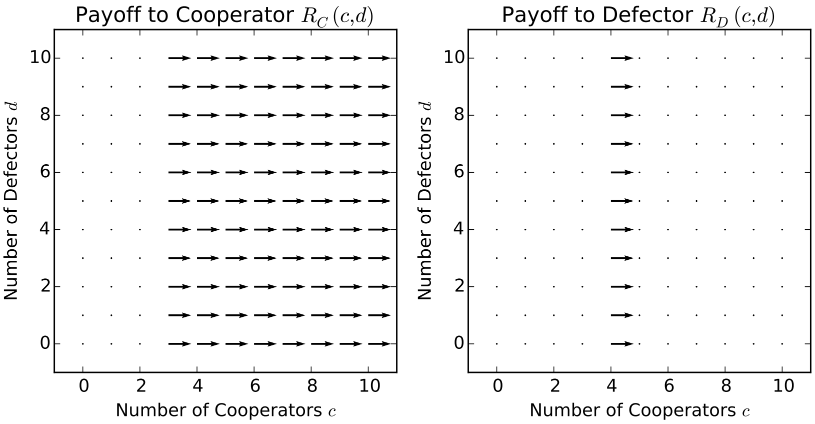


Figure 3.9: Vector field for threshold snowdrift with threshold $L = 5$ where $V = 5/2,\ K = 4/3$.

3.3.2 Commons Dilemmas

Commons dilemmas were popularized by [36], who gave an example of herders with access to a common parcel of land. Each herder is interested in putting as many of their cows on that land because they receive the benefit of each additional cow but the damage to the commons is shared by the group. However, if all the herders chose this option, the commons will be damaged irreparably and all will suffer. In an evolutionary biology context, consider the example of parasitic viruses residing in a bacterial cell host [23]. A virus can be more competitive and use up more resources resulting in a larger number of direct progeny. If all the viruses did this, the host will die faster and the total number of progeny will be smaller. On the other hand, the viruses can be less competitive and use less resources. In this case, the number of direct progeny would be smaller, but the total number of progeny would be larger. These examples are representative of commons dilemmas in general, in particular, they involve the use of commons that are readily available resources freely available for any group member to consume. However, commons are *rivalrous*, therefore, its consumption by one individual diminishes its availability for another individual. The dilemma here is that the group is better off if a common is used in an equitable manner but the individual is better off being greedy and having the entire common to itself.

For commons dilemmas it will be assumed that cooperators consume a common in an equitable manner and defectors do not. In Table 3.1, the inequalities where $R_*(c{+}1,d) \leq R_*(c{-}1,d)$ are the only ones that appear in commons dilemmas. This is because the focal individual is better off having a common to itself and therefore prefers removing a cooperator to adding a cooperator. The following is an example of a commons dilemma.

Hawk-Dove [16] A group of cooperators share a common V equally, however, they flee if there is a defector present getting no share of the common. A defector chases away cooperators and fights other defectors for the common. Each defector has an equal chance of winning the entire common V, with the losers incurring a cost K. The payoffs are given by

$$R_C(c,d) = \begin{cases} \frac{V}{c+1} & d = 0 \\ 0 & d > 0 \end{cases} \tag{3.29}$$

$$R_D(c,d) = \frac{V - dK}{d+1} \tag{3.30}$$

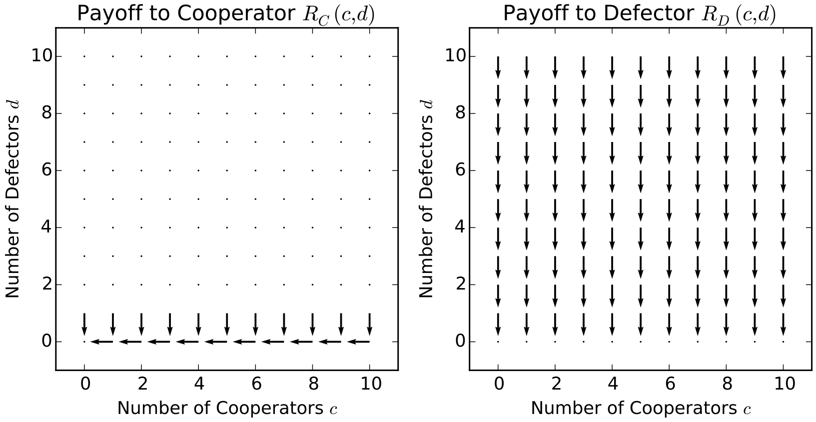


Figure 3.10: Vector field for hawk-dove commons dilemma where $V = 5/2,\ K = 4/3$.

3.4 Constructing the vector fields

This section explains how the 2-dimensional vector fields are constructed where the vectors indicate the direction in which an increase in payoff can be achieved. The number of defectors will be plotted on the y-axis and cooperators on the x-axis such that the following quantities

$$\delta_{*,C^+}(c,d) = \max(R_*(c+1,d) - R_*(c,d), 0)$$
$$\delta_{*,C^-}(c,d) = \max(R_*(c-1,d) - R_*(c,d), 0)$$
$$\delta_{*,D^-}(c,d) = \max(R_*(c,d-1) - R_*(c,d), 0)$$

will be used to determined the vector at some point (c,d). In particular, if $\delta_{*,C^+}(c,d) > 0$, the vector

$$\mathbf{v}_{*,C^+}(c,d) = \left(\frac{\delta_{*,C^+}(c,d)}{\delta_{*,C^+}(c,d) + \delta_{*,D^-}(c,d)}, \frac{-\delta_{*,D^-}(c,d)}{\delta_{*,C^+}(c,d) + \delta_{*,D^-}(c,d)} \right) \tag{3.31}$$

is drawn, which indicates that an increase in payoff can be achieved by either adding a cooperator or removing a defector. However, it is more effective to add a cooperator than remove a defector if $\delta_{*,C^+}(c,d) > \delta_{*,D^-}(c,d)$. Also, if $\delta_{*,C^-}(c,d) > 0$, the vector

$$\mathbf{v}_{*,C^-}(c,d) = \left(\frac{\delta_{*,C^-}(c,d)}{\delta_{*,C^-}(c,d) + \delta_{*,D^-}(c,d)}, \frac{-\delta_{*,D^-}(c,d)}{\delta_{*,C^-}(c,d) + \delta_{*,D^-}(c,d)} \right) \tag{3.32}$$

is drawn, which indicates that an increase in payoff can be achieved by either removing a cooperator or removing a defector. However, if $\delta_{*,C^+}(c,d) = \delta_{*,C^-}(c,d) = 0$, neither $\mathbf{v}_{*,C^+}(c,d)$ nor $\mathbf{v}_{*,C^-}(c,d)$ are drawn and only the vector

$$\mathbf{v}_{*,D^-}(c,d) = \begin{cases} (0,0) & \delta_{*,D^-}(c,d) = 0, \\ (0,-1) & \delta_{*,D^-}(c,d) \neq 0 \end{cases} \tag{3.33}$$

is drawn, which indicates whether removing a defector increases the payoff or not. Note that only the cases where the payoff can be increased are considered, therefore $R_*(c, d+1)$ is not considered since $R_*(c, d+1) \leq R_*(c,d)$ by equation (3.8).

3.5 Discussion

Two main categories of social dilemmas were identified: public goods dilemmas and commons dilemmas. The key difference between these two dilemmas is that the former involves the production of a joint good and the latter does not. In public goods dilemmas, the dilemma faced by a focal individual within a group is whether or not to contribute towards the production of a public good because, regardless of what it does, it can still enjoy its benefits. However, if all individuals decide not to contribute, the entire group is worse off as there will be no public good to consume. In commons dilemmas, a common is a freely available resource that can be consumed by the entire group, however, it is rivalrous thereby diminishing in availability as more individuals consume it. A focal individual faces the dilemma where consuming as much of the commons leaves itself better off but the group worse off. These characteristics of public goods and commons dilemmas are captured in the conditions given.

Several examples of games of public goods and commons dilemmas are given. A bulk of the examples given are public goods games because of the diversity of the production function. In particular, multiplayer public goods games have been considered in a number of papers: [37, 48, 49, 57, 89, 91, 96, 102]; where as the multiplayer Hawk-Dove has only been considered in [16]. In order to visualize the behaviour found within these games, a vector field for each of the games is plotted. The vectors indicate the direction of a preferred group change for the focal that results in an increase in its payoff. The vector fields act a visual substitute for the conditions given in Table 3.1. Some of the games are sensitive to the reward V, cost K and other parameters specific to the game, like the threshold L, and it here that the vector fields are quite effective at spotting the changes that arise, for example, see Figure 3.2. In the following chapters, some of these games will be investigated in the context of models where interactions between individuals take place in groups of variables sizes.

Chapter 4

Developments in the Broom-Rychtář framework and the Territorial Raider Model

4.1 Introduction

This chapter serves two purposes, the first part develops the Broom-Rychtář (BR) framework [16], which was introduced in Section 1.6 (pg. 38), so that it can be used to create population evolution models. The second part applies the BR framework to create a population evolution model called the territorial raider model.

4.2 Developments in the Broom-Rychtář framework

When the BR framework was first introduced in [16], it described the structure of the population in terms of individuals distributed over places and how this distribution changes over time. The change in the population distribution could depend upon various different things, for example, there could be history and time dependency. It was shown how this changing distribution affects the interaction between individuals thereby provided a mechanism with which to determine the fitness of the individuals. What was missing is how this changing distribution affects the dynamics of the population, that is, the births and deaths. The developments discussed here aims to address this and, to achieve this, the notation is slightly changed from that of the original paper with some new terminology being introduced.

The objective of the BR framework is to provide a cohesive solution to developing population evolution models. Alternative approaches, for example, [73] uses two graphs, one called the 'interaction' graph to determine the fitness of individuals and another called the 'replacement' graph to determine the births and deaths of individuals. With this approach there is no clear link between the two graphs that can be explained by some common population-derived factors. The development of the BR framework therefore improves on this kind of approach by providing a way of deriving both the fitness and dynamics from the same set of factors, which is the movement of individuals. There is therefore a clear link between the interactions and replacements that happen in the population.

The following sections describe the main components of the framework: structure, fitness, and evolutionary dynamics. Notation used in this chapter is summarised in Table 4.1.

Notation	*Definition*	*Description*
$m_{n,t}$	$\in \{1, \ldots, M\}$	Place where I_n is at time t.
$\mathbf{m}_t$	$= [m_{n,t}]_{n=1}^{N}$	Population distribution at time t.
$\mathbf{m}_{<t}$	$= (\mathbf{m}_{t-1}, \ldots, \mathbf{m}_0)$	Population distribution history.
$p_t(\mathbf{m}\|\mathbf{m}_{<t})$	$\in [0, 1]$	Probability population has distribution $\mathbf{m}$ at time t given $\mathbf{m}_{<t}$.
π_t	$\in [0, 1]$	Population distribution probability function (PDPF).
$P(\mathbf{m}_{<t})$	$\in [0, 1]$	Probability that population has history $\mathbf{m}_{<t}$.
$\pi_{n,t}$	$\in [0, 1]$	Individual distribution probability function (IDPF).
$f_{n,t}$	≥ 0	Fitness contribution of I_n at time t.
$F_{n,t}$	> 0	Fitness of I_n at time t.
$\mathcal{G}_n$	$\subset \{1, 2 \ldots, N\}$	*Direct group*: group that I_n is in.
$w_{i,j,t}$	≥ 0	Replacement weight that I_i replaces I_j at time t.
$\mathbf{W}_t$	$= [w_{i,j,t}]_{i,j=1,\ldots,N}$	Weighted adjacency matrix of evolutionary graph.
$u_{i,j,t}$	≥ 0	Replacement weight contribution that I_i assigns to I_j at time t.

Table 4.1: New notation used in this chapter.

4.2.1 The population: structure and distribution

The population structure describes the restrictions placed on the interactions between the members of the population. In [16], restrictions originate from the movement of individuals in the population, which is considered to be stochastic. The structure of the population is mathematically described using the *population distribution* that gives the position of every individual in the population. Let I_n represent individual n in the population and P_m represent place m in the population. In a population of N individuals who can move around M places, the population distribution at time t is given in [16] by an $N \times M$ binary matrix $\mathbf{X}_t = (X^{(t)}_{n,m})$ where

$$X^{(t)}_{n,m} = \begin{cases} 1 & \text{if } I_n \text{ is in } P_m \text{ at time } t, \\ 0 & \text{otherwise.} \end{cases} \tag{4.1}$$

In this chapter an alternative matrix representation of the population distribution is presented as it is more convenient to use when considering the models in the later chapters. Here, the population distribution at time t will be denoted by the matrix $\mathbf{M}_t = [M_{n,t}]_{n=1,\dots,N}$, where $M_{n,t} = m$ if individual I_n is in place P_m at time t.

The framework assumes that the movement of individuals is probabilistic such that there is dependence upon time and the current and past movements of individuals in the population. In particular, the transition probability function denoted $p_t(\mathbf{m}|\mathbf{m}_{<t})$ gives the probability that the movement of individuals at time t results in a population distribution $\mathbf{m}$ given the population distribution history $\mathbf{m}_{<t} = (\mathbf{m}_{t-1}, \dots, \mathbf{m}_1, \mathbf{m}_0)$. The *transition probability function* is defined as follows

$$p_t(\mathbf{m}|\mathbf{m}_{<t}) = \mathbb{P}(\mathbf{M}_t = \mathbf{m}|\mathbf{M}_{t-1} = \mathbf{m}_{t-1}, \dots, \mathbf{M}_0 = \mathbf{m}_0) \tag{4.2}$$

whose exact form will depend upon the model being used but will always satisfy

$$1 = \sum_{\mathbf{m}} p_t(\mathbf{m}|\mathbf{m}_{<t}) \quad \forall\, t, \mathbf{m}_{<t}. \tag{4.3}$$

The *population distribution probability function* (PDPF) $\pi_t(\mathbf{m})$ gives the probability that the population distribution is $\mathbf{m}$ after t time steps regardless of the population distribution history. The PDPF is expressed using the transition probabilities as follows

$$\pi_t(\mathbf{m}) = \mathbb{P}(\mathbf{M}_t = \mathbf{m}) = \sum_{\mathbf{m}_{<t}} p_t(\mathbf{m}|\mathbf{m}_{<t}) P(\mathbf{m}_{<t}) \tag{4.4}$$

where $P(\mathbf{m}_{<t})$ denotes the *historical PDPF* that gives the probability that the population distribution history is $\mathbf{m}_{<t}$, that is,

$$\begin{aligned} P(\mathbf{m}_{<t}) =& \mathbb{P}(\mathbf{M}_0 = \mathbf{m}_0, \mathbf{M}_1 = \mathbf{m}_1, \dots, \mathbf{M}_{t-1} = \mathbf{m}_{t-1}) \\ =& p_{t-1}(\mathbf{m}_{t-1}|\mathbf{m}_{<t-1}) \cdots p_1(\mathbf{m}_1|\mathbf{m}_0)\pi_0(\mathbf{m}_0) \end{aligned} \tag{4.5}$$

assuming that the *initial population distribution*, $\pi_0(\mathbf{m}_0)$, is known.

Individual movement model

In general, [16] assume that the movement of individuals could depend on each other. This can be simplified by considering the *individual movement model* where individuals are assumed to move independently of each other. The PDPF can is then given by

$$\pi_t(\mathbf{m}) = \prod_n \pi_{n,t}(m_n) \tag{4.6}$$

where $\pi_{n,t}(m_n)$ is the *individual distribution probability function* (IDPF) that gives the probability of individual I_n being present in place P_{m_n} at time t regardless of the history of the process. The expression for $\pi_{n,t}(m_n)$ will depend upon whether the movement of I_n is dependent upon the whole population distribution history or just its own individual history.

Dependence on the population distribution history

When the movement of individual I_n depends upon the distribution history of the whole population, the *individual transition probability function* $p_{n,t}(m_n|\mathbf{m}_{<t})$ gives the probability that I_n moves to place m_n at time t given the population history $\mathbf{m}_{<t}$, that is,

$$p_t(m_n|\mathbf{m}_{<t}) = \mathbb{P}(M_{n,t} = m_n|\mathbf{M}_{t-1} = \mathbf{m}_{t-1}, \ldots, \mathbf{M}_0 = \mathbf{m}_0). \tag{4.7}$$

The IDPF is then given by

$$\pi_{n,t}(m_n) = \sum_{\mathbf{m}_{<t}} p_{n,t}(m_n|\mathbf{m}_{<t})P(\mathbf{m}_{<t}). \tag{4.8}$$

Dependence on the individual distribution history

When the movement of individual I_n depends only upon its own distribution history $m_{n,<t} = (m_{n,t-1}, \ldots, m_{n,0})$, which is independent from the history of the other individuals, then the individual transition probability function is given by

$$p_t(m_n|m_{n,<t}) = \mathbb{P}(M_{n,t} = m_n|M_{n,t-1} = m_{n,t-1}, \ldots, M_{n,0} = m_{n,0}). \tag{4.9}$$

The IDPF is then given by

$$\pi_{n,t}(m_n) = \sum_{m_{n,<t}} p_{n,t}(m_n|m_{n,<t})P_n(m_{n,<t}) \tag{4.10}$$

where $P_n(m_{n,<t})$ denotes the *individual history distribution*, that is,

$$P_n(m_{n,<t}) = p_{n,t-1}(m_{n,t-1}|m_{n,<t-1}) \cdots p_{n,1}(m_{n,1}|m_{n,0})\pi_0(m_{n,0}) \tag{4.11}$$

assuming the initial IDPF, $\pi_0(m_{n,0})$, is known.

The fully independent movement model

The *fully independent movement model* assumes that individuals move independently of each other, history and time. This means that the probability that individual I_n is in place P_m is always the same so the individual transition function will be denoted by $p_{n,m}$. The IDPF is therefore the same as the individual transition function, that is,

$$\pi_{n,t}(m) = p_{n,m} \overbrace{\sum_{m_{n,<t}} P_n(m_{n,<t})}^{1} = p_{n,m} \tag{4.12}$$

and therefore the PDPF can simply be written

$$\pi_t(\mathbf{m}) = p(\mathbf{m}). \tag{4.13}$$

4.2.2 Fitness

In [16] the contribution to an individual's fitness depends upon the time t, the current population distribution $\mathbf{m}$ and historical population distributions $\mathbf{m}_{<t}$. The *fitness contribution* of I_n is denoted

$$f_{n,t}(\mathbf{m}|\mathbf{m}_{<t}) \tag{4.14}$$

where the exact form will depend upon the assumptions about the factors that contribute to an individual's fitness. The *mean fitness contribution* at time t is then given by

$$\bar{f}_{n,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} f_{n,t}(\mathbf{m}|\mathbf{m}_{<t}) p_t(\mathbf{m}|\mathbf{m}_{<t}) P(\mathbf{m}_{<t}). \tag{4.15}$$

It is assumed that the fitness of an individual at time t is given by averaging the mean fitness contribution across all time periods up to and including t. The *fitness* of individual I_n at time t is then given by

$$F_{n,t} = \frac{1}{t} \sum_{k=1}^{t} \bar{f}_{n,k}. \tag{4.16}$$

Note that there are other definitions of the fitness function that one can use instead of the one given here, for example, one could use a weighted average of the mean fitness contribution instead.

In the fully independent movement model, the mean fitness contribution simplifies to

$$\bar{f}_{n,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} f_{n,t}(\mathbf{m}|\mathbf{m}_{<t}) p(\mathbf{m}) P(\mathbf{m}_{<t}). \tag{4.17}$$

In [16], a further simplifying assumption made is that the fitness contribution of individual I_n only depends upon itself and the individuals that it can directly interact with. The set of individuals that individual I_n is present with in the same place, given population distribution $\mathbf{m}$, is called the *direct group* (or simply the *group*) of individual I_n and is given by

$$\mathcal{G}_n(\mathbf{m}) = \{i : m_i = m_n\}. \tag{4.18}$$

The fitness contribution is then denoted by $f_n(\mathcal{G}_n(\mathbf{m}))$. In this case, the mean fitness change is constant over time and therefore the fitness is equal to the mean fitness contribution, that is

$$F_n = \bar{f}_n = \sum_{\mathbf{m}} f_n(\mathcal{G}_n(\mathbf{m})) p(\mathbf{m}). \tag{4.19}$$

4.2.3 Evolutionary Dynamics

This section develops the evolutionary dynamics and is crucially important in completing the development of the framework. In [16], where the dynamics were not defined, only static analysis of an evolutionary process was carried out, though, one of the main goals of the framework is to be able to carry out dynamic analysis. When developing the dynamics, consistency with the framework was essential, thereby, the notions of dependency on population members, history and time was carried forward to the dynamics. However, whether replacement is synchronous or not is independent of the framework and needed to be decided.

Evolutionary graph theory has proved to be a popular approach for implementing dynamics in a structured population. The framework can benefit by incorporating evolutionary graph theory into its dynamics as its knowledge base is quite mature. It also makes it easier to understand for those who are already accustomed to evolutionary graph theory, i.e. there will be some continuity. To incorporate evolutionary graph theory, the two key assumptions required are the population size remains constant and that there is only one birth and death per replacement event, that is, the replacements are asynchronous. Note that a completely different approach could have been used, in particular, where replacement events are synchronous, but, for the aforementioned reasons, the dynamics were actively developed to incorporate evolutionary graph theory.

As seen in section 1.4 (pg. 31), an evolutionary graph controls the replacement events that take place, which is independent of time. In the framework the time t at which the replacement event takes place has to be taken into account. A replacement event at time t is then governed by an evolutionary graph defined using an $N \times N$ weighted adjacency matrix $\mathbf{W}_t = [w_{i,j,t}]_{i,j=1,\ldots,N}$ where the replacement weight $w_{i,j,t}$ gives the weight of the edge from node i to node j in the evolutionary graph that represent individuals I_i and I_j respectively. Note that the time subscript indicates that the evolutionary graph can change over time.

To construct $\mathbf{W}_t$, an approach similar to calculating the fitnesses of the individuals is used. In particular, $\mathbf{W}_t$ is made up of *replacement weight contributions* that depend upon the time t the replacement takes place, the current population distribution $\mathbf{m}$ and the historical population distributions $\mathbf{m}_{<t}$. The replacement weight contribution that individual I_i assigns individual I_j is denoted by

$$u_{i,j,t}(\mathbf{m}|\mathbf{m}_{<t}). \tag{4.20}$$

The exact form will depend upon the assumptions made about the replacement weight contributions. The mean replacement weight contribution is given as follows

$$\bar{u}_{i,j,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} u_{i,j,t}(\mathbf{m}|\mathbf{m}_{<t}) p_t(\mathbf{m}|\mathbf{m}_{<t}) P(\mathbf{m}_{<t}). \tag{4.21}$$

Dynamics			
BDB	$b_{i,t} = \frac{F_{i,t}}{\sum_n F_{n,t}},\ d_{i,j,t} = \frac{w_{i,j,t}}{\sum_n w_{i,n,t}}$	BDD	$b_{i,t} = \frac{1}{N},\ d_{i,j,t} = \frac{w_{i,j,t}F_{j,t}^{-1}}{\sum_n w_{i,n,t}F_{n,t}^{-1}}$
DBD	$d_{j,t} = \frac{F_{j,t}^{-1}}{\sum_n F_{n,t}^{-1}},\ b_{i,j,t} = \frac{w_{i,j,t}}{\sum_n w_{n,j,t}}$	DBB	$d_{j,t} = \frac{1}{N},\ b_{i,j,t} = \frac{w_{i,j,t}F_{i,t}}{\sum_n w_{n,j,t}F_{n,t}}$
LB	$\mathfrak{r}_{i,j,t} = \frac{w_{i,j,t}F_{i,t}}{\sum_{n,k} w_{n,k,t}F_{n,t}}$	LD	$\mathfrak{r}_{i,j,t} = \frac{w_{i,j,t}F_{j,t}^{-1}}{\sum_{n,k} w_{n,k,t}F_{k,t}^{-1}}$

Table 4.2: Dynamics defined using the evolutionary graph $\mathbf{W}_t$ and fitnesses $F_{n,t}$.

In is assumed that the replacement weight at time t is chosen to be the mean replacement weight contribution at time t, that is,

$$w_{i,j,t} = \bar{u}_{i,j,t} \tag{4.22}$$

but, as for the fitness function, there are other definitions that one can use. The reason why this approach is chosen here is that it alludes to the fact that the more individuals interact with one another the more likely they are likely they are to replace one another. The key observation here is that the evolutionary graph is derived from the interactions between the individuals, thereby, if the interactions between individuals change, so should the evolutionary graph.

Now that it known how $\mathbf{W}_t$ is constructed, the next step is to calculate the probability that the offspring of individual I_i replaces individual I_j at time t, denoted $\mathfrak{r}_{i,j,t}$. Since $\mathbf{W}_t$ is an evolutionary graph, an analogue of the standard dynamics given in Table 2.2 (pg. 51) suitable for $\mathbf{W}_t$ can be used to calculate $\mathfrak{r}_{i,j,t}$. These definitions of the replacement probabilities are given in Table 4.2.

In the fully independent movement model the mean replacement weight contribution simplifies to

$$\bar{u}_{i,j,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} u_{i,j,t}(\mathbf{m}, \mathbf{m}_{<t}) p(\mathbf{m}) P(\mathbf{m}_{<t}). \tag{4.23}$$

Furthermore, it can be assumed that the replacement weight contributions are independent of time and history, and depend only on I_i, I_j and the group interactions between them. This implies that the mean replacement weight is invariant over time and is given by

$$w_{i,j} = \bar{u}_{i,j} = \sum_{\mathbf{m}} u_{i,j}(\mathcal{G}_{i,j}(\mathbf{m})) p(\mathbf{m}) \tag{4.24}$$

where $\mathcal{G}_{i,j}(\mathbf{m}) = \{k : m_k = m_i \wedge m_k = m_j\}$. Note that $\mathcal{G}_{i,j}(\mathbf{m}) = \emptyset$ if I_i and I_j are not present in the same place for a population distribution $\mathbf{m}$.

Note on the dynamics

In this chapter the development of the framework of [16] is completed by defining the dynamics that can be used with the framework. It is now possible to carry out dynamic analysis of an evolutionary process in a population with mobile individuals. The dynamics developed here incorporate evolutionary graph theory and can therefore readily use its vast knowledge base that includes the material in Chapter 2. In particular, the known behaviour of the standard dynamics in evolutionary graph theory can be leveraged to get an understanding of their behaviour in a different context. This is particularly true in the next few chapters where models are developed using the framework in its fully developed form.

In the classic metapopulation framework [51], it is assumed that there are discrete patches with extinction-prone populations. This means that it is possible for a population to colonise an unoccupied patch and a subpopulation within a patch to go extinct, allowing the total population size to fluctuate. This is different from the Broom-Rychtář (BR) framework because the dynamics used specify that the offspring of an individual immediately replaces another individual, keeping the population size fixed. Since every birth and death is a replacement event, the population cannot go extinct, instead, different types within the population can go extinct but the population itself persists. Furthermore, a patch in the metapopulation framework is a 'fixed' location in space that an individual and its offspring can occupy. This idea of a patch is not the same as in the BR framework. Instead, a patch is simply thought of as a place that an individual can move to, however, its offspring must take the place of another individual. To bring the BR framework in line with the metapopulation framework would require a different definition of the dynamics. A possible solution would be to have dynamics with separate birth and death rates such that an offspring can be placed in an immediate neighbourhood patch. This way a patch can be colonised by a population and also a population in a patch can go extinct through death and individuals moving away.

4.3 The Territorial Raider model

The territorial raider population evolution model is a simple application of the BR framework. It is assumed that each individual has their own unique territory that overlaps with other individuals. Where these territories overlap, individuals can meet and interact with one another. Meetings between individuals can take place in groups and, therefore, multiplayer Hawk-Dove and public goods games, see chapter 3, are used to determine the payoffs an individual receives. Each individual has a unique home within their territory and the proportion of time that an individuals spends at home is controlled by a global home fidelity parameter that is the same for all individuals. The higher this home fidelity parameter, the more time individuals spend at home and less time interacting with one another. Furthermore, it is assumed that individuals are allowed to make one movement within their territory before returning home. Replacement events are assumed to happen at discrete time intervals. Between these intervals individuals are assumed to meet with one another in order to determine their fitness. Dynamics where birth happens first followed by death with selection acting on birth (BDB) are considered such that an individual's offspring replaces another individual proportional to how often they meet. The quantity that will be calculated to measure the evolutionary success of a strategy is the fixation probability. Special cases of small graphs where all of the population states can be identified allowing exact analyses to be carried out are considered. Interesting general features of the model are identified by comparing the fixation probability value for both games on several graphs under different parameter values and assumptions. The new notation used in this chapter is given in Table 4.3.

The motivation behind the territorial raider model is the territorial behaviour of animals. Animals of many species live alone or in distinct groups on a certain territory. Although animals generally forage for food within their territory, it can happen that the territory size varies considerably over time. In some cases, it can expand and overlap with other territories, when food becomes rarer, or for the purpose of mating for example. Thus the same place is used by two or more individuals that will interact and sometimes compete when some major items of food are at stake. The territorial raider model incorporates these more general types of interaction, therefore, allowing multi-player games to be played among the population.

In comparison to the population evolution model considered in chapter 2, the territorial raider model determines the fitness of individuals through multiplayer game-theoretic interactions that depends upon the movement structure of the individuals. Whilst both models consider an evolutionary graph to determine the replacement events, the evolutionary graph for the latter model is derived from the movement structure of the population. Therefore, studying the evolutionary graph on its own is not sufficient to understand what is happening in the territorial raider model. In particular, factors that affect the movement structure of the population are also studied.

4.3.1 The population structure and distribution

The territorial raider model (see Figure 4.1) was developed by [16] and is used to represent interactions within a population with overlapping territories. The territorial raider model considers a population of N individuals $I_1, \dots, I_N$ (see also Section 4.3.3 for an interpretation of I_n in relation to the evolutionary dynamics) who can move and eventually interact in N different

Notation	*Definition*	*Description*
p_{nm}	$\in [0,1]$	Probability of I_n being at P_m.
h	$\in [0,\infty)$	*Home fidelity*: likelihood of individual staying in its home vertex.
d	$\in \mathbb{Z}^+ \setminus \{0\}$	Number of neighbours.
$\mathcal{G}$	$\subset \{1,2,\ldots,N\}$	Group of indiviuals.
$\chi(m,\mathcal{G})$	$\in [0,1]$	Probability of group $\mathcal{G}$ meeting at P_m.
$R_A(a,b)$	$\in [0,\infty)$	Payoff to type A individual present with a (b) other type A (B).
R	$\in [0,\infty)$	Background payoff that individuals start with.
V	$\in [0,\infty)$	Reward.
K	$\in (0,\infty)$	Cost.
v	$= V/K$	Reduced parameter.
r	$= R/K$	Reduced parameter.
T_j	$= \sum_{i\neq j} w_{ij}$	Temperature of I_j.

Table 4.3: New notation used in this chapter.

places $P_1,\ldots,P_N$, see Figure 4.1(a). The individual I_n lives in a place P_n and can also move to neighbouring places.

The population is represented using a graph where vertices represent individuals as well as places of interaction. The graphs studied are representations of territorial raider models. Therefore, it is important to bear in mind that they relate to a more general representation where places and individuals are disconnected as shown in Figure 4.1(b). In other words, the graphs shown here stands for the kind of models in Figure 4.1(a). All of the three and four vertex connected undirected graphs shown in Figure 4.2 are considered.

It is assumed that there is *fully independent movement*, that is, individuals move independently of each other, history and time (see Section 4.2.1 on Page 88). In general each individual could have a different probability of movement, but a natural model where all movements are governed by a single parameter is selected. It will be assumed that an individual with d neighbours will stay with probability $p_{n,n} = h/(h+d)$ and move to one of its neighbouring places with probability $1/(h+d)$. Thus h is a measure of the preference of an individual to stay on its home vertex, and will be called its *home fidelity*. In each case setting $h = 1$ gives the natural parameters of each individual visiting all allowable places (including its home vertex) with equal probability. Note that, for a given value of h, an individual is more likely to move away if it has a larger number of neighbouring places d. The probability that an individual I_n is at place P_m,

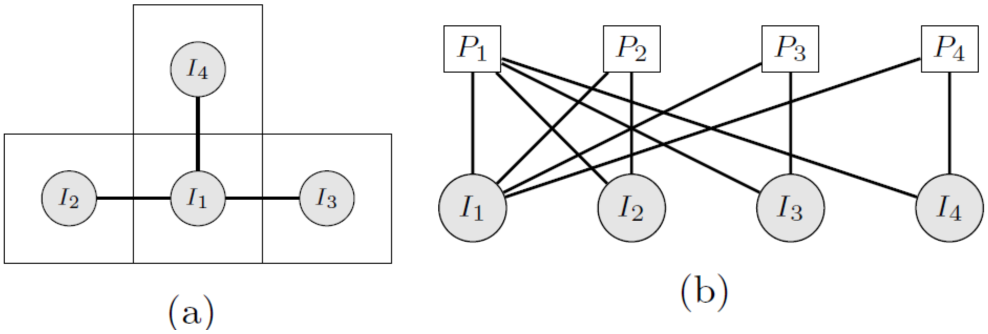


Figure 4.1: The territorial raider model from [16]. (a) Individual I_n lives in place P_n but can visit neighbouring places. The territory of I_1 consists of all places P_1, P_2, P_3 and P_4, the territory of I_2 consists of P_1 and P_2, the territory of I_3 consists of P_1 and P_3, the territory of P_4 consists of P_1 and P_4. (b) An alternative visualization as multi-player interactions on a bi-partite graph where individuals and places are clearly separated. The vertices $I_1, \ldots I_n$ will be called the *I-vertices.*

i.e. the IDPF, will be given by

$$p_{n,m} = \begin{cases} h/(h+d) & n = m, \\ 1/(h+d) & n \neq m \text{ and vertices } n, m \text{ connected}, \\ 0 & \text{otherwise}. \end{cases} \tag{4.25}$$

4.3.2 Fitness

To calculate the fitness of individuals it is assumed that the fitness contribution only depends upon itself and the group of individuals that it interacts with. The fitness of an individual is therefore given by equation (4.19, pg. 89) that is rewritten more simply as follows

$$F_n = \sum_{m=1}^{N} \sum_{\substack{\mathcal{G} \\ n \in \mathcal{G}}} \chi(m, \mathcal{G}) f_n(\mathcal{G}), \tag{4.26}$$

where $\mathcal{G}$ is a group of individuals and

$$\chi(m, \mathcal{G}) = \prod_{i \in \mathcal{G}} p_{i,m} \prod_{j \notin \mathcal{G}} (1 - p_{j,m}) \tag{4.27}$$

gives the probability that group $\mathcal{G}$ forms in place m. The fitness contribution, $f_n(\mathcal{G})$, will be determined by the payoff received in a multi-player game. It is assumed that there are two types of strategies, A and B, that individuals can choose from. The payoff to an individual of type A present with a (b) other type A (B) will be denoted $R_A(a, b)$ and, similarly, $R_B(a, b)$ for a type

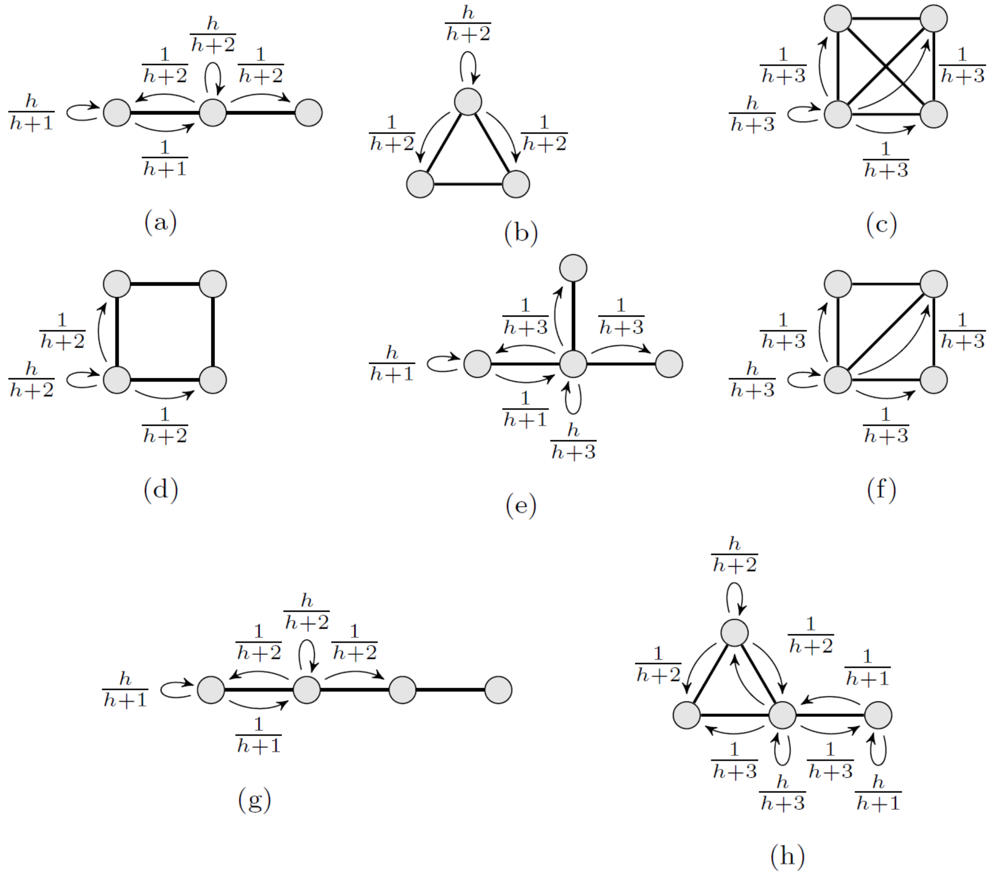


Figure 4.2: The population structures and movement probabilities for small graphs on 3 and 4 vertices. An individual moves to a neighbouring vertex with probability $1/(h+d)$ and stays at home with probability $h/(h+d)$ where d is the number of neighbours. (a) The line of 3 vertices, which in this case, is also the star. (b) the triangle. (c) the square with both diagonals, the complete graph for four vertices. (d) the “circle” graph, or a square with no diagonals. (e) the star graph with 4 vertices. (f) the diamond, a square with one diagonal. (g) the line with 4 vertices. (h) the paw.

B individual. The fitness contribution is then given by

$$f_n(\mathcal{G}) = \begin{cases} R_A(|\mathcal{G}|_A - 1, |\mathcal{G}|_B) & I_n \text{ type } A, \\ R_B(|\mathcal{G}|_A, |\mathcal{G}|_B - 1) & I_n \text{ type } B \end{cases} \tag{4.28}$$

where $|\mathcal{G}|_A$ ($|\mathcal{G}|_B$) is the number of type A (B) individuals in group $\mathcal{G}$.

The charitable prisoner's dilemma (see Section 3.3.1, pg. 76), which is referred to as the public goods game in the remainder of this chapter and thesis, and the Hawk-Dove game (see Section 3.3.2, pg. 80) are considered. The payoffs for the fixed fitness case are also introduced, which can be seen as a limiting case in this model. The payoffs for each case are given below where a background payoff R has been added. The background payoff R has no effect in static games, but is important for the dynamics. In general for discrete dynamics, including the one considered here, the larger the value of R, the weaker the effect of evolution [17, Chapter 2]. Here, it will be always assumed that R is sufficiently large that no fitness can ever go negative. Furthermore, scaling all payoffs by a constant has no effect on the game outcomes. All payoffs have therefore been divided by the cost K so that the reduced background payoff is given by $r = R/K$, which is fixed to 10, and the reduced reward is given by $v = V/K$.

- *The Public Goods game:* A stands for a Cooperator and B for a Defector. Both types start with a reduced background payoff r. A Cooperator (always) pays a cost of 1 so that other individuals in the group share the the reduced reward v and Defectors do nothing. The payoffs are given by

$$R_A(a,b) = \begin{cases} r - 1 & a = 0, b = 0, \\ r - 1 + \frac{a}{a+b} v & \text{otherwise,} \end{cases} \tag{4.29}$$

$$R_B(a,b) = r + \frac{a}{a+b+1} v. \tag{4.30}$$

- *The Hawk-Dove game:* A stands for a Hawk, and B for a Dove. They both start with a background payoff r and compete for a single reduced reward v. If all individuals in the group are Doves, they split the reward so that each one gets the same share. If there is at least one Hawk then all the Doves concede. The Hawks fight so that the winner gets the reduced reward v while the other Hawks incur a cost of 1 such that each Hawk has an equal chance of winning. The payoffs are given by

$$R_A(a,b) = r + \frac{v-a}{a+1}, \tag{4.31}$$

$$R_B(a,b) = \begin{cases} r & \text{if } a > 0, \\ r + \frac{v}{b+1} & \text{if } a = 0. \end{cases} \tag{4.32}$$

- *Fixed fitness case:* In this game, the individuals do not really interact with each other but rather receive a constant payoff depending on their type and irrespective of the groups size or types of the other group members. The payoffs are given by

$$R_A(a,b) = r + v, \tag{4.33}$$

$$R_B(a,b) = r. \tag{4.34}$$

4.3.3 Evolutionary dynamics

It will be assumed that the replacement weight contributions depend only the birth individual I_i, the death individual I_j and the group interactions between them. This means that the replacement weights, which are used in the evolutionary dynamics, are given by equation (4.24, pg. 91), which is rewritten more simply here as follows

$$w_{ij} = \sum_{m=1}^{N} \sum_{\substack{\mathcal{G} \\ i,j \in \mathcal{G}}} u_{ij}(m, \mathcal{G}). \tag{4.35}$$

An individual I_j can be replaced by a copy of individual I_i if and only if I_i and I_j could meet in the spatial structure (which here means that P_i and P_j are at most two edges apart from each other). Thus the types of the individuals change through time, and so I_i is more properly thought of as a position in our structure which has a particular relationship to the places $P_1, \ldots, P_N$, rather than an actual individual. The relationship between the position I_i and the potential individuals that can be thought of as similar to that between a gene and its possible alleles. The positions I_n will be called the *I-vertices* of this structure, but will often simply be referred to as "individuals", unless this distinction needs to be emphasised (see Figure 4.1(b)).

For the replacement weight contribution $u_{ij}(\mathcal{G})$, it is assumed that each individual I_j in group $\mathcal{G}$ contributes equally except I_i. This represents the fact that individual I_i can replace any one of the other individuals in a group $\mathcal{G}$ that it is present in. Therefore, the contribution of each individual I_j in group $\mathcal{G}$ will be set to $1/(|\mathcal{G}| - 1)$. However, when I_i is alone, it is assumed that it can replace itself and so contributes 1. The replacement weight contribution for all $\mathcal{G}$ such that $i, j \in \mathcal{G}$ is then given by

$$u_{ij}(m, \mathcal{G}) = \begin{cases} 0 & i = j \wedge |\mathcal{G}| > 1, \\ \chi(m, \mathcal{G}) & i = j \wedge |\mathcal{G}| = 1, \\ \frac{\chi(m,\mathcal{G})}{|\mathcal{G}|-1} & i \neq j. \end{cases} \tag{4.36}$$

With this definition of the replacement weight contribution, the replacement weights have the

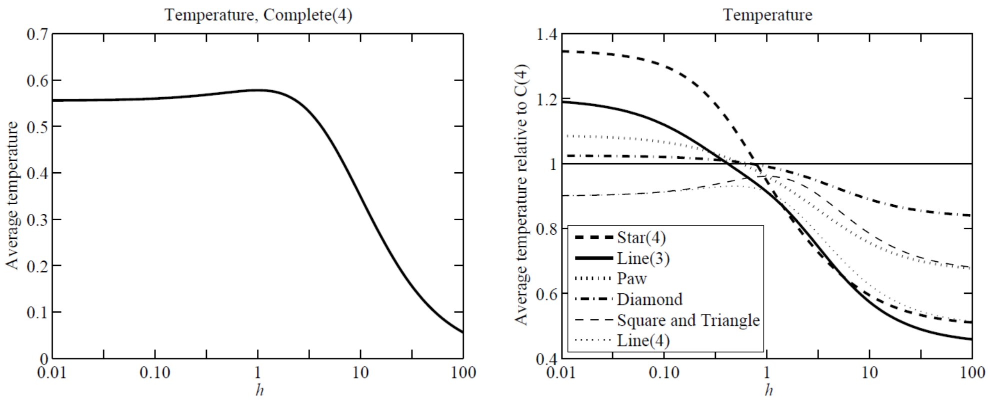


Figure 4.3: The average temperatures as given by (4.37) for small graphs on 3 and 4 vertices. The average temperature for Line(3), Star(4) and paw monotonically decrease with h, the average temperature for other graphs peaks around $h \approx 1$ for other graphs.

property that $w_{i,j} = w_{j,i}$. Also, the quantity

$$T_j = \sum_{i \neq j} w_{ij} \tag{4.37}$$

could be regarded as the temperature [52] of the I-vertex I_j as it is proportional to the frequency of an individual I_j being replaced by another individual (if all individuals are equally likely to produce an offspring). Note that in this setting, the (mean) temperature depends not only on the graph but also on the parameter h, see Figure 4.3.

4.3.4 The fixation probability of A

To calculate the fixation probability of type A among B individuals at a given spatial structure, the first step is to list all the states that describe all the possible distributions of individuals of both types on the different places throughout the evolutionary process, from the insertion of one individual from type A in a population made up of B individuals until its fixation or elimination. Not accounting for the symmetries, a given population structure with N individuals yields a transition graph with 2^N different states that can be indexed by subsets $S \subset \{1, 2, \ldots, N\}$. State $\emptyset$ will be used to represent a population composed entirely of B individuals, and state $\mathcal{N}$ a population of A individuals only. Let $P_{SS'}$ denote the transition probability from state S to state S' in the dynamic process. Figure 4.4 shows the transition graphs (when all graph symmetries are taken into account) for the corresponding graphs from Figure 4.2.

Having previously defined the replacements weights w_{ij}, the appropriate definition from Table 4.2 (pg. 91) can be chosen to give the replacement probabilities $\mathfrak{r}_{ij}$. Using the replacement probabilities, for $S \neq S'$, the transition probabilities are given by

$$P_{SS'} = \begin{cases} \sum\limits_{i \notin S} \mathfrak{r}_{ij}; & \text{if } S' = S \setminus \{j\} \text{ for some } j \in S \\ \sum\limits_{i \in S} \mathfrak{r}_{ij}; & \text{if } S' = S \cup \{j\} \text{ for some } j \notin S \\ 0; & \text{otherwise} \end{cases} \tag{4.38}$$

and, therefore,

$$P_{SS} = 1 - \sum_{S' \neq S} P_{SS'}. \tag{4.39}$$

The probability ρ_S^A that type A fixates from state S is given by

$$\rho_S^A = \sum_{S' \subset \{1,2,\ldots,N\}} P_{SS'} \rho_{S'}^A \tag{4.40}$$

with boundary conditions

$$\rho_\emptyset^A = 0, \tag{4.41}$$

$$\rho_\mathcal{N}^A = 1. \tag{4.42}$$

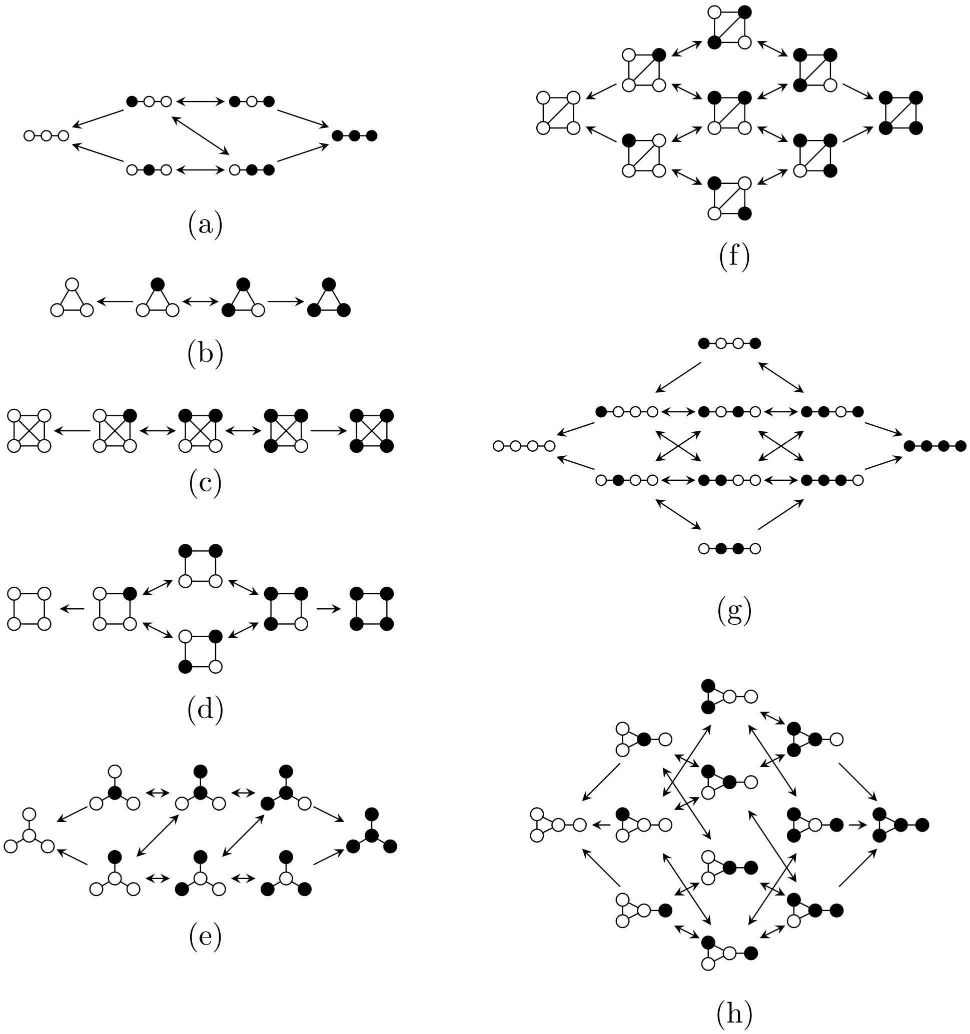
The mean fixation probability of type A, ρ^A, will be an appropriately weighted average of the fixation probabilities from all states including exactly one individual of type A. Following [5], the mean fixation probability is defined

$$\rho^A = \sum_i \frac{T_i}{\sum\limits_j T_j} \rho_{\{i\}}^A. \tag{4.43}$$

The temperature weighted mean fixation probability assumes that a new type of individual is more likely to appear at a place whose inhabitants are replaced more often (relative to others). Note, however, that the difference between ρ^A and the uniformly weighted average $\sum_i \frac{1}{N} \rho_{\{i\}}^A$ is negligible for all the small graphs considered here. In fact, the latter quantity is never less than ρ^A which is in agreement with results from [3].

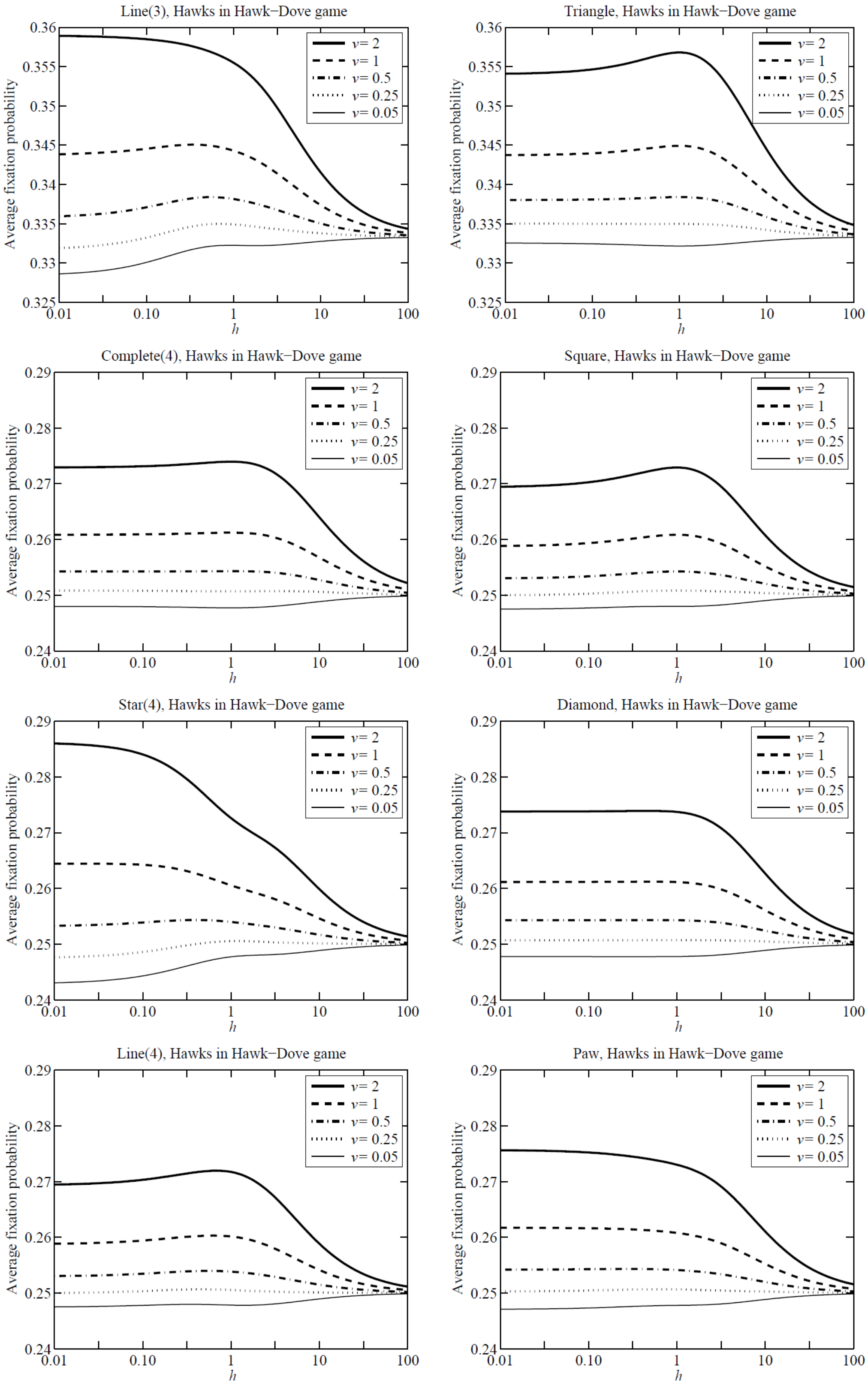
4.4 Results

For the Hawk-Dove game, the results for the fixation probabilities of Hawks on small graphs are shown in Figure 4.5. The fixation probabilities of Doves on small graphs are shown in Figure 4.6. For the Public Goods game, the results for the fixation probabilities of Cooperators on small graphs are shown in Figure 4.7 and the fixation probabilities of Defectors are shown in Figure 4.8. The fixation probability ρ^A, depends on the underlying graph structure, the home



(a) (b) (c) (d) (e) (f) (g) (h)

Figure 4.4: The transition graphs for small graphs on 3 and 4 vertices. (a) The line of 3 vertices. (b) the triangle. (c) the square with both diagonals, the complete graph for four vertices. (d) the “circle” graph, or a square with no diagonals. (e) the star graph with 4 vertices. (f) the diamond, a square with one diagonal. (g) the line with 4 vertices. (h) the paw.


Line(3), Hawks in Hawk−Dove game

Triangle, Hawks in Hawk−Dove game

Complete(4), Hawks in Hawk−Dove game

Square, Hawks in Hawk−Dove game

Star(4), Hawks in Hawk−Dove game

Diamond, Hawks in Hawk−Dove game

Line(4), Hawks in Hawk−Dove game

Paw, Hawks in Hawk−Dove game

Figure 4.5: The fixation probabilities of a single Hawk in a population of Doves for small graphs on 3 and 4 vertices.

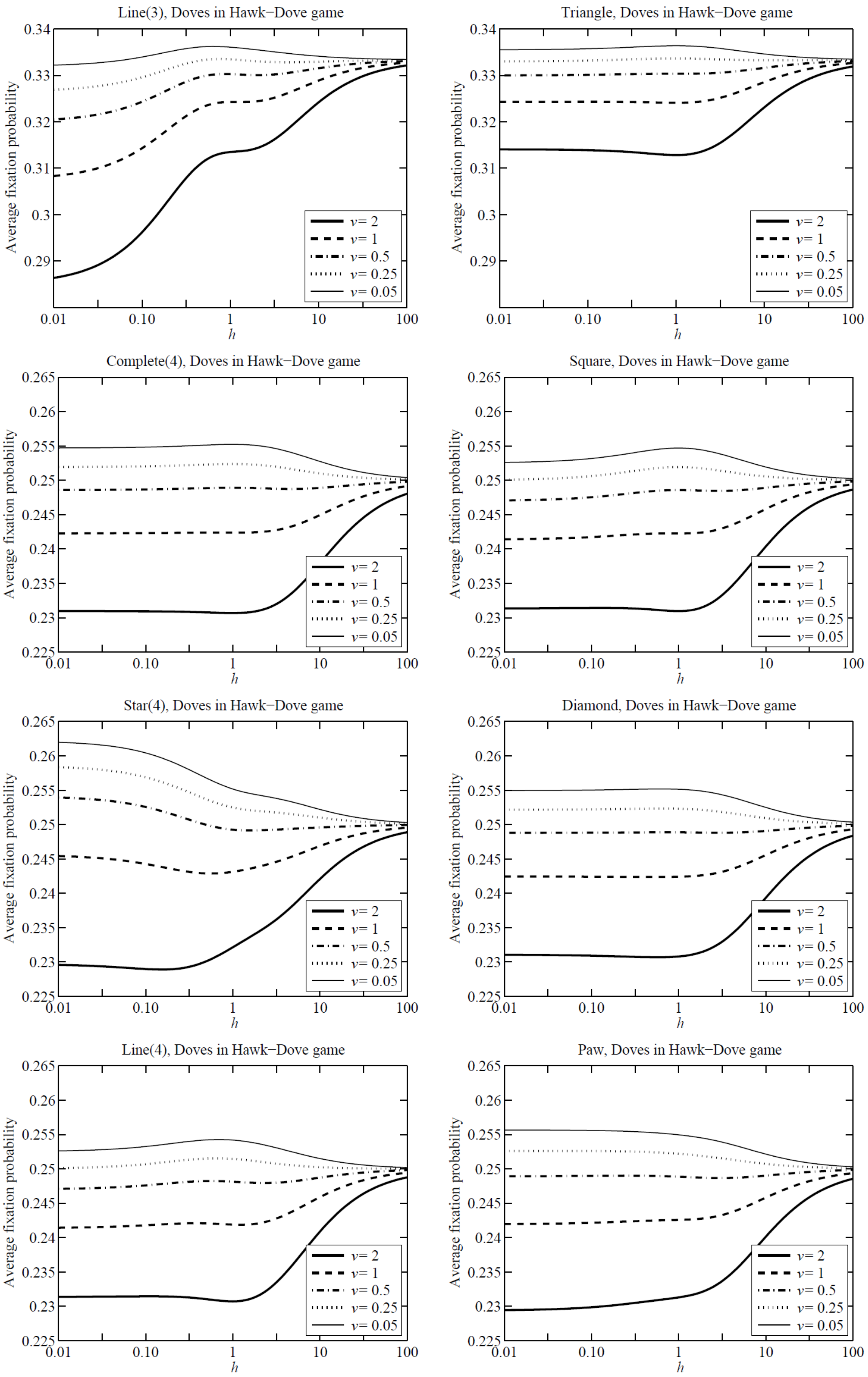


Figure 4.6: The fixation probabilities of a single Dove in a population of Hawks for small graphs on 3 and 4 vertices.

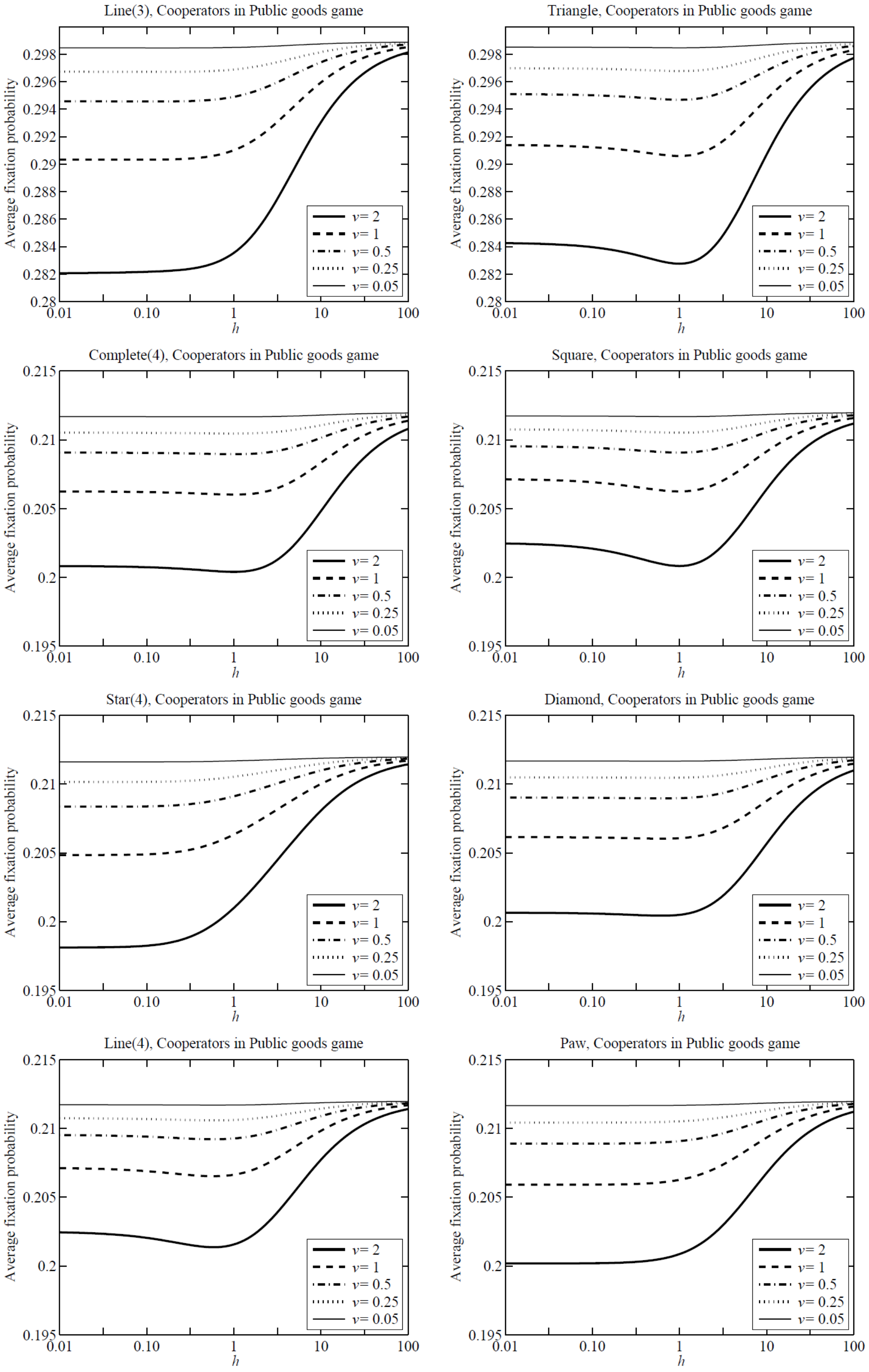


Figure 4.7: The fixation probabilities of a single Cooperator in a population of Defectors for small graphs on 3 and 4 vertices.

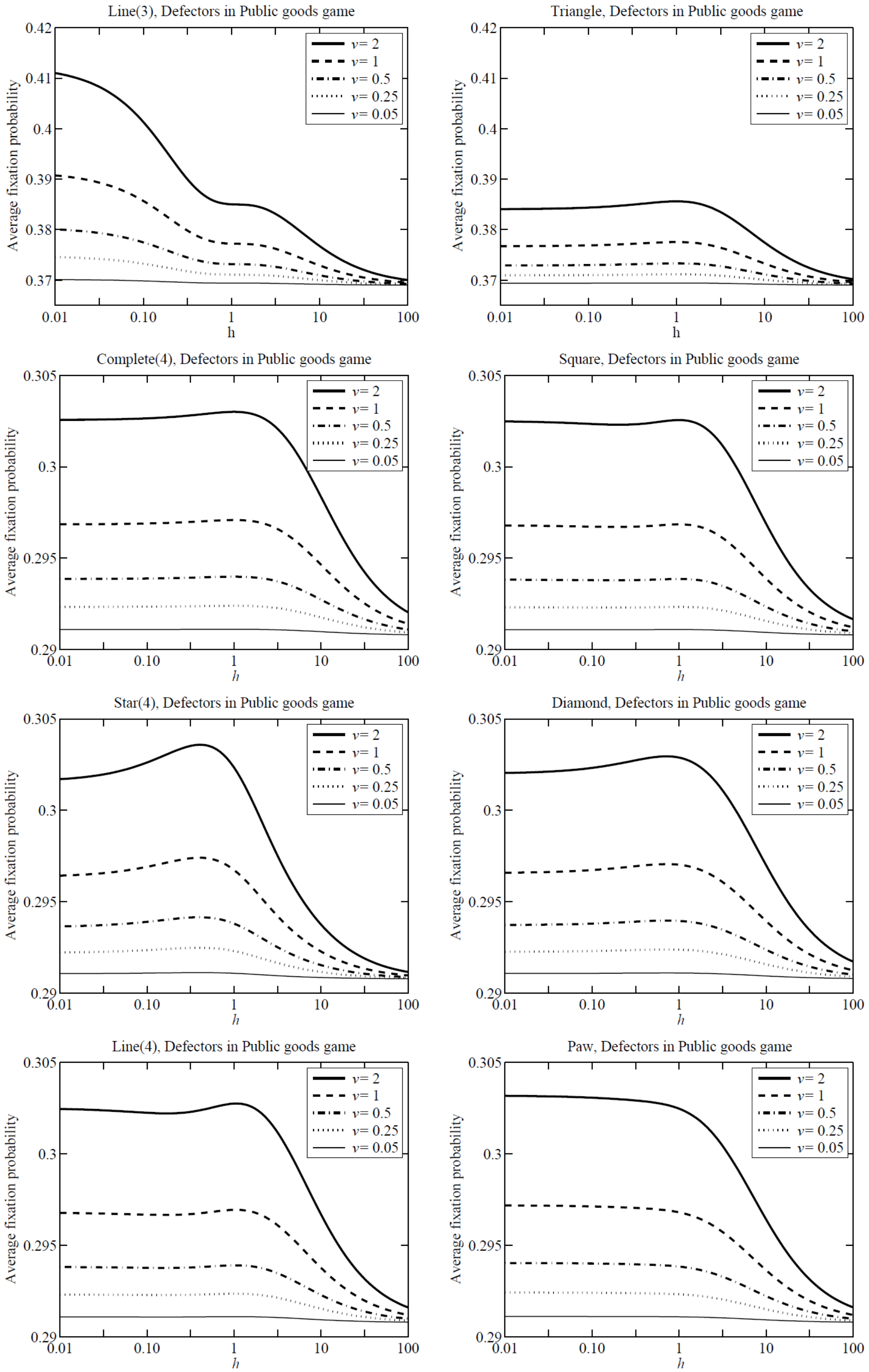


Figure 4.8: The fixation probabilities of a single Defector in a population of Cooperators for small graphs on 3 and 4 vertices.

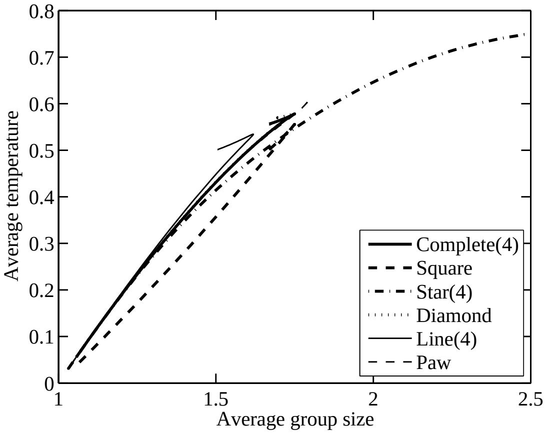


Figure 4.9: The mean temperature versus the mean group size for graphs with 4 vertices (as h varies from 0 to 100). For complete graphs, the line with 4 vertices and the diamond, i.e. the graphs where the mean temperature peaks at $h \approx 1$, there is a spike in the correlation figure corresponding to the fact that the mean temperature and the mean group size increase (decrease) at different speeds as $h < 1$ (or $h > 1$). Note that Star(4) has the largest possible mean group size.

fidelity parameter h, the game and the parameters of the game v (the parameter r was fixed at 10), as well as the type of the invading individual/ resident population.

There are a number of features common to both games, and both types of invading mutant within the Hawk-Dove game. The fixation probability in each case naturally depends upon the size of the reward, and the strength of this dependency itself depends upon h. For low values of h, which have a high mean temperature, there is a wide spread of values of fixation probability depending upon the value of v. For high h, corresponding to low mean temperature, the fixation probability depends very little upon v. This can be seen from Figure 4.10, where the biggest differences between fixation probabilities are for the highest temperatures. In the Hawk-Dove game, a large v is good for Hawks, and a small v is good for Doves (since Hawks still pay costs against other Hawks) and the effect of changing v is most profound when the temperature is highest. In general, it is observed that low temperatures suppress the effect of fitness and thus suppress selection, whereas high temperatures enhance it.

4.4.1 Fixation probability, temperature and mean group size

The mean size of an individual's group (the group size from the individual's perspective) is studied in [16, 18], whose definition is given by

$$\overline{G} = \sum_{m} \sum_{\mathcal{G}} \frac{\chi(m,\mathcal{G})|\mathcal{G}|^2}{\sum_{m}\sum_{\mathcal{G}} \chi(m,\mathcal{G})|\mathcal{G}|}. \tag{4.44}$$

Note the distinction between (4.44) and the mean group size from an observer's perspective as, here, the groups are weighted by the numbers of individuals within a group. For example, if half of groups are of size 6 and half are of size 12, from the observer's perspective the mean group size is 9, but from the individual's perspective this is 10, as 2/3 of individuals are in the larger groups.

In [16] it was observed that the mean group size was an important factor affecting the fitness, and thus it was expected that this would be the case for the fixation probability too. In fact this is so, but it turns out that the mean temperature and the mean group size are strongly correlated, see Figure 4.9. The effect of the mean group size on the fixation probability is less strong than that of the mean temperature, hence, the mean temperature will be focused on in the discussion of the results. It is observed in Figure 4.10 that ρ^A strongly correlates with the mean temperature for the underlying graphs. The correlation is negative for the Public Goods game and ranges from positive to negative as v decreases for Hawks or increases for Doves in the Hawk-Dove game.

4.4.2 High home fidelity h

For low temperatures, the relationship between mean temperature and fixation probability is effectively linear, although this linear dependence breaks down for high temperatures, and breaks down fast for larger or more heterogeneous graphs like the star with 7 vertices, see Figure 4.10.

For example consider the case of the complete graph, where every I-vertex has the same temperature, which will be simply denoted by T. In this case the fixation probability is given by equation (1.6, pg. 29), rewritten here as follows

$$\rho^A = \frac{1}{1+\sum_{j=1}^{N-1}\prod_{k=1}^{j}\gamma_k}, \tag{4.45}$$

where γ_k is the ratio of the probability of a decrease in the number of type A individuals and the probability of an increase in that number (given there are currently k type A individuals). Since $d_{ij} = d_{ji}$, in this case $\gamma_k = b_{A,k}/b_{B,k} = F_{A,k}/F_{B,k}$, where the latter expressions are the ratios of the birth probabilities of types B and A and the fitnesses of types B and A (that depends on k but does not depend on position).

For both games this is the ratio of two terms that are approximately linear in the I-vertex temperature, when this temperature is low, as is shown below. Any individual is only likely to be with at most one other individual, and a payoff above the baseline will only occur if this is a cooperator (each with probability roughly $1/h$). The temperature at each I-vertex is approximately $(N-1)/h$. Recalling that the (reduced) background fitness and reward values are denoted by r and v, respectively, if type A is a Cooperator in the Public Goods game, the following is obtained

$$F_{A,k} \approx r - 1 + \frac{(k-1)v}{h} \approx r - 1 + \frac{k-1}{N-1}vT, \tag{4.46}$$

$$F_{B,k} \approx r + \frac{kv}{h} \approx r + \frac{k}{N-1} vT. \tag{4.47}$$

For sufficiently small temperatures, it is thus clear that γ_k is approximately linear in the mean temperature, and so consequently it is seen that the fixation probability will also be approximately linear in the mean temperature, although this linearity breaks down as soon as the temperature becomes sufficiently large.

For the fixed fitness case, the situation can actually be seen from the point of view of classical evolutionary graph theory [52]. No matter what the underlying population structure, an evolutionary graph W can be constructed with the vertices given by the set of I-vertices $\{I_i; i = 1, \dots N\}$ and the edges between I_i and I_j weighted by $w_{ij} = d_{ij}$ corresponding to the fact that I_j is being replaced by I_i with probability d_{ij}. Since $d_{ij} = d_{ji}$, the resulting evolutionary graph W is a circulation [52, Appendix]. Consequently, type A, having a relative fitness $(r + v)/r$ when compared to type B, will fixate with the Moran probability [58]

$$\rho^A = P_{Moran}\left(\frac{r+v}{r}\right) = \frac{1 - \frac{r}{r+v}}{1 - \left(\frac{r}{r+v}\right)^N}. \tag{4.48}$$

The above results hold for any graph and the fixed fitness case; and it holds approximately for any graph and any game where the payoffs of different types of individuals are nearly constant. Within the framework here, this happens if $h \to \infty$ because then the individuals rarely move and thus rarely interact. For the Public Goods game, it also happens if $v \to 0$. In this case, Cooperators receive payoff $r - 1$ while Defectors receive payoffs r, resulting in

$$\rho^A = P_{Moran}\left(\frac{r-1}{r}\right) = \frac{1 - \frac{r}{r-1}}{1 - \left(\frac{r}{r-1}\right)^N}. \tag{4.49}$$

When $r = 10$ and $N = 4$, then $P_{Moran} \approx 0.2119$ which corresponds to the results for $h \to \infty$ or $v \to 0$ as seen in Figure 4.11. For the Hawk-Dove game, as $h \to \infty$, the fitnesses of both the Hawk and the Dove tend to r as the individuals rarely meet. Thus, the fixation probability of either Hawk or a Dove tends to $1/N$ as $h \to \infty$ as seen in Figures 4.5 and 4.6.

Note that for the Hawk-Dove game, when $v \to 0$ but h is not too large, the fixation probability of Hawks and Doves is *not* $1/N$. This is caused by the fact that Hawks still interact and thus have a disadvantage over Doves. The disadvantage grows with growing mean group size (i.e. with growing mean temperature). Consequently, the fixation probability is not the Moran probability if $h \ll \infty$.

4.4.3 Effects of the graph and the game

The fixation probability also depends upon the population structure more generally over and above the mean temperature. For low h in particular the heterogenous star graph, and to a

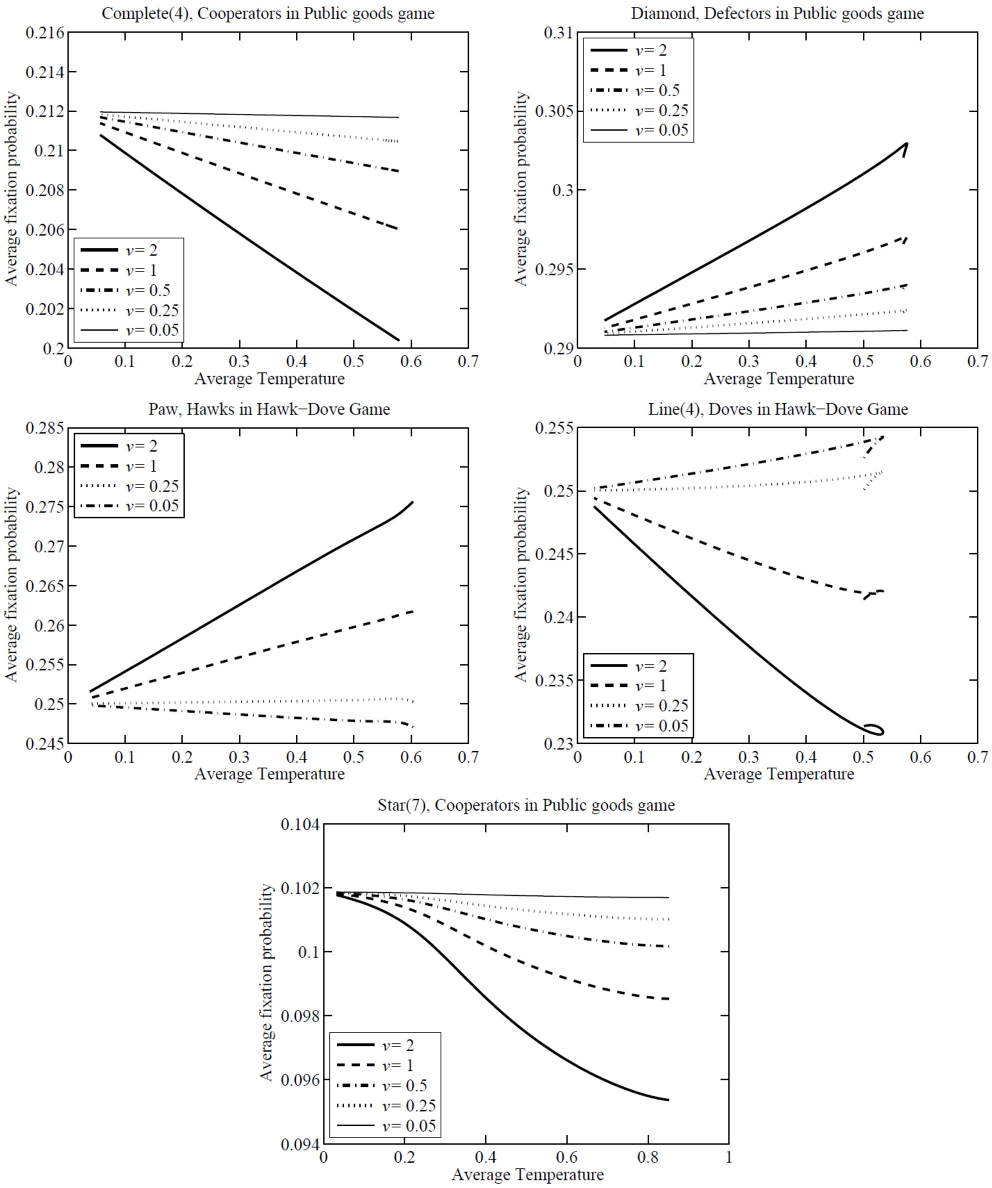


Figure 4.10: The fixation probability as a function of the mean temperature for various graphs. For all small graphs, the correlations look similar and depend primarily on the game played.

lesser extent the paw, have a wider range of fixation probabilities for differing values of v than any of the other graphs. Note, however, that the line is less variable than the homogeneous well-mixed population. This may be the effect of the temperature (note that the star has the highest mean temperature as well as the widest range of fixation probabilities), or the variance in the group size, or possibly both effects working in conjunction.

A second observation that can be made on these graphs is that the ordering of fixation probabilities for different graphs can change as the parameters vary. For example, for the Hawk-Dove game with three vertices, whatever the value of the reduced gain v, the fixation probability of the triangle and the line cross for $h \approx 0.66 \approx 10^{-0.18}$. Note that this approximately corresponds to the point where the mean temperature gets higher on the triangle than on the line. Similar observations are true for some (but not all) of the graphs (and other games considered here), see Figure 4.12.

There are some features specific to the particular game in question. For the Hawk-Dove game, the highest fixation probabilities can occur for intermediate values of $\log(h) \approx 0$, both for Dove invaders and for Hawk invaders. This is particularly the case for the square and the line. This occurs when the reward value v is high for Hawk invaders, and the effect disappears for low v. The figures are noticeably different for different graphs, and it can thus be said that there is a significant graph effect for the Hawk-Dove game. For the Public Goods game these features do not appear, and eight broadly similar figures are seen. Thus for the Public Goods game, we can say that there is not a significant graph effect, at least for the small graphs that have been considered. The main features where the graphs differ is in the broader spread on the star as mentioned above, and the dip in the fixation probability for intermediate values of v.

4.5 Discussion

In this chapter the modelling framework of Broom-Rychtář is used to consider interactions of individuals in a non-homogeneous environment. A birth-death dynamics is used so that dynamic analysis can be carried out. The dynamics of some simple games on different spatial structures were analysed and compared to try to determine some general features. In particular the fixation probability was shown to be strongly correlated with the mean temperature. Within the population, individuals play games, and each game as well as being distinct, has specific features (in this case reward, cost and baseline reward) which govern how well individuals do. The value of the reward v was shown to have a potentially significant effect on the fixation probability; the size of this effect depended upon aspects of the population structure. In particular, a high mean temperature made the effect of this parameter much more critical, and the effect will be stronger when the graph is highly heterogeneous, on the star for example.

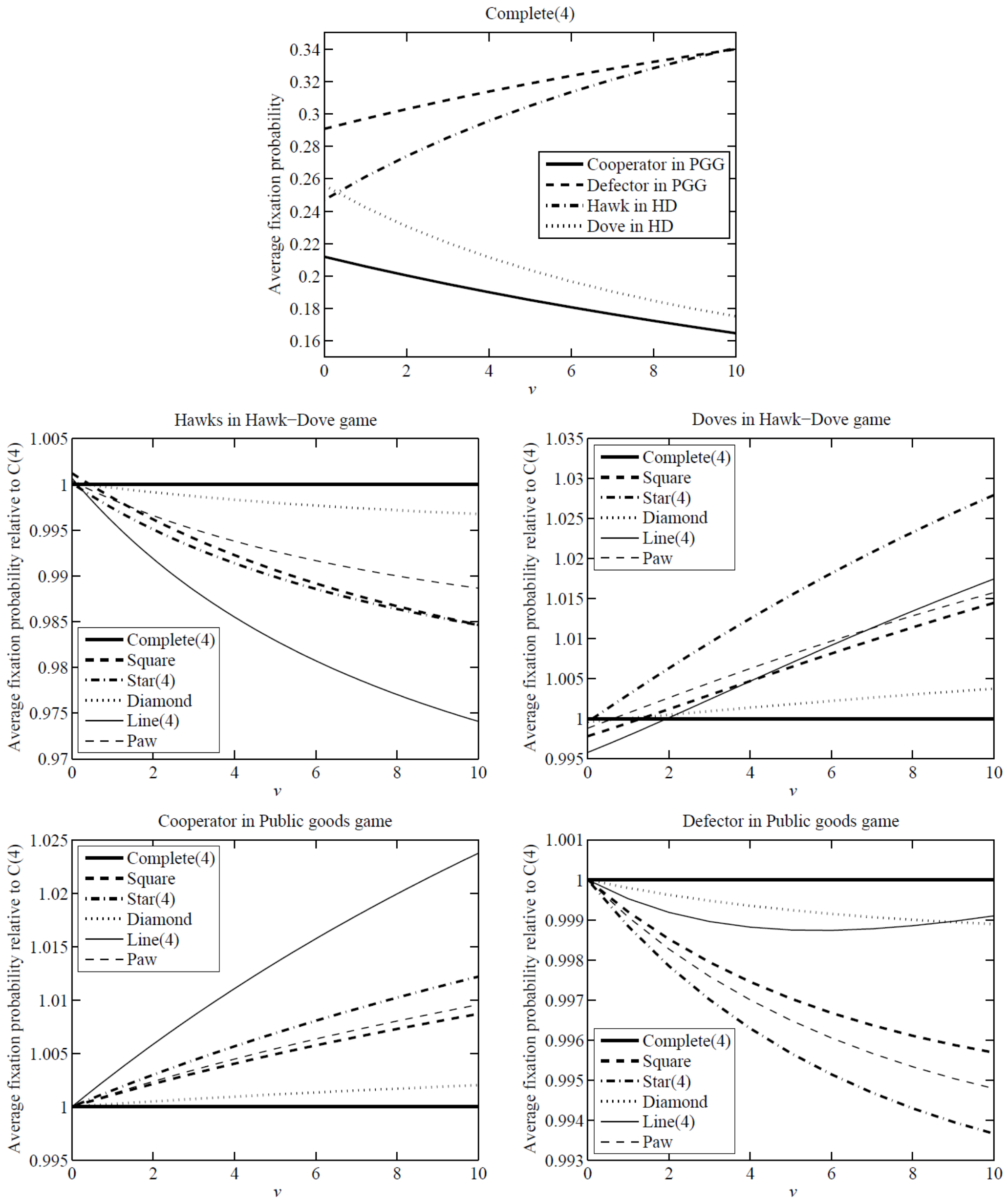


Figure 4.11: Dependence of the fixation probability on v for $h = 1$.

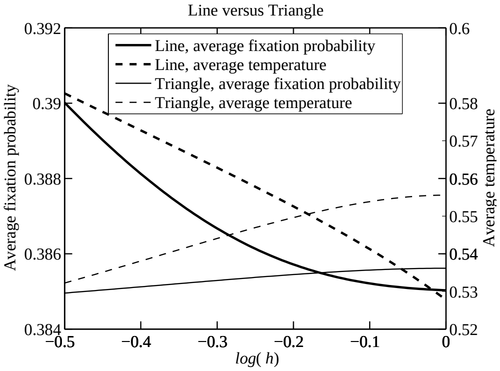


Figure 4.12: Dependence of the fixation probability on the graph.

The territorial raider model is set up in a way that given any graph structure and any multi-player game, one can automatically generate a system of linear equations yielding fixation probabilities. The results for graphs on 3 and 4 vertices are shown in this chapter. The results for graphs on more vertices can theoretically be obtained in a similar fashion. For some highly symmetrical classes of graphs (such as complete graphs, or stars), the analysis can still be performed even for large graphs. However, the system of linear equations grows exponentially with the number of vertices [see 13, for similar scenario] and the number of possible graphs grows even faster [35, p. 240]. It is difficult to say where the exact limits of these brute force numerical methods lie, however, the methods we used seemed to manage around 10 vertices before becoming cumbersomely slow. Rewriting the code underlying the numerical methods more efficiently should push this limit higher. The alternative to using brute force numerical methods would be to run multi-agent simulations. For this approach, [92] showed that, in the fixed fitness case, for a 100 vertex graph it took around 4000 seconds to compute the fixation probability. In the territorial raider model, due to the extra computation required for calculating the fitness, it would be reasonable to assume that it would take around this much time for a 25 to 30 vertex graph. With more efficient and advanced programming methods this should reduce the time even further thereby allowing larger populations sizes to be considered. Using multi-agent simulations would help understand how these results generalise to more general networks. Due to the small size of the current networks considered, it is difficult to say whether a given strategy would do better or worse on a larger network. However, we expect certain fundamental relationships such as that between the fixation probability and mean temperature, and the fixation probability and the game parameters to hold. This is in particular due to the consistency shown by these relationships for the different graphs considered.

The two games consider here, Hawk-Dove and the Public Goods game, can be said to represent cooperative dilemmas, with the cooperative strategies being Dove and Cooperate, respectively. In the territorial raider model, for the cases shown, the cooperative strategies generally do poorly. For the Public Goods game, the fixation probability of a single Cooperator (Defector) is always less (more) than $1/N$. Similarly, for the Hawk-Dove game, the fixation probability for a single Hawk is often greater than $1/N$, although it can fall below this value for small v. The fixation probability of a single Dove is often less than $1/N$, although it can climb above this value for small v. One reason for this is that the Invasion process, like birth-death processes in general, does not favour cooperation [see e.g. 70]. Thus it may be that cooperation is generally disfavoured in the Public Goods game. For the Hawk-Dove game, an important factor could be the small size of the graphs used, which means that in turn the groups formed remain small. Large groups will tend to disfavour Hawks, as all but one Hawk in any group incurs a cost. Thus for larger graphs, more cooperative behaviour may be obtained, in the form of relatively higher fixation probabilities for Doves as opposed to Hawks.

The territorial raider model illustrates how to calculate the fitness of an individual receives more realistically in comparison to, for example, games on graphs [70] that simply aggregates the pairwise payoffs to calculate the fitness. The problem with the latter approach is that it assumes an individual spends the same amount of time with all the individuals it can interact with. The territorial raider model addresses this issue by accounting for the proportion of time that individuals spend in the same place i.e. individuals only interact with one another if they are present in the same place at the same time. Furthermore, it also highlights the fact that individuals can be alone and, therefore, this situation needs to be accounted for. Note that this approach used by the territorial model is only one possibility that is available within the Broom-Rychtář framework.

The different graphs in the model here can be considered to represent different ways in which biological territories overlap. Alternatively the graphs can represent distinct social relationships within a group. As mentioned above, mean temperature seems to be a more important factor than the specific structure. In the biological context, this represents a measure of interaction between the individuals within the population. High mean temperature corresponds to highly mobile individuals which interact potentially in larger groups than when the mean temperature is low. This provides a natural measure of the strength of the effect of a particular game in a population. In addition to that, temperatures can be estimated in real populations, as long as the meetings between individuals in groups can be reliably recorded, so that the frequency of the formation of different groups can be estimated. It would be of great interest to work out the temperatures in various real population scenarios, and to ascertain how accurate our general conclusions are.

Chapter 5

Generalized Territorial Raider Model

5.1 Introduction

The generalised territorial raider model is a population evolution model based on the BR framework and is an extension of the territorial raider model of chapter 4. In this model individuals are allowed to share the same territory and home, as opposed to each individual having a unique territory and home as seen in chapter 4. Individuals who have the same territory are said to be a subpopulation. The movement of the individuals are as before, such that they are allowed one movement within their territory before returning home and the proportion of time spent at home is controlled by the home fidelity parameter. The fitness and dynamics are also determined as before. For fitness, the individuals have multiplayer interactions, though, the only game considered here is the public goods game. These interactions take place between replacement events that occur between discrete time points. For the dynamics, the complete set of standard evolutionary dynamics given in Table 4.2 (pg. 91) are considered, before, only the BDB dynamics was considered. For each of these dynamics, the fixation probability is calculated to measure the relative success between cooperators and defectors in the multiplayer public goods game that takes place on various different population structures.

This chapter uses the generalized territorial raider to study whether cooperation can evolve, i.e. cooperators have a higher fixation probability than cooperators. It was previously shown, in the territorial raider model, that the defectors always did better than the cooperators. One of the reasons could be due to the structure. In [66], several rules were identified that allow cooperation to evolve, one of which was a population structure that allows cooperators to have more frequent interactions, particularly when hubs or clusters of cooperators can form [91]. This in turn made them resistant to exploitation by defectors [70, 86]. Considering subpopulations within the context of the territorial raider model will allow such hubs or clusters to form. Another reason could be the dynamics used. In [70] showed that death-birth or birth-death dynamics with selection on the second event, i.e BDD or DBB, promotes cooperation but not when selection happens in the first event. Therefore, in this chapter all the standard dynamics are considered to see which ones allow cooperation to evolve. Any new notation used in this chapter is given in Table 5.1.

The main difference between the territorial raider model and the generalised territorial raider model is that the latter allows individuals to share the same territory. In the former case, increasing the home fidelity parameter implied that individuals spent more time alone. In the latter case, this would now mean that individuals spend more time interacting with individuals who are part of the same subpopulation. It is this effect that is investigated to see whether it can help the evolution of cooperation.

Notation	*Definition*	*Description*
$\mathcal{Q}_m$	$\subset \{1, 2, \ldots, N\}$	Subpopulation of individuals.
$T_{\mathcal{Q}_m}$	$= \sum_{i \in \mathcal{N} \setminus \mathcal{Q}_m} \sum_{j \in \mathcal{Q}_m} w_{ij}$	Strict subpopulation temperature.

Table 5.1: New notation used in the chapter.

5.2 The Model

5.2.1 The population structure and distribution

In this section the territorial raider model (Chapter 4) is generalised to include subpopulations, based upon their movement distributions. A *subpopulation* of individuals in the fully independent model is defined as a division of individuals from the main population that is *well-mixed* [16], which simply means that all of these individuals have an identical distribution over the places. In particular, for a subpopulation $\mathcal{Q}$ we have that $p_{im} = p_{jm}$ $\forall$ $i, j \in \mathcal{Q}$ and $m = 1, \ldots, M$.

For simplicity it will be assumed that individuals move as they do in the territorial raider model. Thus a population of N individuals is divided into M non-overlapping subpopulations $\mathcal{Q}_1, \ldots, \mathcal{Q}_M$ where $|\mathcal{Q}_m| \geq 0$ such that $N = \sum_m |\mathcal{Q}_m|$. The individuals in subpopulation $\mathcal{Q}_m$ are assumed to treat place P_m as their home place, so that there is a one-to-one correspondence between subpopulations and places. However, subpopulations are allowed to be empty and, therefore, places in which no individuals reside can exist. As in the territorial raider model, the movement probabilities of the individuals are governed by the home fidelity h (see Section 4.3.1 pg. 93). In particular, a subpopulation $\mathcal{Q}_m$ that can visit d neighbouring places will stay in home place P_m with probability $h/(h+d)$ or move to one of its neighbouring places with probability $1/(h+d)$. Note that when there is one individual in each subpopulation, that is $|\mathcal{Q}_m| = 1 \; \forall m$, the territorial raider model is obtained. This information can be visually represented in two different ways as shown in Figure 5.1, which includes a graph whose vertices represent both subpopulations and places.

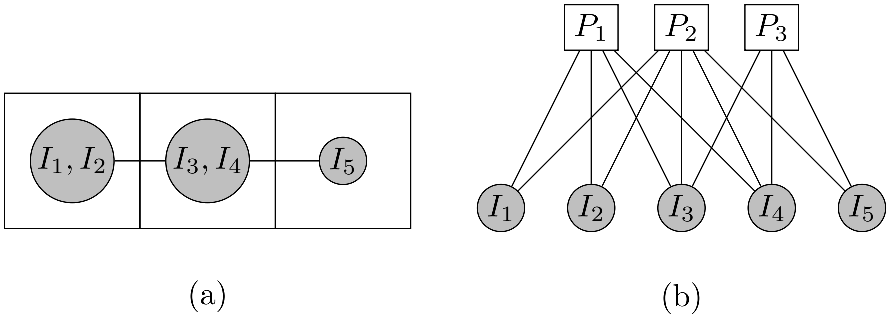


Figure 5.1: The territorial raider model with subpopulations. (a) Individuals that are members of subpopulation $\mathcal{Q}_m$ live in place P_m but can visit neighbouring places. The territory of subpopulation $\{I_1, I_2\}$ consists of places P_1 and P_2, the territory of subpopulation $\{I_3, I_4\}$ consists of places P_1, P_2 and P_3, the territory of subpopulation $\{I_5\}$ consists of P_2 and P_3. (b) An alternative visualization as multiplayer interactions on a bi-partite graph where individuals and places are clearly separated.

In this chapter only complete graphs will be considered. To indicate the number of nodes and size of each subpopulation at each node, one of the following naming conventions will be used. If there are subpopulations of different sizes, then a list with the size of each subpopulation will be used. For example, 2-2-2-0 implies that there are 3 subpopulations of size 2 and 1 of size 0; and 6-6-3-1 implies that there are 2 subpopulation of size 6, 1 of size 3 and 1 of size 1. On the other hand, if all the subpopulations are of the same size then (M, δ) will be used where M, as mentioned earlier, is the number of subpopulations and δ is the size of each subpopulation.

5.2.2 Fitness

The fitness will be calculated as in the territorial raider model and focuses on the multiplayer public goods game as defined using the reduced parameters (see Section 4.3.2 pg. 95). This means that the fitness contribution only depends upon the individual itself and the group of individuals that it is interacting with.

5.2.3 Evolutionary dynamics

The replacement weights are calculated as in the territorial raider model (see Section 4.3.3 pg. 98). That is, the replacement weight contributions depend only on the the birth individual, the death individual and the group interactions between them.

In this chapter, all the standard dynamics as defined in Table 4.2 (pg. 91) have been considered. However, in terms of presenting the results, only DB dynamics have been used. This is because the results for BDB and DBD are identical (as are those for BDD and DBB), because the replacement structure **W** is symmetric and doubly stochastic, so whether birth or death occurs first is irrelevant. Furthermore, the LB and LD dynamics are equivalent to the BDB and DBD dynamics, respectively, because **W** is isothermal (see Section 2.5.1 pg. 55).

Concepts of temperature

In the territorial raider model the concept of the temperature of an individual was given as the likelihood of an individual being replaced. This is developed further here.

The original definition given in [52] states that the temperature of a vertex of an evolutionary graph measures how likely an individual occupying a particular vertex is to be replaced by another individual's offspring. [54] extended this definition and introduced the out temperature of a vertex of an evolutionary graph to measure how likely the offspring of the individual occupying that vertex will replace another individual. These definitions of the *in* and *out* temperatures of individual I_n for an evolutionary graph $\mathbf{W}$ are respectively defined as follows

$$T_n^- = \sum_i w_{in} \quad \text{and} \quad T_n^+ = \sum_i w_{ni}. \tag{5.1}$$

In general, the in and out temperatures can be different. However, **W** is doubly stochastic and symmetric and, therefore, the in and out temperatures are identical. Thereby, the definition of the in temperature is used and is simply referred to as the temperature.

An alternative version of the definition of temperature is the *strict* temperature that measures how often an individual is likely to be replaced by other individuals excluding itself. The strict temperature of individual I_n for an evolutionary graph $\mathbf{W}$ is given by

$$T_n = \sum_{i \neq n} w_{in} = 1 - w_{nn}. \tag{5.2}$$

The definition of strict temperature can be extended to subpopulations to give the strict subpopulation temperature. This measures how likely an individual in subpopulation $\mathcal{Q}_m$ is to be replaced by an individual in another subpopulation. Clearly all individuals in a subpopulation have the same temperature (for any of the temperature definitions), since they all have the same movement distribution. The strict subpopulation temperature is calculated by summing all weights w_{ij} such that I_i is not part of subpopulation $\mathcal{Q}_m$ and I_j is part of subpopulation $\mathcal{Q}_m$ giving

$$T_{\mathcal{Q}_m} = \sum_{i \in \mathcal{N} \setminus \mathcal{Q}_m} \sum_{j \in \mathcal{Q}_m} w_{ij}. \tag{5.3}$$

This means that if there is only one subpopulation then its strict subpopulation temperature is 0 by definition, that is, $T_{\mathcal{Q}_m} = 0$ if $\mathcal{Q}_m = \mathcal{N}$.

A strategy introduced in one subpopulation can spread throughout the population because $\mathbf{W}$ is strongly connected. This implies that if there is more that one non-empty subpopulation then the strict subpopulation temperature is non-zero for all non-empty subpopulations, that is, $T_{\mathcal{Q}_m} > 0$ if $|\mathcal{Q}_m| > 0$. The mean strict subpopulation temperature is used to measure the likelihood of the individuals in a subpopulations being replaced by an individual from another subpopulation. The definition of the means strict subpopulation temperature is given by

$$\langle T_{Q_m} \rangle = \frac{1}{N} \sum_{m=1}^{M} |\mathcal{Q}_m| T_{\mathcal{Q}_m}. \tag{5.4}$$

Note that the means strict subpopulation temperature also indicates how connected the subpopulations are with one another.

5.2.4 Fixation probability

The fixation probability is calculated as in the territorial raider model (see Section 4.3.4 pg. 99). However, an arithmetic mean of the fixation probabilities is taken instead of using the temperature weighted fixation probabilities as the difference between the two means is insignificant.

5.3 Results: Cooperation in generalized territorial raider models

This section studies the effect that different model parameters have on the evolution of cooperation. For models investigating the evolution of cooperation using evolutionary graph theory, both the evolution and interaction of individuals are dictated by a fixed structure, following games with a fixed number of players (almost always two). In the generalized territorial raider model the replacement structure emerges from the interactions between individuals, involving games with a varying number of players, and therefore gives a different perspective on the evolution of cooperation.

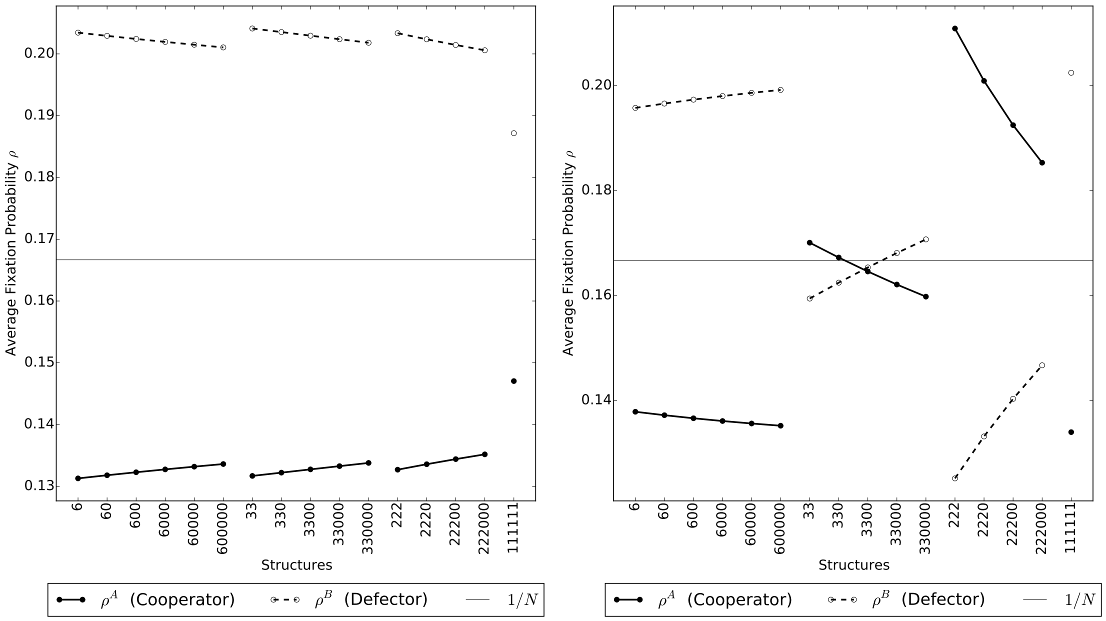


Figure 5.2: Comparing different complete structures for the public goods game. Each number indicates a subpopulation of a certain density e.g. 6-0 is a complete structure with 2 subpopulations of size 6 and 0 respectively. In each case the parameters are $r = 30, v = 10$ and $h = 30$. It is seen that in the first figure for the DBD dynamics, cooperators perform poorly in all cases. In the second figure, cooperators do better for small groups (greater than one). Increasing the number of empty places is beneficial for defectors.

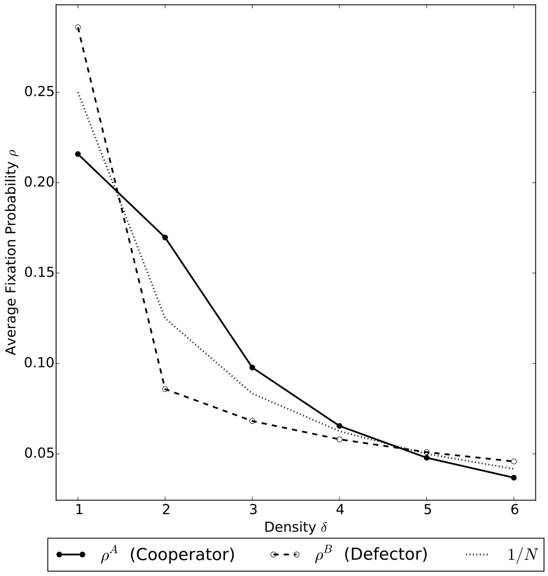


Figure 5.3: Public goods game plot for the complete graph with 4 subpopulations each having size (or density) δ. The game parameters are set to $r = 30$ and $v = 11$, the movement parameters are set to $h = 30$ and dynamics used are DBB. As in Figure 5.2, cooperators evolve better in small groups (larger than 1), namely groups of size two and three, with a small advantage for groups of size four.

5.3.1 The effect of the dynamics

For evolutionary graph theory models, cooperation is favoured when using DBB or BDD dynamics, but not DBD or BDB dynamics, if the structure allows a cluster of cooperators to form (see [70]). This is consistent with territorial raider model (Chapter 4) that studied the effect of BDB dynamics on the public goods game and cooperators generally performed poorly. It was shown that defectors dominate regardless of the structure of the population and the game parameters. The public goods game can now be revisited with more flexibility both in terms of the dynamics and the structure of the population.

For DBD dynamics, the defectors do better than cooperators regardless of the population structure. However, for DBB dynamics, cooperators are favoured over defectors for certain population structures. In particular, these structures that favour cooperators contain small subpopulations, ideally of two individuals. This is seen in Figure 5.2, where the fixation probability is plotted against different complete population structures for the DBD and DBB dynamics. For example, for the complete structure 2-2-2 where there are 3 subpopulations of size 2, the cooperators outperform defectors by a large amount.

To understand why this is the case, consider a population of two individuals where one individual is of type A and the other type B. Within such a population, the cooperative type A will be less fit than the selfish type B. For DBD dynamics, the least fit individual is most likely to be chosen for death and the fixation probability is proportional to the fitness of the individual. This means that a type A individual has a low fixation probability compared to a type B individual. However, when using DBB dynamics, one of the two individuals is randomly chosen for death and immediately replaced by the offspring of the other individual. This means that regardless of the fitness of the individual, each type will fixate with probability 1/2. For sufficiently high home fidelity parameter h, individuals primarily interact with their groupmates. Therefore, in such a population where there exists a subpopulation of two individuals, a cluster of two cooperators is more likely to form when using DBB dynamics. This cluster of cooperators has a fitness larger than that of a cluster of defectors, provided that $v > 1$, thereby establishing a stronghold against defectors. In fact, a subpopulation of larger than two individuals can establish a stronghold against defectors as shown in Figure 5.3. Here the fixation probability is plotted against a complete structure with four subpopulations that each have size ranging from 1 to 6. Subpopulations of size two are best for cooperation, with their advantage over defectors declining as the size of the subpopulation decreases. Given the parameters used, subpopulations of two to four cooperators can successfully resist invasion, but larger subpopulations cannot.

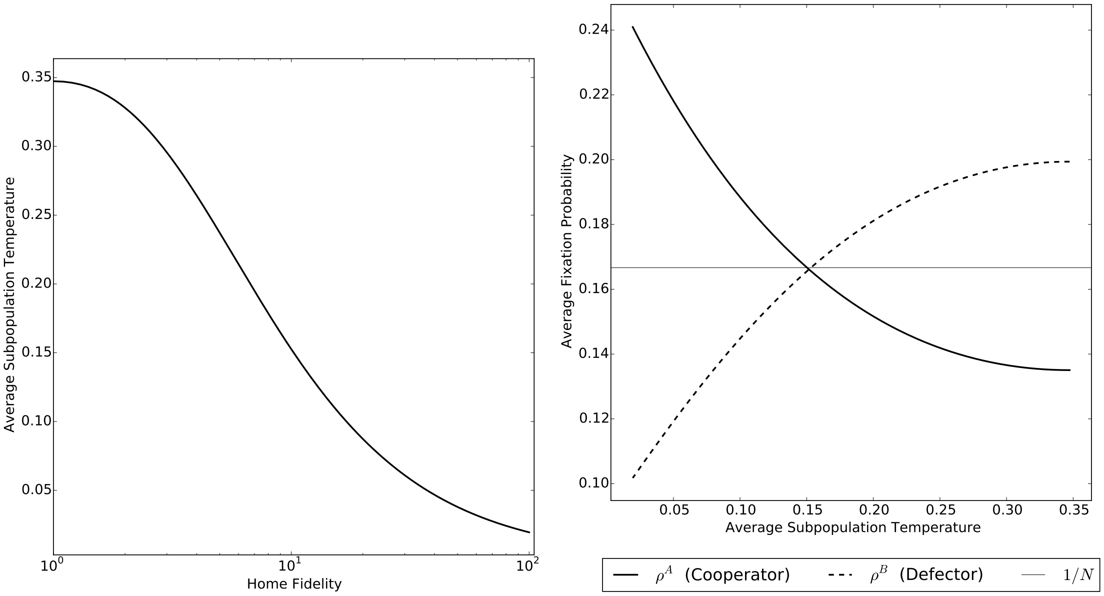


Figure 5.4: The figure on the left hand side plots the mean subpopulation temperature against the home fidelity h for a complete population structure with 3 subpopulations of size 2 each. The figure on the right then plots the fixation probabilities against these values of the mean subpopulation temperature where $r = 30$ and $v = 10$ for the public goods game, and the dynamics used are DBB. In particular, notice that the fixation probability of the cooperators is decreasing with the mean subpopulation temperature.

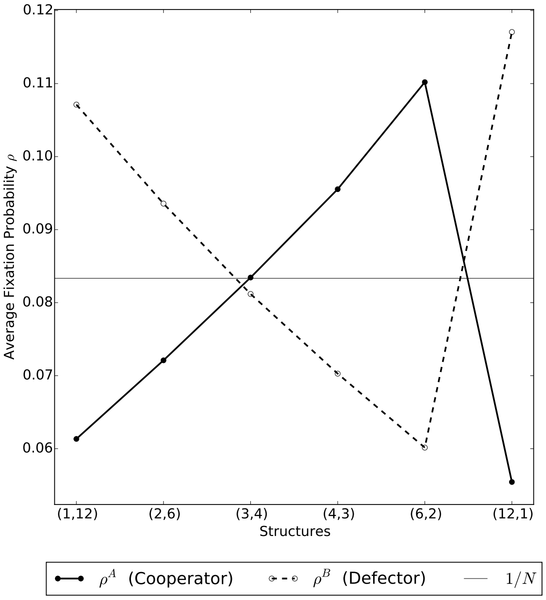


Figure 5.5: Comparing different population structures for the public goods game with various complete graphs for a population size of 12 where (1,12) means there is 1 subpopulation with 12 individuals, (2,6) means there are 2 subpopulations with 6 individuals and so on. The parameters are set to $r = 30$ and $v = 10$, the dynamics used are DBB and for home fidelity $h = 30$.

5.3.2 The effect of the temperature

In the territorial raider model, the strict temperature and mean group size were both shown to be strongly correlated with the fixation probability, with the effect of the former shown to be stronger (see Figure 4.9 pg. 106). This chapter therefore focuses on the temperature, namely the strict subpopulation temperature. Note that in the territorial raider model there is one-to-one correspondence between individuals and places, which implies that the strict temperature and strict subpopulation temperature are identical, but this is not the case for the generalized territorial raider model.

The individual temperature is a measure of how often an individual interacts with other individuals including those who are part of the same subpopulation; thus an individual may have a high temperature but that does not mean it is interacting with individuals from other subpopulations. In particular whenever individuals are not alone very often, this temperature does not vary so much between different individuals, and so is not a useful concept for when there are non-trivial subgroups. The strict subpopulation temperature, on the other hand, considers interactions with individuals only from other subpopulations, and thus can be very variable. It will be shown that this temperature is a good predictor of important population properties.

The mean strict subpopulation temperature decreases when home fidelity increases as shown on the left hand side plot in Figure 5.4. This is because the individuals are more likely to remain on their home place than visit another place as home fidelity increases, therefore reducing interactions with other subpopulations, and in particular the probability that a member of one subpopulation replaces a member of another at any given time.

In the territorial raider model it was shown that for BDB dynamics for structures where each subpopulation is of size one, there was a linear relationship between the strict (subpopulation) temperature and the fixation probability, with the higher the temperature, the stronger the effect of selection (see Figure 4.10 pg. 109). This was investigated for DBB dynamics and found that there is an opposite linear effect, which is consistent with [54] who showed that the DBB dynamics suppresses the effect of selection the most for the complete graph. Note that this relationship only holds for relatively weak selection, and we can reverse the relationship (and make it non-linear) by increasing the value of the reward.

To promote cooperation a structure involving a subpopulation of size at least two is required. However, whether these structures promote cooperation or not also depends upon the base fitness and reward, and so it is assumed that the base fitness and reward are sufficiently large for this to be the case (this is further investigated in Section 5.3.4). In this case, decreasing the temperature by increasing the home fidelity promotes cooperation. In particular, the relationship between the mean fixation probability of cooperators and the mean strict subpopulation temperature

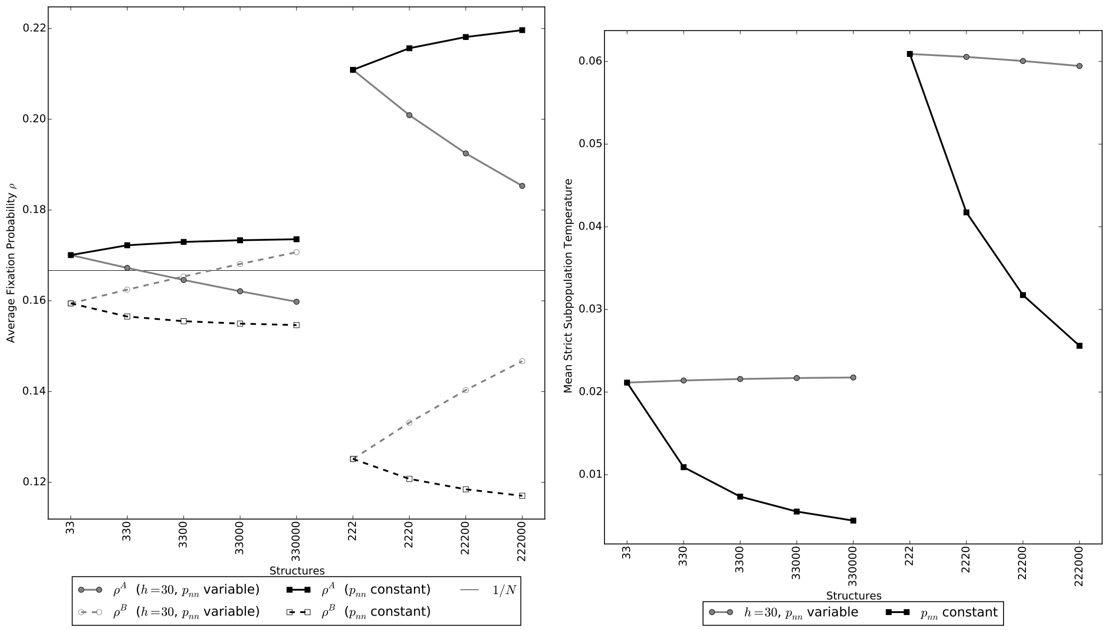


Figure 5.6: The figure on the left shows the effect of compensating for empty places by increasing the home fidelity such that the probability of staying in their home place, p_{nn}, remains the same. We start at $h = 30$ for the 3-3 and 2-2-2 structures. As an empty place is added, h is increased so that $p_{nn} = 30/31$ for the 3-3-0, …, 3-3-0-0-0-0 structures and $p_{nn} = 30/32$ for 2-2-2-0, …, 2-2-2-0-0-0 structures. In all cases $r = 30$ and $v = 10$. We can see that after compensating for the above effect, the influence of introducing empty places is both reversed and weakened. The figure on the right shows the mean strict subpopulation temperature dropping off when we compensate for the empty places by increasing the home fidelity such that p_{nn} remains the same.

is negative and nonlinear as shown in Figure 5.4. The nonlinearity arises not only from the nonlinear payoff function of the public good game, but also from the fact that there exists a subpopulation that has size at least two. For cooperators, the mean fixation probability is negatively correlated with the mean strict subpopulation temperature because the mean strict subpopulation temperature is highest when home fidelity is lowest, when cooperators cannot separate themselves from the population and form clusters, consequently defection evolves. On the other hand, for low mean strict subpopulation temperature, and so high home fidelity, it is easier to form clusters of cooperators that allows cooperation to evolve. This kind of behaviour is also evident in Figures 5.2 and 5.5.

5.3.3 The effect of the number of places

In the territorial raider model, each individual had their home place and there were no empty places (non home places) that individuals could visit (see Figure 4.1 pg. 95). In the generalized territorial raider model, individuals can visit non home places and therefore the effect this has on the evolution of cooperation is investigated.

As seen in Figure 5.2, increasing the number of empty places that subpopulations can visit reduces, whilst keeping all other parameters constant, makes it more difficult for cooperation to evolve. In particular, this effect is prominent for structures where cooperators were initially doing well. For example, for the structure 2-2-2 where the cooperators do best, increasing the number of places significantly reduces their fixation probability whilst increasing that of the defectors. Here increasing the number of places acts in the same way as decreasing the home fidelity, decreasing the amount of time an individual spends in its home place with members of its subpopulation. Thus the amount of time an individual spends alone or with individuals not from its subpopulation increases, so that the overall fitness of a cooperative subpopulation will decrease (they still pay a cost but do not receive a benefit when alone). In terms of the dynamics, spending more time alone would increase the effect of selection in DBB dynamics because an individual with higher fitness randomly chosen for death is more likely to be replaced by its own offspring, which affects the cooperators adversely. A cooperative subpopulation will also have lower fitness because its members are more likely to interact with individuals from other subpopulations, therefore exposing them to defectors. The increased interaction between individuals will also increase the effect of selection in DBB dynamics because an individual with higher fitness randomly chosen for death is less likely to be replaced by an individual with lower fitness in the same subpopulation.

The increase in the number of places can be compensated for by increasing the home fidelity, so that individuals stay in their home place with the same probability. This has the effect of decreasing the mean strict subpopulation temperature as individuals are more likely to spend time with members of their subpopulation. This is shown in Figure 5.6, where it is seen that the effect of adding empty places is now reversed, although the strength of this reverse effect is weak.

5.3.4 The effect of a large home fidelity

Consider a well-mixed population of M subpopulations each containing L individuals, so that $N = ML$, as described in Section 5.2.1, where h is very large. Consequently, the probability of group $\mathcal{G}$ forming, $\chi(m, \mathcal{G})$, is approximately 1 if $\mathcal{G} = \mathcal{Q}_m$, and is approximately 0 otherwise. Thus the fitness of an individual can be evaluated assuming that we have a group containing precisely all individuals from its subpopulation with probability 1. Due to the symmetric nature of a population in the generalized territorial raider model, the weights for any two individuals in the same subpopulation will be the same, as will the weights for any two members of different subpopulations. Denoting the latter as w_O, which will be small, such that $w_{ij} = w_O$ when I_i and I_j are not in the same subpopulation, and $w_{ij} = w_I \approx [1-(M-1)Lw_O]/(L-1)$ otherwise, with the probability of self-replacement negligible.

It follows that only replacements within subpopulations will happen, except very rarely. Thus it can be assumed that the battle within any mixed subpopulation of type A and type B individuals will be resolved with fixation of one type or the other before any new mixed subpopulation appears.

A two stage process is considered. Firstly, a new mixed group appears. This occurs rarely, through the invasion of a type A cooperator into a defector subpopulation, or a type B defector into a cooperator subpopulation. Assuming that there are currently $M_A(M_B = M - M_A)$ type A (B) subpopulations, such a transition happens with probability

$$p_{AI} = \frac{M_B}{M}\frac{M_A L w_O F_L(A)}{(L-1)w_I F_L(B) + O(w_O)} \tag{5.5}$$

of a type A into a type B subpopulation, or

$$p_{BI} = \frac{M_A}{M}\frac{M_B L w_O F_L(B)}{(L-1)w_I F_L(A) + O(w_O)} \tag{5.6}$$

of a type B into a type A subpopulation. The terms $F_L(A)$ and $F_L(B)$ are the fitnesses of type A and B individuals within their own subpopulations, and the terms $O(w_O)$ are of the order of w_O, and so small. Let $x = v/[r(L-1)]$ then the ratio of the two expressions in equations (5.5) and (5.6), and thus the relative frequency that the new invasions happen, is thus

$$\frac{p_{AI}}{p_{BI}} \approx \left(\frac{F_L(A)}{F_L(B)}\right)^2 = \left(1 + \frac{v-1}{r}\right)^2 \approx (1+(L-1)x)^2 \tag{5.7}$$

for large v and r.

The second process considers fixation within a well-mixed group of size L. Following [41], this is given by

$$x_i = \frac{1 + \sum_{j=1}^{i-1}\prod_{k=1}^{j}\frac{\delta_k}{\beta_k}}{1 + \sum_{j=1}^{L-1}\prod_{k=1}^{j}\frac{\delta_k}{\beta_k}}, \tag{5.8}$$

where x_i is the fixation probability of i type A individuals within a population of size L. Here β_k (δ_k) is the probability that the next event is the replacement of a type B (A) by a type A (B), when the number of type A is k. These probabilities are given by

$$\beta_k = \frac{k(L-k)}{L}\frac{r + \frac{(k-1)v}{L-1} - 1}{(L-1)r + ((L-k-1)k + k(k-1))\frac{v}{L-1} - k}. \tag{5.9}$$

$$\delta_k = \frac{k(L-k)}{L} \frac{r + \frac{kv}{L-1}}{(L-1)r + ((L-k)k + (k-1)^2)\frac{v}{L-1} - (k-1)}, \tag{5.10}$$

For sufficiently large r, the following is obtained

$$\frac{\delta_k}{\beta_k} \approx \frac{1+kx}{1+(k-1)x} f_k(x), \tag{5.11}$$

where

$$f_k(x) = \frac{L-1+(L-2)kx}{L-1+((L-2)k+1)x} < 1. \tag{5.12}$$

The fixation probability of a single type A individual in a group of type Bs is given by $\rho_{A,L} = x_1$, and the fixation probability of a single type B individual in a group of type As is $\rho_{B,L} = 1 - x_{L-1}$. This gives

$$\frac{\rho_{B,L}}{\rho_{A,L}} = \prod_{k=1}^{L-1} \frac{\delta_k}{\beta_k} = \prod_{k=1}^{L-1} \frac{1+kx}{1+(k-1)x} f_k(x) = (1+(L-1)x) \prod_{k=1}^{L-1} f_k(x). \tag{5.13}$$

This implies that

$$\frac{p_{AI}}{p_{BI}} > \frac{\rho_{B,L}}{\rho_{A,L}}. \tag{5.14}$$

Following our assumptions, the population evolves following a succession of invasions of subpopulations either of type A cooperators by type B defectors or defectors by cooperators. The probability that the next such event will be the invasion of a defector by a cooperator is simply

$$\frac{p_{AI}\rho_{A,L}}{p_{AI}\rho_{A,L} + p_{BI}\rho_{B,L}} = \frac{r_S}{1+r_S}, \tag{5.15}$$

where $r_S = p_{AI}\rho_{A,L}/p_{BI}\rho_{B,L}$ is the *forward bias* (see Section 2.5.2 pg. 56) of cooperative groups within our population. For a single type A to fixate in the population it must first fixate within its group with probability $\rho_{A,L}$, after which, there is a competition between groups proceeding precisely as in a Moran process, so this gives

$$\rho_A = \rho_{A,L} \frac{1 - 1/r_S}{1 - (1/r_S)^M}, \tag{5.16}$$

with the equivalent expression for ρ_B,

$$\rho_B = \rho_{B,L} \frac{r_S - 1}{r_S^M - 1}. \tag{5.17}$$

It is clear from equation (5.14) that $r_S > 1$, so that ρ_A is greater than $\rho_{A,L}(1 - 1/r_S)$ for any M. Letting M become large means that $1/N = 1/ML$ will be less than ρ_A, but larger than ρ_B, so that $\rho_B < 1/N < \rho_A$ holds. This means that for sufficiently large h, r and v, cooperation evolves for any given subpopulation size L. Thus cooperation can potentially evolve for arbitrarily large subpopulations, although as shown previously, it is easier for smaller subpopulations.

5.4 Discussion

The territorial raider model has been developed to incorporate subpopulations. This is beneficial because the territorial raider model, represented in the bipartite graph in Figure 4.1 pg. 95, would require a vertex for every individual as well as an additional vertex for every available place. Now only a vertex per subpopulation is required, potentially allowing a small number of very large subpopulations to be considered, which would not have been possible previously.

This type of structure has been considered in a slightly different context, for example, the island- or community-structured populations of [104]. In this model interactions occur at multiple levels, interactions between community members being more common than those with non-community members where interaction occurs at multiple levels. Members of one community first play a public goods game and then join the members of another community and play a public goods game such that, at the highest level, the entire population plays a public goods game. This is in contrast to the generalized territorial raider model, where individuals only play a game if they are present in the same place at the same time. In the community structured populations, it was shown that cooperation can evolve when DBB dynamics are used and selection is weak within communities, which is consistent with the results in this chapter.

There are some differences between the generalized territorial raider model and a metapopulation model [51]. In the territorial raider model, each place is either a home to a subpopulation or not. This means that an individual can place its offspring in a place if there is already a subpopulation present there by replacing an individual in that subpopulation. In a metapopulation model, an offspring can be placed in a place regardless of whether a subpopulation is already present there or not, unless that place has reached peak capacity. Furthermore, individuals are allowed to migrate in a metapopulation model but not in the generalized territorial raider model. In the latter case, individuals are allowed to move to places in their territory but always return home, i.e. they do not migrate.

It is shown that the choice of dynamics is crucial, and that DBD (and BDB) dynamics would not allow cooperation to evolve, but that DBB (and BDD) would, which is consistent with [70]. Further, using the latter dynamics, the size and the level of isolation of the subpopulations is important, with the smaller the subpopulations and the greater the isolation, the greater the chance for cooperation to evolve. Unsurprisingly, the larger the level of reward v, the better the cooperators do. In particular, the larger the subpopulations, the larger the reward v required for cooperation to evolve; note that this is similar to the requirement that the benefit-to-cost ratio exceeds the average number of neighbours an individual has from [70].

The generalized territorial raider model improves on the territorial raider model in chapter 4 by allowing multiple individuals to have the same territory, who are then said to be part of the same subpopulation. This idea played a crucial role in the evolution of cooperation, which could not be achieved before, by allowing more effective cooperation between cooperators when they are part of the same subpopulation. Previously, individuals had their own unique territory and it was difficult to get two cooperating individuals to spend enough time with each other. Reducing the home fidelity parameter meant that individuals spent more time with one another but it was difficult to control with whom this time was spent with. However, in the generalized territorial raider model, increasing the home fidelity parameter means that individuals that are part of the same subpopulation spend more time with one another. Consequently, with either DBB or BDD dynamics, a cooperative subpopulation can form that allows cooperators to propagate throughout the population.

The results in this chapter only apply to complete graphs where each node represents a place where a subpopulation can reside. Heterogeneity was considered in terms of the size of each subpopulation present on each node, and it was shown that for large home fidelity cooperation can evolve for arbitrarily large subpopulations. In order to generalise these results to more general graphs, further study will have to be carried out on more heterogeneous graph structures. However, as is seen from Figure 5.4, the idea that strict subgroup temperature is important in explaining the level of cooperation that evolves, would hold for graphs in general. In particular, low (high) temperature helps promote the invasion of cooperators (defectors) such that higher temperatures allow cooperators to cluster more strongly and benefit more from cooperating with one another. The reason for this is that, with higher strict subgroup temperatures, the individuals are likely to interact locally within their subpopulation and, therefore, the global structure of the population will have a less substantial effect on the overall fixation probability.

Chapter 6

Markov Movement Model

6.1 Introduction

The Markov movement population evolution model is based on the BR framework. As the name suggests, the movement of the individuals is Markov such that they would decide to stay where they are or move depending upon the current interaction they had. The likelihood of staying is larger for a beneficial interaction. It is assumed that individuals have a unique home and are allowed to make a finite number of movements before returning home, called the exploration time. The topology of the places that individuals can visit is represented by a complete graph and therefore individuals can directly move from one place to another. The fitness of the individuals is impacted by the amount they move such that a cost is incurred for each movement made. In addition to this, the individuals have multiplayer interactions as governed by the multiplayer public good game. Movement and interactions are assumed to take place between successive discrete time points at which replacement events take place. The dynamics considered for the replacement events are the complete set of standard evolutionary dynamics given in Table 4.2 (pg. 91). The success of the cooperate and defect strategy in the multiplayer goods game will be studied by calculating the fixation probability of each type under various different assumptions and parameter values. Any new notation used in this chapter is given in Table 6.1.

The motivation behind the Markov movement model is to study whether cooperation can evolve in the mutliplayer public goods game, if individuals are allowed to make strategic movements. In this case, individuals make strategic movements by staying where they are if it is beneficial and moving away if not. Similar strategic movement was considered by [1, 2] but multiplayer interactions were not accounted for. Therefore, the Markov movement model aims to better understand how strategic movement can help cooperation evolve in the context of multiplayer interactions.

In the generalized territorial raider model of the previous chapter, the problem being studied is similar, i.e. the evolution of cooperation, but the mechanisms available to achieve this are different. In the generalized territorial raider model, the mechanism required is quite straightforward and requires subpopulations of individuals to spend more time with one another allowing clusters of cooperators to form. However, this mechanism is quite sensitive to the dynamics being used because a subpopulation cannot be colonized by cooperators if selection happens in the first event of birth-death or death-birth dynamics. On the other hand strategic movement is more realistic, and its superiority can be tested by checking its robustness to the dynamics being used.

Notation	*Definition*	*Description*
h_n	$\in [0,1]$	Probability that I_n stays.
α_n	$\in [0,1]$	*Staying propensity*: probability of I_n staying when alone.
C (D)		Cooperator (Defector) interactive strategy.
β_C (β_D)	$\in \mathbb{R}$	Benefit of being with cooperator (defector).
S	$\in (0,1)$	Sensitivity shown to group members.
R_n	≥ 0	Payoff to I_n.
λ	$\in [0, \min(R_n))$	Movement cost.
T	$\in \mathbb{Z}^+$	Exploration time.
C_α (D_α)		Cooperator (defector) with staying propensity α.
γ (δ)	$\in [0,1]$	Nash equilibrium staying propensity of cooperator (defector).

Table 6.1: New notation used in this chapter.

6.2 The model

6.2.1 The population structure and distribution

The (generalized) territorial raider model is a special case of the fully independent movement model, i.e. individuals move independently of time, history and the population. The movement of individuals is limited to their neighbourhood and exogenously controlled by the *home fidelity* parameter that measures how likely the individual is to remain in their home. A natural extension to this is to allow individual distributions to vary with time. A Markov model is considered based on the assumption that history dependence is Markov, that is, the current population distribution is only dependent upon the previous population distribution. In particular, the population distribution probability function (PDPF) given in equation (4.4, pg. 87) will simplify to

$$\pi_t(\mathbf{m}) = \sum_{\mathbf{m}_{<t}} p_t(\mathbf{m}|\mathbf{m}_{t-1}) P(\mathbf{m}_{<t}). \tag{6.1}$$

Individual movement with dependence only upon individual history

Assuming that an individual moves independently of the other individuals in the population but its current position is dependent upon its previous position, the individual distribution probability function (IDPF) given in equation (4.8, pg. 88) would then simplify to

$$\pi_{n,t}(m) = \sum_{m_{n,<t}} p_{n,t}(m|m_{n,t-1}) P(m_{n,<t}). \tag{6.2}$$

This expression can be rewritten using the $M \times M$ probability matrix $\mathbf{p}_{n,t} = [p_{n,t}(m_n|m_{n,t-1})]$ for $m_n, m_{n,t-1} = 1, \ldots, M$ as follows

$$\boldsymbol{\pi}_{n,t} = \boldsymbol{\pi}_{n,0} \prod_{k=1}^{t} \mathbf{p}_{n,k} \tag{6.3}$$

where $\boldsymbol{\pi}_{n,t} = [\pi_{n,t}(m)]_{m=1,\ldots,M}$. Furthermore, if it is assumed that there is time homogeneity, that is $\mathbf{p}_{n,t} = \mathbf{p}_n$ for all t, then this simplifies to

$$\boldsymbol{\pi}_{n,t} = \boldsymbol{\pi}_{n,0} \mathbf{p}_n^t. \tag{6.4}$$

In this case, assuming that $\mathbf{p}_n$ is irreducible and aperiodic for all n, then as $t \to \infty$ the IDPF $\boldsymbol{\pi}_{n,\infty}$ is stationary for all n. Essentially, this model is then equivalent to the fully independent movement model, which was considered in the models in the (generalized) territorial raider model and therefore will not be used in this chapter.

Individual movement with dependence on population history

Assuming that the individuals move to a new position independently of each other but dependent upon the current distribution of the whole population, the IDPF is then given by

$$\pi_{n,t}(m) = \sum_{\mathbf{m}_{<t}} p_{n,t}(m|\mathbf{m}_{t-1}) P(\mathbf{m}_{<t}). \tag{6.5}$$

In this chapter, this type of IDPF with the assumption that the individual transition probabilities are time homogeneous but dependent upon the previous group and previous position of the individuals, that is

$$p_n(m|m_{n,t-1}, \mathcal{G}_n(\mathbf{m}_{t-1})) = \begin{cases} h_n(\mathcal{G}_n(\mathbf{m}_{t-1})) & m = m_{n,t-1} \\ \frac{1-h_n(\mathcal{G}_n(\mathbf{m}_{t-1}))}{d} & m \neq m_{n,t-1} \end{cases} \tag{6.6}$$

where $h_n(\mathcal{G}_n(\mathbf{m}_{t-1}))$ denotes the staying probability of individual I_n and $N-1$ is the number of neighbouring places that an individual can move to in a complete graph where each node represents a place. The population is assumed to be of size N where each individuals has a home that they can return to such that every place is home to precisely one individual.

The staying probability $h_n(\mathcal{G}_n(\mathbf{m}_{t-1}))$ will depend upon the *staying propensity* α_n of individual I_n and the attractiveness of remaining in group $\mathcal{G}_n(\mathbf{m}_{t-1})$. The staying propensity α_n measures the likelihood that individual I_n will stay where it is, in particular, $h_n(\mathcal{G}_n(\mathbf{m}_{t-1})) = \alpha_n$ when I_n is alone ($\mathcal{G}_n(\mathbf{m}_{t-1}) = \{n\}$). The staying propensity is assumed to be one of the characteristics that makes up the type of an individual. However, when present in a group ($|\mathcal{G}_n(\mathbf{m}_{t-1})| > 1$), individual I_n would take into account the benefit of remaining in that group. The benefit β_i of group member I_i to others depends upon its *interactive strategy*, the second characteristic that makes up the type of an individual. It will be assumed that there are two interactive strategies, cooperate (C) and defect (D). The benefit function, β_i is then defined as follows

$$\beta_i = \begin{cases} \beta_C & \text{if } I_i \text{ is a cooperator,} \\ \beta_D & \text{if } I_i \text{ is a defector} \end{cases} \tag{6.7}$$

where β_C and β_D are the *benefits* of being with a cooperator and defector, respectively. The benefit of group $\mathcal{G}_n(\mathbf{m}_{t-1})$ to individual I_n is then defined as follows

$$\beta_{\mathcal{G}_n(\mathbf{m}_{t-1})\backslash\{n\}} = \sum_{i \in \mathcal{G}_n(\mathbf{m}_{t-1})\backslash\{n\}} \beta_i. \tag{6.8}$$

Finally, combining the effects of the staying propensity and the group benefit, in the rest of the chapter the staying probability is expressed as the following sigmoid function

$$h_n(\mathcal{G}_n(\mathbf{m}_{t-1})) = \frac{\alpha_n}{\alpha_n + (1-\alpha_n) S^{\beta_{\mathcal{G}_n(\mathbf{m}_{t-1})\backslash\{n\}}}} \tag{6.9}$$

where $0 < S < 1$ is the sensitivity shown to group members. So, for example, $S \to 0$ implies that I_n shows great sensitivity and would move away immediately if remaining in group $\mathcal{G}_n(\mathbf{m}_{t-1})$ is unattractive, which is the case when $\beta_{\mathcal{G}_n(\mathbf{m}_{t-1})\backslash\{n\}} < 0$. An alternative way of representing the $S \to 0$ limit involves the staying probability being defined using the following step function

$$h_n(\mathcal{G}_n(\mathbf{m}_{t-1})) = \begin{cases} 0 & |\mathcal{G}_n(\mathbf{m}_{t-1})| > 1 \text{ and } \beta_{\mathcal{G}_n(\mathbf{m}_{t-1})\backslash\{n\}} < 0, \\ \alpha_n & |\mathcal{G}_n(\mathbf{m}_{t-1})| = 1, \\ 1 & |\mathcal{G}_n(\mathbf{m}_{t-1})| > 1 \text{ and } \beta_{\mathcal{G}_n(\mathbf{m}_{t-1})\backslash\{n\}} \geq 0. \end{cases} \tag{6.10}$$

For example, if $\alpha_n = 0 \ \forall n$, $\beta_C = 0$ and $\beta_D < 0$ then the attractiveness of a group is completely determined by the presence or absence of defectors. An individual would therefore leave with probability 1 if a defector is present in the group. This was referred to as the ‘walk away’ strategy in [1].

6.2.2 Fitness

For the Markov movement model the mean fitness contribution given by equation (4.15, pg. 89) simplifies to

$$\bar{f}_{n,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} f_{n,t}(\mathbf{m}|\mathbf{m}_{<t}) p_t(\mathbf{m}|\mathbf{m}_{t-1}) P(\mathbf{m}_{<t}) \tag{6.11}$$

It will be assumed that the fitness contribution $f_{n,t}(\mathbf{m}|\mathbf{m}_{<t})$ of an individual depends upon (direct) group interactions and whether a movement has been made.

For the group interactions, the multiplayer public goods game as in Section 4.3.2 (pg. 95) will be considered. However, instead of dividing the payoffs by the cost K, they will be dividing by the background payoff R such that the reduced reward is given by $v = V/R$ and the reduced cost is given by $c = K/R$. This means that the base payoff has been normalised to 1 and the reward v and cost c are multiples of the base payoff. The cost cannot exceed 1 in order to prevent the fitness contribution from going negative (this is done for convenience of calculation; it is important that total fitness is not negative, and large costs could be dealt with, if necessary, by truncating the resulting total fitness at 0). The direct group interaction payoff functions are then defined as follows

$$R_n(\mathcal{G}_n(\mathbf{m})) = \begin{cases} 1 + \frac{|\mathcal{G}_n(\mathbf{m})|_C - 1}{|\mathcal{G}_n(\mathbf{m})| - 1} v - c & I_n \text{ cooperator and } |\mathcal{G}_n(\mathbf{m})| > 1, \\ 1 - c & I_n \text{ cooperator and } |\mathcal{G}_n(\mathbf{m})| = 1, \\ 1 + \frac{|\mathcal{G}_n(\mathbf{m})|_C}{|\mathcal{G}_n(\mathbf{m})| - 1} v & I_n \text{ defector and } |\mathcal{G}_n(\mathbf{m})| > 1, \\ 1 & I_n \text{ defector and } |\mathcal{G}_n(\mathbf{m})| = 1 \end{cases} \tag{6.12}$$

where $|\mathcal{G}|_C$ is the number of cooperators in group $\mathcal{G}$.

An individual will pay a cost of λ for every movement that it makes. The movement cost is chosen so that it does not exceed the direct group interaction payoff an individual receives (for the same reasons as for the cooperative cost c, and large movement costs could be similarly accommodated if necessary), that is $0 \leq \lambda < \min(R_n(\mathcal{G}_n(\mathbf{m})))$. The fitness contribution is then given by

$$f_n(m, \mathcal{G}_n(\mathbf{m})|m_{t-1}) = \begin{cases} R_n(\mathcal{G}_n(\mathbf{m})) - \lambda & m \neq m_{t-1}, \\ R_n(\mathcal{G}_n(\mathbf{m})) & m = m_{t-1}. \end{cases} \tag{6.13}$$

6.2.3 Evolutionary dynamics

For the Markov movement model the mean replacement weight contribution given by equation (4.21, pg. 90) simplifies to

$$\bar{u}_{i,j,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} u_{i,j,t}(\mathbf{m}|\mathbf{m}_{<t}) p_t(\mathbf{m}|\mathbf{m}_{t-1}) P(\mathbf{m}_{<t}). \tag{6.14}$$

It will be assumed that the replacement weight contribution will only depend upon the direct group. As in the territorial raider model (see Section 4.3.3 pg. 98), the replacement weight contribution will depend upon the amount of time spent with each individual. In particular, it is assumed that an individual spends an equal amount of time with each individual in the group excluding itself. However, if the individual is alone, then it effectively allocates all the time to itself. The replacement weight contribution function is then defined as follows

$$u_{i,j}(\mathcal{G}_i(\mathbf{m})) = \begin{cases} 1/|\mathcal{G}_i(\mathbf{m}) \setminus \{i\}| & i \neq j \text{ and } j \in \mathcal{G}_i(\mathbf{m}), \\ 0 & i \neq j \text{ and } j \notin \mathcal{G}_i(\mathbf{m}), \\ 1 & i = j \text{ and } |\mathcal{G}_i(\mathbf{m})| = 1, \\ 0 & i = j \text{ and } |\mathcal{G}_i(\mathbf{m})| > 1. \end{cases} \tag{6.15}$$

6.2.4 The evolutionary Markov chain

The evolution of the population can now be described in terms of a Markov chain. It will be assumed that there are only two types of individuals in the population, which are labelled A and B. What exactly makes a type A or B individual would depend upon its interactive strategy and staying propensity. For example, setting $A = C_{0.1}$ and $B = D_{0.5}$ means that type A is a cooperator with a staying propensity of 0.1 and type B is a defector with staying propensity 0.5, or setting $A = C_{0.1}$ and $B = C_{0.2}$ means that both types have the same behavioural strategy but different staying propensities. However, the important thing to note is that, at any one time, there are only two unique types A and B in the population. Since there are only two types in the population, the fixation probability is calculated in the same way as described in section 4.3.4 pg. 99. However, in this chapter an arithmetic mean of the fixation probabilities is used because there is an insignificant difference to the temperature weighted mean.

Simulating the evolutionary Markov chain

The method used in this chapter to calculate the fixation probability is a semi-analytic one where the fitnesses of individuals are found by simulation, and these results are then used to evolve the population using the evolutionary Markov chain, which results in a more accurate solution than simulating the whole process (the movement process is too complex to allow for a fully analytic solution).

In this model an *exploration time* T is selected, which is the number of steps an individual takes moving around the region before returning to its home place. Individuals start on their home place and are then allowed to move T times such that their fitness contribution is calculated for each of these movements; the total of these T fitness contributions gives their fitness for one simulation. The position of the individuals is then reset, that is, they return to their home place before the next simulation is run. Their average fitness for 10,000 simulations is used in the evolutionary Markov chain.

To calculate the replacement weights, individuals start on their home place and move only one time to determine their replacement weight. This represents individuals returning to their home place to reproduce, with individuals being replaced according to the corresponding local connections. This counts as one simulation and, before the next simulation is run, the position of the individuals is reset so they all start in their home place. The replacement weights are calculated exactly because they comprise only one movement. This involves calculating the probability that an individual is alone, which gives the self-replacement weight. The other replacement weights are simply 1 minus the self-replacement weight divided by $N-1$ because the probability of replacing the other individuals is the same for a complete graph.

The fitnesses and the replacement weights are all that is required to construct the transition probabilities of the evolutionary Markov chain. The transition probabilities are substituted into equation (1.6, pg. 29), given in its more general form here, to give the fixation probability of i type A mutants in a population of $N-i$ type B residents as follows

$$\rho_i^A = \frac{1+\sum_{j=1}^{i-1}\prod_{k=1}^{j}\frac{P_k^-}{P_k^+}}{1+\sum_{j=1}^{N-1}\prod_{k=1}^{j}\frac{P_k^-}{P_k^+}} \tag{6.16}$$

where P_k^- (P_k^+) is the backward (forward) transition probability for a state with k type A individuals. Note that this formula can easily be modified to find the fixation probability of type B individuals.

The advantage of such an approach is that the fixation probability can be calculated relatively quickly starting from any state. However, this approach necessarily requires that the population being modelled has individuals who can differ only in terms of their type. This is ensured by assuming that there is a complete population structure with N places such that each individual has their own home place.

6.3 Results

In this section the effect of the model parameters on the fixation probability are investigated. In particular, how the model parameters affect *assortment* is investigated, which is the mechanism that allows cooperation to evolve as shown in [26]. There is positive assortment between cooperators if they are more likely to interact with other cooperators than defectors. In the model considered here, this occurs due to an increase (decrease) in the time it takes for defectors (cooperators) to find cooperators. According to [24] the time to find cooperators should depend upon the density of the population and an individual's movement speed. In their model, N individuals pair up with one another to form a coalition such that the probability of a pair forming is exponentially distributed with rate μ, which is a function of N and the population density. The time to find cooperators in their model is essentially determined by the rate μ. There is a one-to-one correspondence between individuals and places and therefore the density remains constant; on the other hand, since a complete graph is considered, the movement speed is high as individuals can directly get from one place to another. Therefore, the time it takes to find cooperators is mostly determined by the staying propensity of the individuals', however, this relationship is not so straightforward as it is not globally controlled and the individuals may have different staying propensities (which are subject to the evolutionary process). This means that some individuals may find cooperators faster than others. The parameters used in the simulations are summarised in Table 6.2.

Apart from an individual's interactive strategy and staying propensity, all other parameters are considered to be fixed. Each individual inherits these two characteristics from its parent, and different interactive strategies or staying propensities are introduced into the population through mutations. Staying propensities can take any value $0.01m$ for $m = 1, \dots, 99$; this means that no individual moves all the time or never, and so makes some adjustment to their behaviour depending upon the group they are in. In particular, $\max(\alpha) = 0.99$; some movement is a necessary requirement otherwise the replacement weights would be zero and there would be no evolution within the population. In a real world setting, a minimum movement requirement can be explained by, for example, foraging behaviour where an individual searches its environment to find food and therefore needs to move in order to survive.

The mutations of these characteristics are sufficiently infrequent that the population is assumed to consist of a maximum of two types; resident and mutant, whose competition will result in fixation of one of the types before a new mutant appears. Two different scenarios are considered to account for the different mutation rates of each characteristic.

6.3.1 Scenario A: Interactive strategy mutations are rare

As previously stated, it is assumed that fixation happens much faster than new mutations arise. A mutation can result in a change of the interactive strategy and/ or the staying propensity. In this scenario, the mutation rate of an individual's interactive strategy is much slower than the rate of mutations that involve their staying propensity. Since it is much more likely that the staying propensity mutates than the interactive strategy does, once one of the interactive strategies (cooperate or defect) is removed from the population, it will be a long time before a new mutant involving this strategy appears. During this time, there will be a sequence of

Parameter Set	1	2	3	4	5	6
N	10	10	10	20	10	10
T	10	5	25	10	10	10
λ	Variable	Variable	Variable	Variable	0.20	0.20
c	0.04	0.04	0.04	0.04	0.04	0.09
v	0.40	0.40	0.40	0.4	Variable	Variable

Table 6.2: Parameters used for the simulations. The other parameters are fixed such that the population has a complete structure with each individual having its own home, $\beta_C = 1$, $\beta_D = -1$, $S = 0.03$ and the dynamics used are BDB.

contests among individuals with the same interactive strategy but different staying propensities and the population will eventually evolve to the point where all individuals have the same interactive strategy and are using a (strict) Nash equilibrium staying propensity (a strict Nash equilibrium propensity is one where the fixation probability is maximised and changing the staying propensity is disadvantageous). Eventually, a mutant with a different interactive strategy and staying propensity will appear, and the quantity of interest at this point is the fixation probability of this mutant type. It will be assumed that the staying propensity of the mutant can be different from the Nash equilibrium staying propensity of the resident population it is invading. The resident population will therefore be stable if it can resist invasion from a mutant using any staying propensity. Rather than considering any arbitrary mutant, the focus will be on the mutant most likely to invade, i.e. one maximising its fixation probability.

Cooperator residents are of the type C_{γ_R} where their Nash equilibrium staying propensity γ_R is the staying propensity where $a = b$ in the set

$$\left\{(a,b) : \rho_1^{C_a,C_b} = \max\left(\rho_1^{C_c,C_b} : c \in (0,1)\right) \text{ and } b \in (0,1)\right\}.$$

In this set all the points (a, b) are identified where a is the best response staying propensity of 1 individual of type C_a when playing against $N-1$ individual of type C_b, who are using some arbitrary staying propensity b. Therefore, at the point where $a = b$, C_a is a best response to itself, i.e. a Nash equilibrium.

A defector mutant is of the type D_{δ_M} where the staying propensity δ_M satisfies

$$\rho_1^{D_{\delta_M},C_{\gamma_R}} = \max\left(\rho_1^{D_c,C_{\gamma_R}} : c \in (0,1)\right).$$

Defector residents are of the type $D_{0.99}$ (i.e. in the equivalent terminology to the above $\delta_R = 0.99$) where their Nash equilibrium staying propensity is $\max(\alpha) = 0.99$ whenever the movement cost is greater than 0 because the only way for them to maximize their fixation probability is by moving as little as possible.

A cooperator mutant is of the type C_{γ_M} where the staying propensity γ_M satisfies

$$\rho_1^{C_{\gamma_M},D_{0.99}} = \max\left(\rho_1^{C_c,D_{0.99}} : c \in (0,1)\right).$$

The Nash equilibrium staying propensity of the resident cooperators γ_R is calculated as follows. The fixation probability of one individual of the type C_a against $N-1$ residents of the type C_b is calculated for all values of a in the range $[\max(0.01, b-0.09), \min(b+0.09, 0.99)]$, and the value of a that gives the highest fixation probability is picked. Note that using a wider range of values for a gives the same result so this range is used for efficiency. The $N-1$ residents then use the staying propensity a that was picked and this process is repeated several times. After around 20 repetitions, the staying propensity that gives the maximum fixation probability remains the same, that is, it is a (strict) Nash equilibrium because it is a best response to itself and any other strategy will be disadvantageous. Therefore, γ_R is set to the value of a obtained after 20 repetitions. It is hypothesized that there is only one solution to the Nash equilibrium staying propensity. The reason for this is that, as seen in Figure 6.1, the Nash equilibrium staying propensity of one type C_a against $N-1$ type C_b is relatively flat. This means that the Nash equilibrium staying propensity is predominantly determined by the movement cost λ regardless of what the other players are doing. Therefore, there is only one intersection point with the line $a = b$ as shown in Figure 6.1, which gives the Nash equilibrium staying propensity γ_R of resident cooperators.

The effect of the movement cost

In Figure 6.2 the effect of the movement cost is shown. In particular, it increases the time it takes to find cooperators by increasing the staying propensity, that is, $\gamma_R, \gamma_M, \delta_M$ are positively correlated with movement cost; the (partial) exception is resident defectors, which have a staying propensity of $\max(\alpha) = 0.99$ regardless of the movement cost.

For very low movement cost, both mutant types have a significantly lower staying propensity than the resident population that they are invading. They can therefore invade the resident population because they take less time to find cooperators.

For higher, but still low, movement costs, whilst mutant cooperators can still invade, mutant defectors cannot. Here the resident cooperators are better at preventing invasion even when $\delta_M < \gamma_R$ for some values of the movement cost. This is because the movement cost impacts the invading mutant defector more adversely than the resident cooperators, who on average leave and regroup less often than a defector who will be repeatedly deserted by its cooperator groupmates.

For intermediate movement costs, neither mutant type can invade. At this point, since $\delta_M > \gamma_R$, a mutant defector is slower at finding cooperators than the resident cooperators and

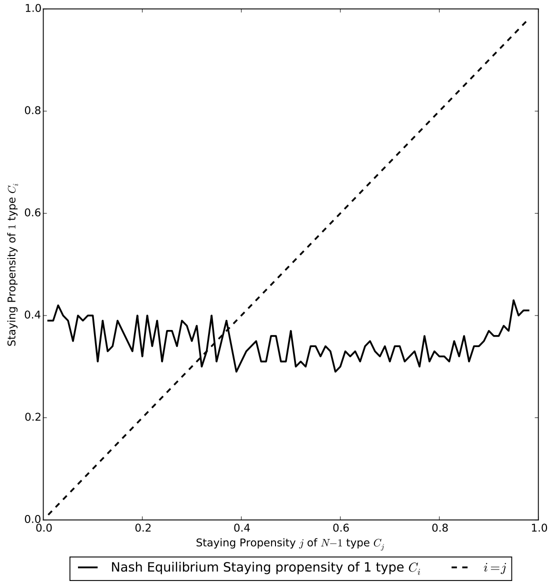


Figure 6.1: This plot shows the Nash equilibrium staying propensities for 1 type C_i individual playing against $N-1$ type C_j individuals. Parameter set 1 is used with $\lambda = 0.2$ and $i, j \in \{0.01, 0.02, \dots, 0.99\}$. The intersection point of the plots gives the cooperator resident Nash equilibrium staying propensity γ_R, which is somewhere between 0.3 and 0.4. This value is similar to the one obtained using the iterative method (see Figure 6.2). The values from the current figure are approximate only because of the jagged nature of the lines; these occur because of the very large number of simulations that would be necessary to obtain a smooth version (the figure uses 10000 simulations for each combination). The figure is used to illustrate the uniqueness of the solution only.

therefore cannot take advantage of them. For a mutant cooperator, γ_M becomes much larger thereby diminishing their advantage over the resident defectors, in particular, not only are they paying a higher movement cost but it takes longer to find the other cooperators, which in turn reduces the amount of time that they can spend with them.

For high movement costs, defecting mutants can invade, but cooperator mutants cannot. At this point all types have a large staying propensity and therefore do not interact much with one another. However, a mutant defector is helped by the fact that the resident cooperators always pay a cooperating cost that they now find difficult to recoup because they are moving very little and also paying a very large movement cost whenever they do so.

The effect of the exploration time

The exploration time T plays an important role in the evolution of cooperation. Changing the exploration time has a minimal effect on the time it takes to find cooperators because it will not alter the speed of movement of the individuals. This is because a complete graph is used and individuals can directly get from one place to any other. However, increasing the exploration time has a positive effect on the coalition time, that is, the amount of time that cooperators spend cooperating with one another. [24] showed that increasing the coalition time helps with

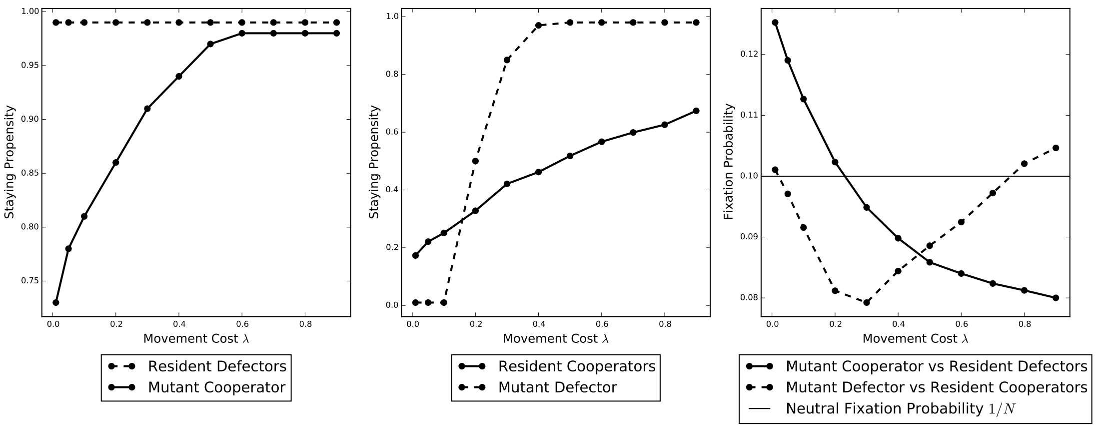


Figure 6.2: These plots show the effect of movement cost on the evolution of cooperation using parameter set 1. The left (centre) plot shows the staying propensities $\delta_R = 0.99$ (γ_R) for resident defectors (cooperators) and γ_M (δ_M) for a mutant cooperator (defector) used to invade the resident population. The right plot shows the fixation probability of a mutant cooperator C_{γ_M} (defector D_{δ_M}) against $N-1$ resident defectors $D_{0.99}$ (cooperators C_{γ_R}).

the evolution of cooperation. In the model considered here, one explanation for this is that the fitness of the individuals, which is the average reward over the exploration time, will naturally have a higher value the larger the coalition time.

In Figure 6.3 reducing the exploration time T from 10 to 5 steps decreases the coalition time which adversely affects the cooperators. One of the key differences is that the resident cooperators now find it much more difficult to prevent invasion from a mutant defector. The shape of the plot for a mutant cooperator is largely the same but with a consistently lower fixation probability. In Figure 6.4 increasing the exploration time T from 10 to 25 steps benefits the cooperators. Not only does it help the resident cooperators prevent invasion from a mutant defector but it also increases the success of an invading mutant cooperator. This again has to do with the increased coalition time that allows the cooperators to increase their fitness.

The effect of population size

Increasing the population size has a positive impact on the evolution of cooperation because it increases the time it takes to find cooperators. Note that it is assumed that there is a one-to-one correspondence between individuals and places and therefore increasing the number of individuals also increases the number of places. Even though the density remains the same, there would be more places for the individuals to search in order to find cooperators thereby increasing the overall time it takes to find cooperators. In particular, an individual that is currently not in a cooperating group will have to search $N-1$ places to find one, therefore, the probability of

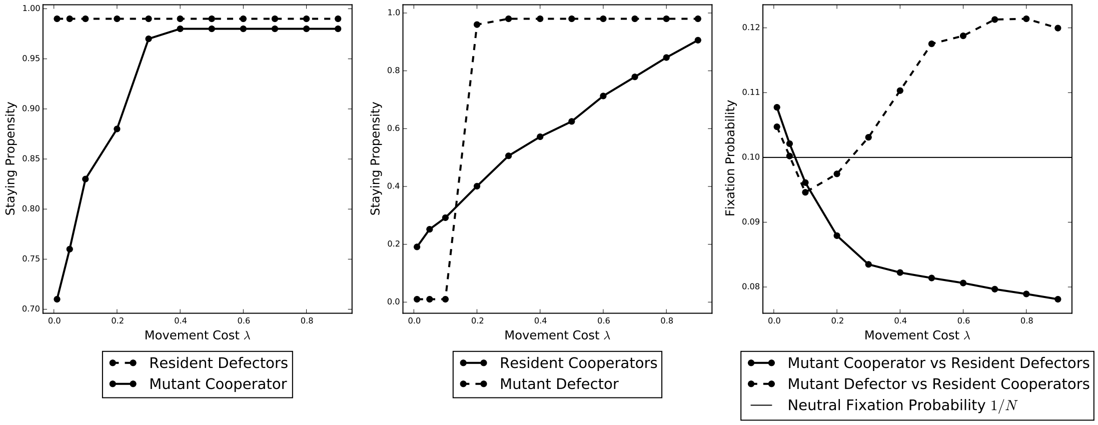


Figure 6.3: Plots created using parameter set 2. The exploration time T has been decreased from 10 to 5.

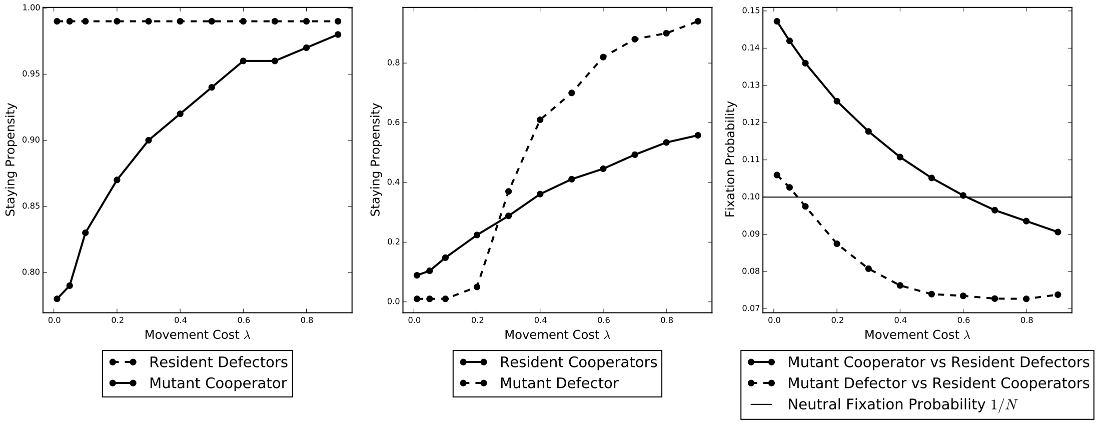


Figure 6.4: Plots created using parameter set 3. The exploration time T has been increased from 10 to 25.

a defector finding a cooperating group decreases as N gets larger. This means that cooperators would do better, which is indeed the case as seen in Figure 6.5 where the population size has been doubled from 10 to 20. One of the key differences to the previous plots is that a mutant defector cannot invade even for very low movement cost in a large population.

The effect of reward and cost

The reward to cost ratio v/c is important because, even if other external factors favour cooperation, cooperation will not evolve if the reward to cost ratio is too low. This is seen in Figure 6.6 where the cost is set to 0.04 with the reward written as a multiple of the cost. When v/c is low, a mutant cooperator cannot invade but a mutant defector can. This is simply because the

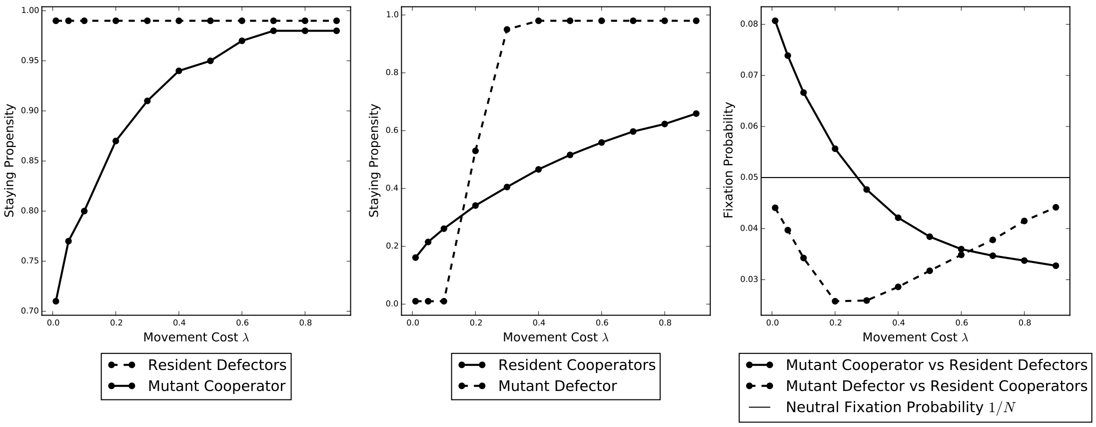


Figure 6.5: Plots created using parameter set 4. The population size has been increased from 10 to 20.

value of v/c is too low to promote cooperation. Increasing v/c makes cooperation more viable and, in particular, it allows a mutant cooperator to reduce the time it takes to find cooperators by reducing its staying propensity. It becomes more difficult for a mutant defector to invade because, on average, resident cooperators move less than the mutant defector as they are more in number and the larger v/c helps them quickly recoup any movement cost they incur whilst evading the mutant defector. This is the case even when $\delta < \gamma_R$, that is, a mutant defector takes less time to find cooperators. For comparison with a different value of v/c, in Figure 6.7 the cost is set to 0.09. However, there is no fundamental change in what happens and the figure is very similar to the one where $c = 0.04$.

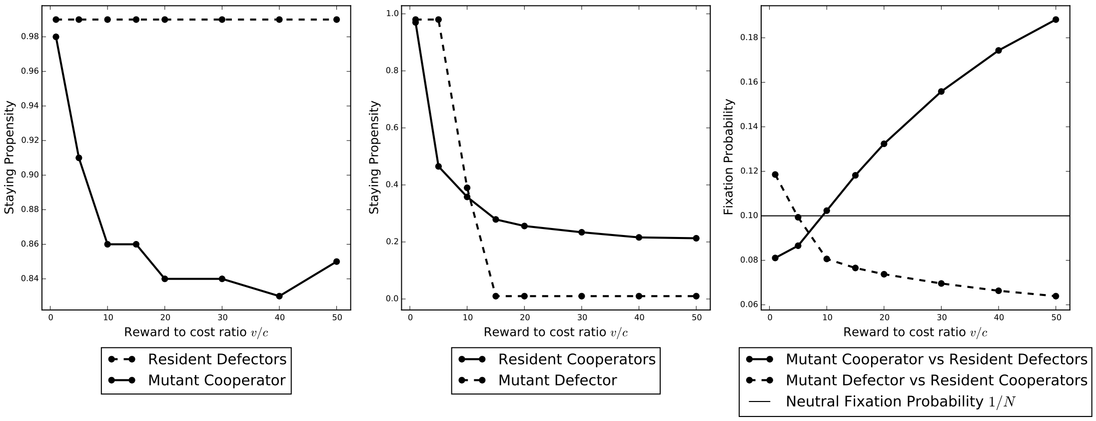


Figure 6.6: Plots have been created using parameter set 5. The plots here are against the reward to cost ratio v/c such that $c = 0.04$.

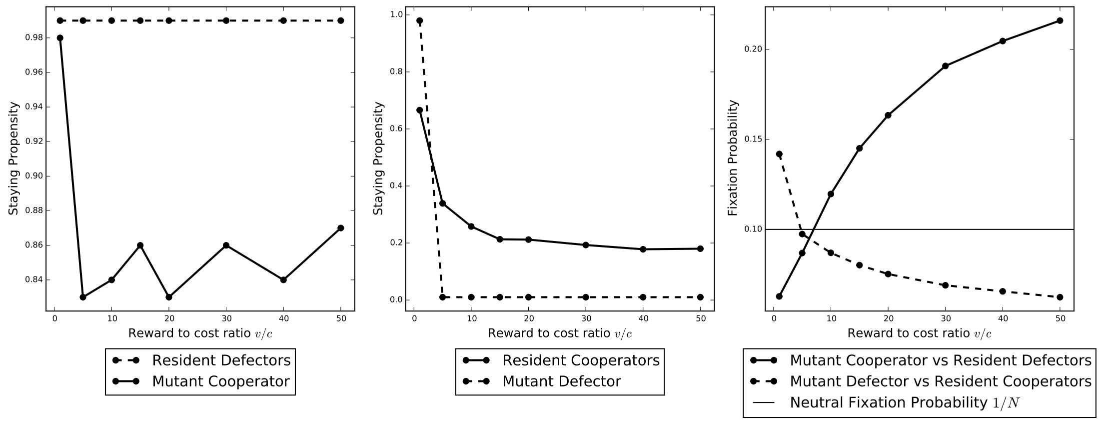


Figure 6.7: Plots have been created using parameter set 6. The plots here are against the reward to cost ratio v/c such that $c = 0.09$.

6.3.2 Scenario B: Interactive strategy mutation is not rare

In this scenario, the mutation rate of an individual's interactive strategy is not much slower than that of their staying propensity. Since the staying propensity would take a number of mutations to reach the right level for any scenario, any successful strategy will have to repeatedly face individuals of both types. The (strict) Nash equilibrium staying propensity will then be determined in a mixed population, i.e. there are individuals of both types. For simplicity only one mixed state is chosen to determine the Nash equilibrium staying propensity which is the one where there are $N/2$ individuals of each type. The Nash equilibrium staying propensity for each type is therefore the one in which the fixation probability from the mixed state of each type is maximised.

Resident and mutant defectors are of the same type D_δ. Similarly, resident and mutant cooperators are of the same type C_γ. The Nash equilibrium staying propensities δ and γ are determined by the intersection of the following two sets

$$\left\{(a,b) : \rho_{N/2}^{C_a,D_b} = \max\left(\rho_{N/2}^{C_c,D_b} : c \in (0,1)\right) \text{ and } b \in (0,1)\right\},$$
$$\left\{(a,b) : \rho_{N/2}^{D_b,C_a} = \max\left(\rho_{N/2}^{D_c,C_a} : c \in (0,1)\right) \text{ and } a \in (0,1)\right\}.$$

In the first set the Nash equilibrium staying propensity a is found for $N/2$ type C_a playing against $N/2$ type D_b, where b is some arbitrary staying propensity. In the second set the Nash equilibrium staying propensity b is found for $N/2$ type D_b playing against $N/2$ type C_a, where a is some arbitrary staying propensity. The point at which these two sets intersect is (γ, δ), that is, both types will be using their Nash equilibrium staying propensities.

To calculate γ and δ a similar iterative procedure from scenario A is used. To initialise the iterative procedure some staying propensities a_0 and b_0 are arbitrarily chosen, and the iterative step is as follows. The fixation probability of $N/2$ type C_a individuals against $N/2$ type D_{b_0} is calculated for all values of a in the range $[\max(0.01, a_0 - 0.09), \min(a_0 + 0.09, 0.99)]$. The staying propensity a that gives the maximum fixation probability is picked, which is labelled a_1. The fixation probability of $N/2$ type D_b individuals against $N/2$ type C_{a_1} is then calculated for all values of b in the range $[\max(0.01, b_0 - 0.09), \min(b_0 + 0.09, 0.99)]$. The staying propensity b that gives the maximum fixation probability is picked, which is labelled b_1. Note that using a wider ranges for a and b gives the same result so these ranges were used for efficiency. After around 20 repetitions of the iterative step, the staying propensities a_{20} and b_{20} remain the same. Note that any other values would be disadvantageous and, therefore, for these values the population is at a (strict) Nash equilibrium. The values of γ and δ are then set to a_{20} and b_{20} respectively, i.e. $\gamma = a_{20}$ and $\delta = b_{20}$.

It is hypothesized that γ and δ are unique. For cooperators, their Nash equilibrium staying propensity is relatively stable because it is predominantly determined by the movement cost regardless of what the defectors are doing. As seen in Figure 6.8, the plot for this is a roughly vertical line. For defectors, their Nash equilibrium staying propensity is negatively correlated with the staying propensity of the cooperators given that the movement cost is not too large, otherwise it would be $\max(\alpha)$. In Figure 6.8, the plot for this slopes downwards as the staying propensity of the cooperators increases. There is therefore only one intersection point of the two curves that gives γ and δ.

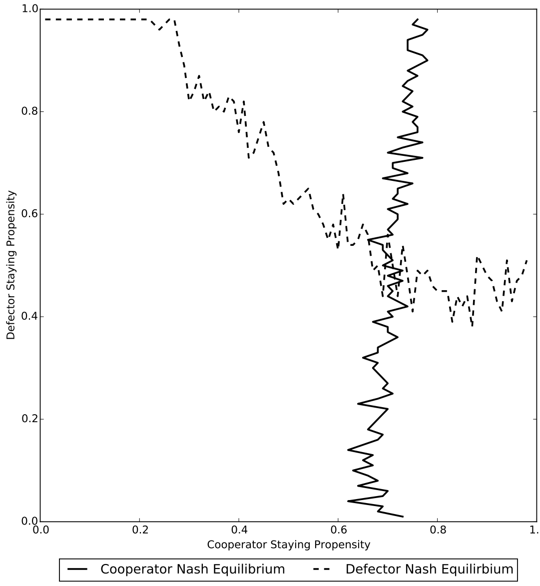


Figure 6.8: This plot shows the Nash equilibrium staying propensities for $N/2$ cooperators and $N/2$ defectors. Parameter set 1 is used with $\lambda = 0.2$ and the staying propensities are chosen from the set $\{0.01, 0.02, \ldots, 0.99\}$. The Nash equilibrium staying propensities cross at one point only where $\gamma \approx 0.7$ and $\delta \approx 0.5$. These values are similar to those obtained using the iterative method described earlier (see Figure 6.9). As before, the values from the current figure are approximate only because of the jagged nature of the lines; the figure is used to illustrate the uniqueness of the solution only.

The effect of movement cost

As in scenario A, the movement cost increases the staying propensity of the individuals and, therefore, increases the time it takes to find cooperators. As seen in Figure 6.9, what happens in this case is quite different to the situation in scenario A. Here, the mutant cooperator does not benefit from the fact that the resident defectors have a very high staying propensity as in scenario A. In this case, δ changes with the movement cost in a similar way that γ changes. Therefore, the key difference here is that a mutant cooperator cannot invade for very low movement cost because the resident defectors have a very low staying propensity, which means that they take much less time to find cooperators.

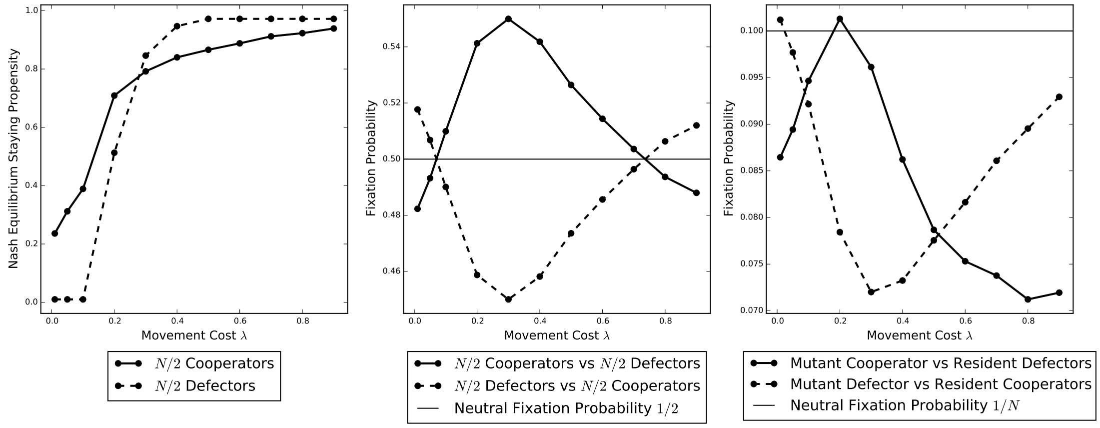


Figure 6.9: These plots show the effect of movement cost λ on the evolution of cooperation and are created using parameter set 1. The plot on the left shows the Nash equilibrium staying propensity γ for cooperators and δ for defectors in a mixed population where there are $N/2$ individuals of each type. The plot in the centre shows the fixation probability of each type from the mixed state with $N/2$ individuals of each type. The plot on the right shows the fixation probability of a mutant cooperator C_γ (defector D_δ) in a population of $N-1$ resident defectors D_δ (cooperators C_γ).

The effect of exploration time

As in scenario A, the cooperators do worse when the exploration time is lower; this is shown in Figure 6.10 where T is decreased from 10 to 5, and in Figure 6.11 where T is increased from 10 to 25. The explanation is as in scenario A where the coalition time is lower when the exploration time is lower and the coalition time increases, since, as previously seen, increasing the coalition time helps the cooperators do better.

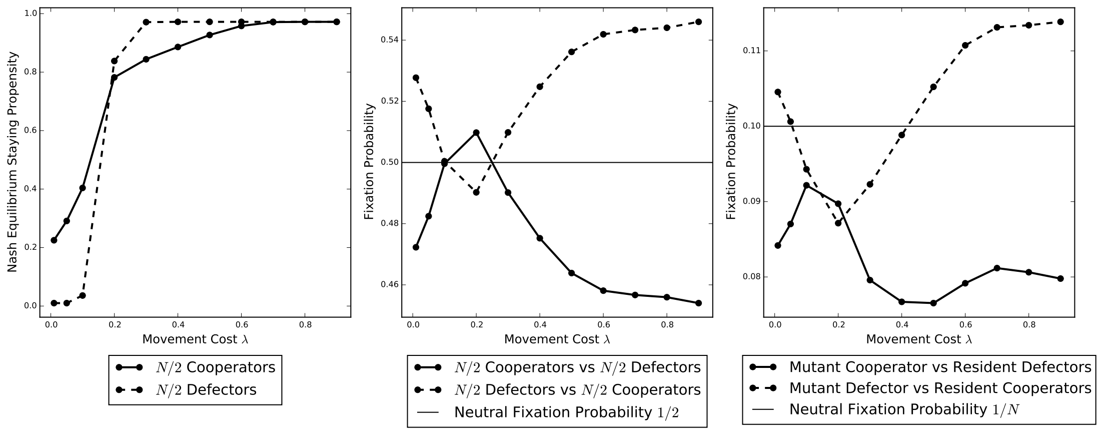


Figure 6.10: Plots created using parameter set 2. Plots are as in Figure 6.9 with exploration time T decreased from 10 to 5.

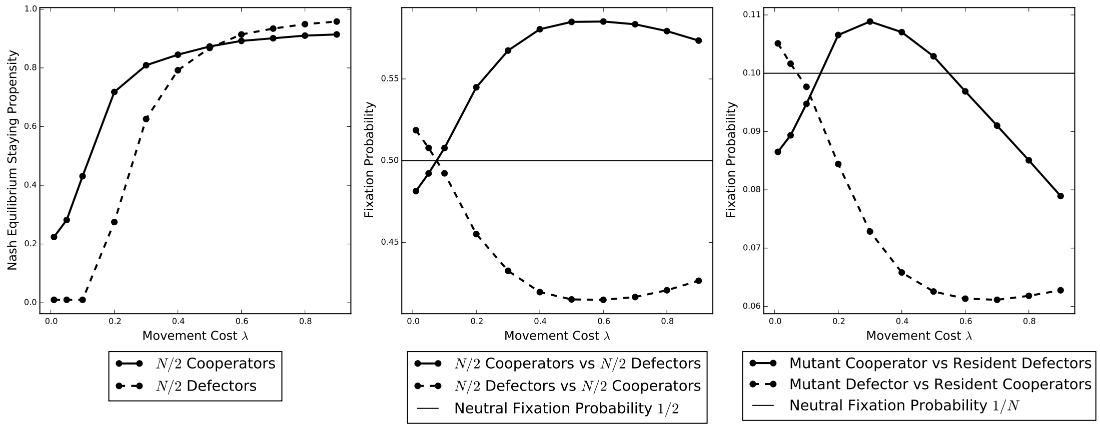


Figure 6.11: Plots created using parameter set 3. Plots are as in Figure 6.9 with exploration time T increased from 10 to 25.

The effect of population size

Similarly to scenario A, increasing the population size helps cooperators as shown in Figure 6.12, where N is increased from 10 to 20. As before, increasing the population size increases the time it takes to find cooperators because there is a one-to-one correspondence between individuals and places. Increasing the population size therefore increases the number of places that need to be searched to find cooperators. Furthermore, as in scenario A, a mutant defector can no longer invade resident cooperators for a very small movement cost.

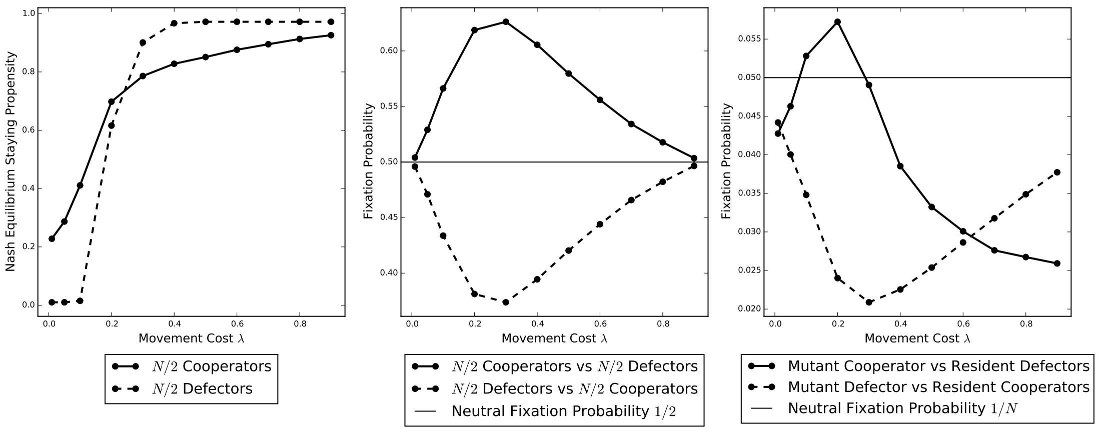


Figure 6.12: Plots created using parameter set 4. Plots are as in Figure 6.9 with population size N increased from 10 to 20.

The effect of reward and cost

For a mutant defector, the effect of the reward to cost ratio v/c is the same as in scenario A. However, a mutant cooperator does not do better with increasing v/c. In this scenario, the fixation probability of a mutant cooperator peaks, then starts dropping, as v/c is increased. This is because the resident defectors have a very low staying propensity, and are therefore faster at finding cooperators, making it difficult for a mutant cooperator to invade because it cannot avoid the defectors. This is shown in Figure 6.13 where $c = 0.04$. Increasing the cost c though, makes it even more difficult for the cooperators regardless of v/c. In Figure 6.14, a mutant cooperator cannot invade for any v/c. This is because a larger c reduces the cooperators' background fitness by a larger amount, increasing the handicap that the cooperators already have.

6.3.3 The effect of other parameters

The effects of other parameters are not shown using plots but will be explained in this section.

Making the individuals more sensitive to their group members by decreasing the sensitivity parameter S improves the chances of cooperation evolving. In equation (6.9), it can be seen that decreasing S will increase the size of the denominator if the group benefit is negative, thereby increasing the probability that an individual moves away from its current position if it is undesirable to stay. Therefore, as $S \to 0$ the more sensitive individuals become, which helps the evolution of cooperation because it reduces the exploitation of cooperators (cooperators are now more likely to move away if the group they are in becomes undesirable).

Another way in which the group member sensitivity can be changed is by choosing $\beta_A > 0$

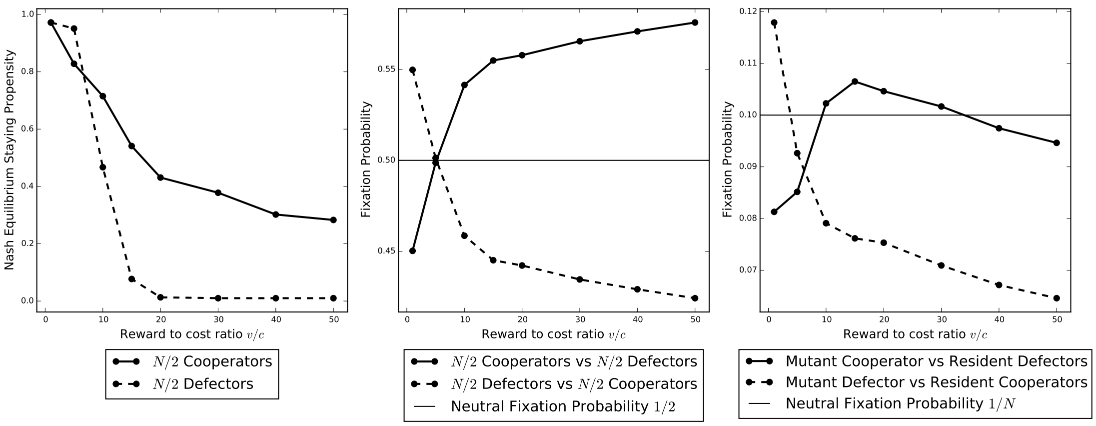


Figure 6.13: Plots created using parameter set 5. Plots are as in Figure 6.9 but λ is fixed and reward to cost ratio v/c varied such that $c = 0.04$.

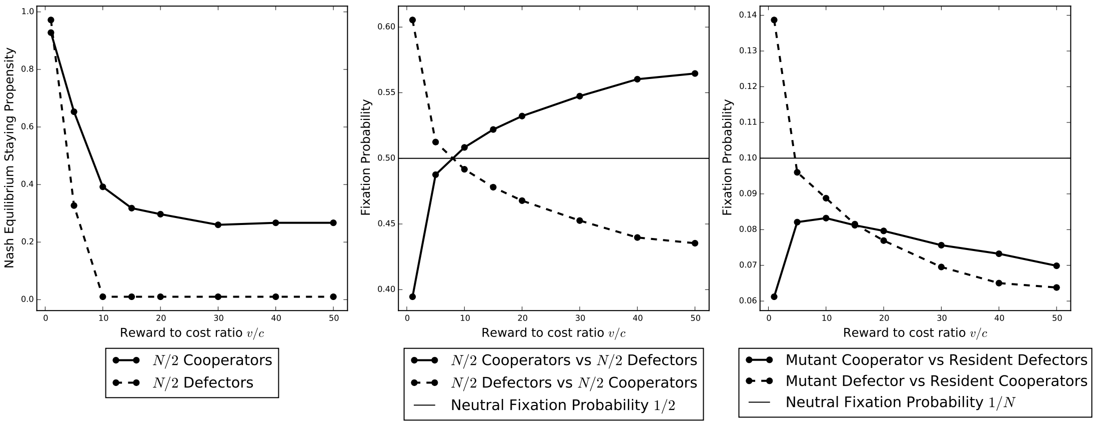


Figure 6.14: Plots created using parameter set 5. Plots are as in Figure 6.9 but λ is fixed and reward to cost ratio v/c varied such that $c = 0.09$.

and $\beta_B < 0$ such that $\beta_B/\beta_A \to -\infty$. As seen in equation (6.9), this will cause the group benefit to become negative very quickly in the presence of a defector, even if there are significantly more cooperators present. Once again, this reduces the exploitation of cooperators by defectors, hence, improving the chances that cooperation evolves.

In all of the plots shown, only BDB dynamics is used because the effect of a change to other dynamics is quite small. The reason for this is that the evolutionary graph is always complete, that is, whilst the replacement weights change, all individuals can still replace one other. For example, in the case of DBB dynamics, to make a significant difference a defector randomly chosen for death should be more likely to be replaced with the offspring of a cooperator. However, this is not the case here and, in particular, the only way the evolutionary graph can be changed is by changing the staying propensity such that increasing the staying propensity increases the probability that an individual replaces itself. Therefore, the dynamics overall have a small effect. Note that this would not be the case for some other underlying structure that was not complete.

6.4 Discussion

In this chapter the framework of Broom-Rychtar (Chapter 4) is used to model the evolution of a mobile population in which the movement of the individuals is Markov such that the place an individual moves to next depends upon their current position. In the (generalized) territorial raider model (Chapters 4 and 5), individuals moved independently of their current position so the Markov movement model in this chapter gives a different perspective on the movement of individuals in relation to the evolution of cooperation.

The Markov movement model considers the movement of individuals that depend upon population history. Here, individuals make a decision of whether they should stay or leave their current position depending upon the other individuals present with them in the same place. This movement strategy is akin to the "walk away" strategy of [1, 2]. However, note that this is only one interpretation that can be used for the Markov movement model. The framework provides the tools to construct different kinds of Markov movement behaviour. For example, in [25], individuals would study all surrounding areas before making a decision about where to move to next. In terms of the framework, individuals would consider a larger subset of the current population distribution rather than just the distribution of individuals that are currently present with each other. Both simple and complex Markov movement behaviour provide useful insight into the movement behaviour of individuals.

For cooperation to evolve, [26] showed that there should be assortment, in particular there should be a mechanism that allows the cooperators to increase their preference for interacting with other cooperators. Here, this mechanism is provided by the Markov movement of the individuals. The results presented here are in line with [2] who also modelled the Markov movement of individuals where individuals would stay where they are if the payoff they received was above some minimum threshold. However, the Markov movement model in this chapter uses a structure that is substantially different. A complete graph is used with one-to-one correspondence between individuals and places instead of a two-dimensional array. This means that there is a high potential movement speed as individuals can go directly from one place to another, which is mitigated in the Markov movement model with the introduction of a movement cost. A higher staying propensity slows down an individual because they are more likely to stay where they are. Individuals use the staying propensity that maximises their fixation probability. Two different scenarios were considered where the staying propensity of an individual mutates very quickly or slowly. The key difference between the two scenarios was that a mutant cooperator can invade a resident population of defectors for very low movement cost if their staying propensity mutates very slowly.

The BDB dynamics used here allows cooperation to evolve even though typically selection does not favour cooperators with these dynamics [70]. Other dynamics that favour cooperators showed little improvement over the results obtained for BDB dynamics. This shows that Markov movement is quite effective in allowing cooperation to evolve. Its effectiveness is further backed up by the fact that the structure of the evolutionary graph is complete, which is known to be detrimental for cooperators [70]. In particular, in a complete evolutionary graph all individuals can replace each other and, therefore, the individuals with the highest fitness are more likely to be favoured by selection. This shows that conditional movement makes the choice of dynamics being used less important.

The results of the generalized territorial raider model given in chapter 5 and the Markov movement model are consistent with one another in that they both require cooperators to spend more time with one another in order to allow cooperation to evolve. The territorial raider model achieves this through stronger subpopulation interactions where as the Markov movement model achieves this through strategic movement. Strategic movement is more realistic than the naive approach used in the territorial raider model because it allows for the fact that individuals move away from adversity. Furthermore, strategic movement is more robust in terms of the dynamics used. The territorial raider model requires that BDD or DBB dynamics are used for cooperation to evolve and, on the other hand, either BDB, DBD, BDD or DBB dynamics work for the Markov movement model.

The results in this chapter apply to places whose connections between them represent a complete graph. For more general graphs, further study will have to be carried out, though, the current study on a complete graph does give some intuition in terms of what to expect. For example, with the complete graph, it is possible for cooperators to escape defectors more easily but, in a graph with less connections, there are fewer places a cooperator can escape to and also fewer places for a defector to search for cooperators, which would adversely affect the level of cooperation. Similarly, for graphs with hubs that individuals are forced to go through would make it difficult for cooperators as they may have to go through these hubs, which may be populated by defectors. Overall, the key difference that will be observed is that the starting position of a cooperator or defector will play a crucial role in their success in heterogeneous graph structures.

Chapter 7

Alternative Dynamics

7.1 Introduction

This chapter utilizes the territorial raider population evolution model of chapter 4 to study alternative dynamics that can be used. Whilst these dynamics are applied to the territorial raider model, they are compatible with the fully independent movement model of the framework of Broom-Rychtář. They are therefore compatible with the generalized territorial raider model (Chapter 5) and, under certain assumptions, the Markov movement model (Chapter 6). These alternative definitions are obtained by altering the definition of the replacement weight contributions $u_{i,j}(m, \mathcal{G})$ in equation (4.24, pg. 91), reproduced here,

$$w_{i,j} = \sum_{m} \sum_{\substack{\mathcal{G} \\ i,j \in \mathcal{G}}} u_{i,j}(m, \mathcal{G}) \chi(m, \mathcal{G}). \tag{7.1}$$

Recall that $w_{i,j}$ are the replacement weights that represent the replacement graph, i.e. it determines which individual an offspring can replace. These newly defined replacement weights $w_{i,j}$ can then be used with the standard dynamics given in Table 4.2 (pg. 91). However, some of the alternative definitions given here cannot be used with the standard dynamics.

The objective of this chapter is not to provide an exhaustive list of dynamics that can be used with the BR framework but to illustrate how they can be constructed. Analysis is carried out for the alternative dynamics defined in order to better understand them and compare them with those used in the previous chapters and, therefore, justify why they were used.

7.2 Standard Dynamics with Selection Bias

Before defining different replacement weights, a definition of the standard dynamics with a selection bias parameter are given. The *selection bias* parameter, x, varies the bias that selection

Standard dynamics with selection bias	
BD	$b_i = \frac{F_i^{1-x}}{\sum_n F_n^{1-x}},\ d_{i,j} = \frac{w_{i,j}F_j^{-x}}{\sum_n w_{i,n}F_n^{-x}}$
DB	$d_j = \frac{F_j^{-1+x}}{\sum_n F_n^{-1+x}},\ b_{i,j} = \frac{w_{i,j}F_i^{x}}{\sum_n w_{n,j}F_n^{x}}$
L	$\mathfrak{r}_{i,j} = \frac{w_{i,j}F_i^{1-x}/F_j^{-x}}{\sum_n w_{n,k}F_n^{1-x}/F_k^{-x}}$

Table 7.1: Evolutionary dynamics rewritten using the selection bias parameter x. The selection bias parameter x permits changing the bias that selection has towards the birth and death processes.

has towards the birth process and death process. The standard dynamics with selection bias are given in Table 7.1. In the case of the birth-death (BD) dynamics, $x = 0$ ($x = 1$) implies that selection happens only in the birth (death) process. For $x \in (0, 1)$, selection happens in both processes, for example, when $x = 0.5$ selection is equally biased towards the birth and death processes. The link dynamics are set up in a similar way to the BD dynamics. On the other hand, for death-birth (DB) dynamics, $x = 0$ ($x = 1$) implies that selection happens only in the death (birth) process and $x \in (0, 1)$ implies that selection happens in both the death and birth processes. Note that it is set up in this way because $x = 0$ ($x = 1$) implies that selection happens in the first (second) process which is birth (death) for the BD and the opposite for DB. With link dynamics, the ordering of birth and death is ambiguous so the same convention as BD is used.

Defining the dynamics in this way generalises the standard dynamics by bridging the gap between selection on the birth and death events making them more useful in the context of evolutionary graph theory. One of the advantages is that they are now more suitable when checking for sensitivity. For example, some of the results obtained hold for the extreme cases where selection happens in the birth or death event, i.e. $x = 0$ or 1 in BD dynamics. By weakening this assumption, it can be checked how sensitive the results are to it. The selection bias parameter allows one to gradually weaken such assumptions. In particular, setting $x = 0.5$ implies that selection happens in both the birth and death events. Thereby, each event is given equal importance and the results obtained should be less sensitive to either the the birth and death events.

7.3 Replacement weights that can be used with standard dynamics

In this section various definition of the replacement weight contributions are given where the replacement weights generated are compatible with standard dynamics given in Table 4.2 (pg. 91). In each case the replacement weight contribution $u_{i,j}(m, \mathcal{G})$ is some function proportional to the probability of the birth individual I_i and death individual I_j meeting in place m in group $\mathcal{G}$.

7.3.1 Definition 1

The replacement weight contribution is equal to the probability of I_i and I_j meeting in place m in group $\mathcal{G}$. This is a simple definition where the only feature of group $\mathcal{G}$ that matters is whether I_i and I_j are in $\mathcal{G}$, that is, they meet. Recall, that the probability of group $\mathcal{G}$ forming in place m is $\chi(m, \mathcal{G})$, see equation (4.27, pg. 95). In the case of *self-replacement*, i.e. the birth and death individuals are the same so $i = j$, the replacement weight contribution is $\chi(m, \mathcal{G})$ if $\mathcal{G} = \{i\}$, and 0 otherwise. This captures the notion that self-replacement should be proportional to an individual being alone. The replacement weight contribution is then given by

$$u_{i,j}(m, \mathcal{G}) = \begin{cases} 0 & i = j \wedge |\mathcal{G}| > 1, \\ \chi(m, \mathcal{G}) & \text{otherwise.} \end{cases} \tag{7.2}$$

7.3.2 Definition 2

This is an extension of Def. 1, however, in this case $\chi(m, \mathcal{G})$ is divided by $|\mathcal{G}|$, the size of group $\mathcal{G}$. The logic behind this is that I_i equally considers all the member of $\mathcal{G}$ including itself. Therefore, smaller groups contribute more than larger groups, which makes sense because individuals I_i and I_j would spend more time together in a smaller group than a larger group. In the case of self-replacement, I_i is allowed to replace itself when present with other group members and does not need to be alone, that is, there is *in-group self-replacement.* The replacement weight contribution is then given by

$$u_{i,j}(m, \mathcal{G}) = \frac{\chi(m, \mathcal{G})}{|\mathcal{G}|}. \tag{7.3}$$

Note that there is no need to account for whether I_i is alone or not because of in-group self-replacement.

7.3.3 Definition 3

This definition is used in the previous chapters where it was first defined in Section 4.3.3 (pg. 98). It has been included for continuity as it is an extension of Def. 2. The main difference here is that in-group self-replacement is not allowed. Therefore, $\chi(m, \mathcal{G})$ is divided by $|\mathcal{G}| - 1$, the size of group $\mathcal{G}$ excluding I_i, and self-replacement is allowed only when I_i is alone. The replacement weight contribution is then given by

$$u_{i,j}(m, \mathcal{G}) = \begin{cases} 0 & i = j \wedge |\mathcal{G}| > 1 \\ \chi(m, \mathcal{G}) & i = j \wedge |\mathcal{G}| = 1 \\ \dfrac{\chi(m, \mathcal{G})}{|\mathcal{G}| - 1} & i \neq j \end{cases} \tag{7.4}$$

Def. 1 does not take into account the effect of other members in the group $\mathcal{G}$ in which I_i and I_j meet and was therefore not used in the previous chapters. Furthermore, Def. 3 was favoured over Def. 2 because the latter overemphasizes self-replacement because of in-group self-replacement and the former does not. Note that there are other implications of in-group self-replacement that are highlighted later in this chapter.

7.3.4 Definition 4

This definition, as in Def. 1, assumes that the replacement weight contribution is equal to the probability of I_i and I_j meeting in place m in group $\mathcal{G}$, however, in addition to this, part of the self-replacement weight contribution is assigned to the other individuals proportional to how often they meet. This then reduces self-replacement and increases the likelihood of replacing another individual by emphasizing the connection between individuals based on how often they meet. The replacement weight is given by

$$u_{i,j}(m, \mathcal{G}) = \begin{cases} \chi(m, \mathcal{G})\chi(m, \mathcal{G}) & i = j \wedge \mathcal{G} = \{i\}, \\ \chi(m, \mathcal{G}) + \chi(m, \mathcal{G})\chi(m, \{i\}) & \text{otherwise.} \end{cases} \tag{7.5}$$

This definition differs from the previous three in that the replacement weights are not symmetric, i.e $w_{i,j} \neq w_{j,i}\ \forall i, j$, except when all individuals have the same probability of being alone and meeting one another.

7.3.5 Comparing the different weights

The territorial raider model (see Chapter 4 pg. 85) is used to make the comparisons. The population structures used are the 4-vertex complete, line and star graphs and the game used is the multiplayer public goods game. For the game, the reduced background fitness is set to $r = 10$ and the reduced reward to $v = 2$. The following plots show an arithmetic mean of the fixation probabilities instead of the temperature weighted mean because there is no significant difference. In each of the plots the selection bias is set to 0.5, that is, selection is equally biased towards birth and death.

Figure 7.1 compares the different definitions for the BD dynamics. It is observed that Defs. 1 and 3 and are quite similar to one another in the sense that the fixation probabilities closely follow one another, especially for the line and star graphs. There is a clear ranking amongst the four definitions in terms of favouring the defectors over the cooperators. Def. 2 favours the defectors the most and Def. 4 the least, with Defs. 1 and 3 falling almost halfway in between. This is to be expected because Def. 2 allows in-group self-replacement. This means if individual I_n is chosen for death and it has a higher fitness than the individuals that can replace it, I_n is more likely to replace itself and this is even more likely to be so in the case of in-group self-replacement. Note that for the public goods game the defectors generally have a higher fitness and are therefore favoured. In Def. 4, where the likelihood of self-replacement is diminished, the advantage of defectors is significantly eroded, especially for low home fidelity. Figure 7.2 compares the different definitions for the DB dynamics. The observations here are very similar to the BD dynamics. In particular, there is a clear ranking between the four definitions with Def. 2 favouring defectors the most and Def. 4 the least.

Figure 7.3 compares the different definitions for the Link dynamics. Here, Defs. 1, 2 and 3 all behave in the same way, which is drastically different from what was observed in the BD and DB dynamics. This is the case because for all three definitions the replacement weight matrix $\mathbf{W} = (w_{i,j})$ is symmetric, i.e. $w_{i,j} = w_{j,i} \; \forall i, j$. This means that $\mathbf{W}$ is a *circulation*, see Section 2.2.3 pg. 49. In the case of circulations, the replacement graph does not impact the fixation probabilities and only the fitness of the individuals matter. In the case of constant fitness, this is shown by Proposition 1 pg. 52. Therefore, the differences seen between the complete, line and star graph are due to the fitnesses of the individuals. However, Def. 4 behaves differently because the replacement weight matrix is not symmetric and, therefore, the structure of the population impacts the fixation probability. The overall shape of the fixation probability curves for the different graph structures are quite similar though. In particular, for low home fidelity the defectors do very well but this drops off as the home fidelity increases. This would be due to the fact that the interactions between the individuals would not be vastly different for these small graphs, though, for larger graphs there could be a more substantial difference.

Figure 7.4 compares the BD, DB and Link dynamics for Def. 1. It can be observed that the BD and DB dynamics are almost identical because the replacement graph $\mathbf{W}$ for Def. 1 is symmetric. This means that whether birth occurs first or death is irrelevant so both BD and DB behave almost identically. However, for significantly heterogeneous graphs, like the star, this behaviour seems to break down with BD being slightly more favourable to the defectors than DB. The link dynamics behaviour is vastly different from the BD and DB dynamics, most notably it slopes upwards whilst the other two dynamics slopes downwards. The figures in

Chapter 4 (pg. 85) for BD dynamics essentially behave like the LD dynamics here, therefore, the effect observed here is due to the selection bias. Indeed, the selection bias is set to $x = 0.5$, which means that for the BD (DB) dynamics the first event, birth (death), is influenced less by selection and, therefore, subject more to chance. As shown in Section 5.3.1 (pg. 121) this favours the less fit type, in this case cooperators, especially when self-replacement is low. Note that the probability of self-replacement is low when the home fidelity is low but increases when the home fidelity is high, hence the upward slope. In the star graph, self-replacement is lowest when home fidelity is low as a lot of the individuals converge in the center vertex. The cooperators are therefore at a much lesser disadvantage than for the other two graphs, so much so, that the difference between the fixation probability of cooperators and defectors is narrower than for the LD dynamics. This means that the plots for the LD and the other two dynamics cross over for the star graph. For the other graphs, there is no cross over and LD seems less favourable to the defectors than the other two dynamics.

Figure 7.5 compares the three dynamics for Def. 2. It is observed that BD and DB dynamics are identical and this relationship does not break down for heterogeneous graphs because, in this case, $\mathbf{W}$ is symmetric and doubly stochastic. This means that $\mathbf{W}$ is *isothermal*, see Section 2.2.3 pg. 49. As mentioned before, the order of the birth and death events becomes irrelevant, and is stronger in the case when $\mathbf{W}$ is isothermal. With in-group replacement, the upward slope disappears. Instead, there is a peak around home fidelity $h = 1$ for the line graph and, more clearly, for the star graph. Where as, in the case of the complete graph, it is now downward sloping. This is expected as self-replacement increases even for low home fidelity with in-group self-replacement. Figure 7.6 compares the three dynamics for Def. 3. Here, the observations are similar to those in Def. 1. However, note that $\mathbf{W}$ in this case is doubly stochastic and symmetric as well, so DB and BD are identical in their behaviour. Figure 7.7 compares the three dynamics for Def. 4. The observations here are characteristically similar to those in Defs. 1 and 3, but the identical behaviour of DB and BD breaks down, more so than Def. 1, due to the lack of symmetry in $\mathbf{W}$, particularly for the line and star graphs. The other difference is that the advantage of the defectors is significantly diminished, especially for the DB and BD dynamics. This means that DB and BD dynamics are more responsive to there being less self-replacement than Link dynamics.

Figure 7.8 compares different values of the selection bias for BD Def. 3 dynamics. The values of the selection bias used are 0, 0.5 and 1. The most noticeable feature is that for $x = 0.5$, the fixation probabilities lie in the middle of the cases where $x = 0$ and $x = 1$. This was somewhat to be expected as selection is equally biased towards the birth and death events. For the complete graph, the effect of the dynamics is consistent regardless of the selection bias, i.e. the fixation

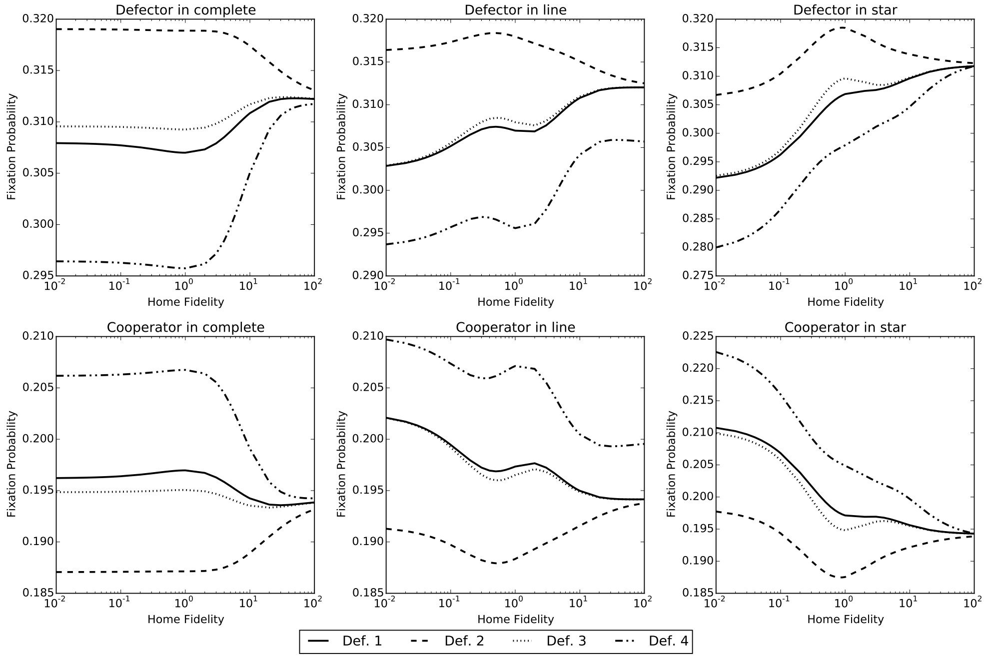


Figure 7.1: Comparison between Definitions 1, 2, 3 and 4 for BD dynamics. For the game $r = 10$ and $v = 2$. The selection bias is $x = 0.5$.

probability of each type converges as the home fidelity increases. For the line and star graphs, this is the case when $x = 0$. However, when $x = 0.5$ or 1, the fixation probabilities initially diverge before starting to converge again in the line and star graphs. This shows that, for low values of home fidelity, as selection shifts to the second event (death in this case), the cooperators do better. This is because, for low values of home fidelity, there is subgrouping behaviour as seen in Chapter 5. Note that, as the home fidelity increases and subgrouping behaviour reduces, there is a point at which the fixation probabilities are identical for all values of the selection bias.

7.4 Replacement weights that cannot be used with standard dynamics

The definition of the replacement weights given in this section are applied in a different way to the ones given in the previous section. In particular, the replacement weight contributions are functions of the fitnesses of the individuals whose effect is controlled by the selection bias parameter x. This means that the replacement weights cannot be used with the standard dynamics. In this case, the replacement weights are not symmetric, i.e. $w_{i,j} \neq w_{j,i}\ \forall i, j$, and changes whenever the state of the population changes because the fitnesses of the individuals

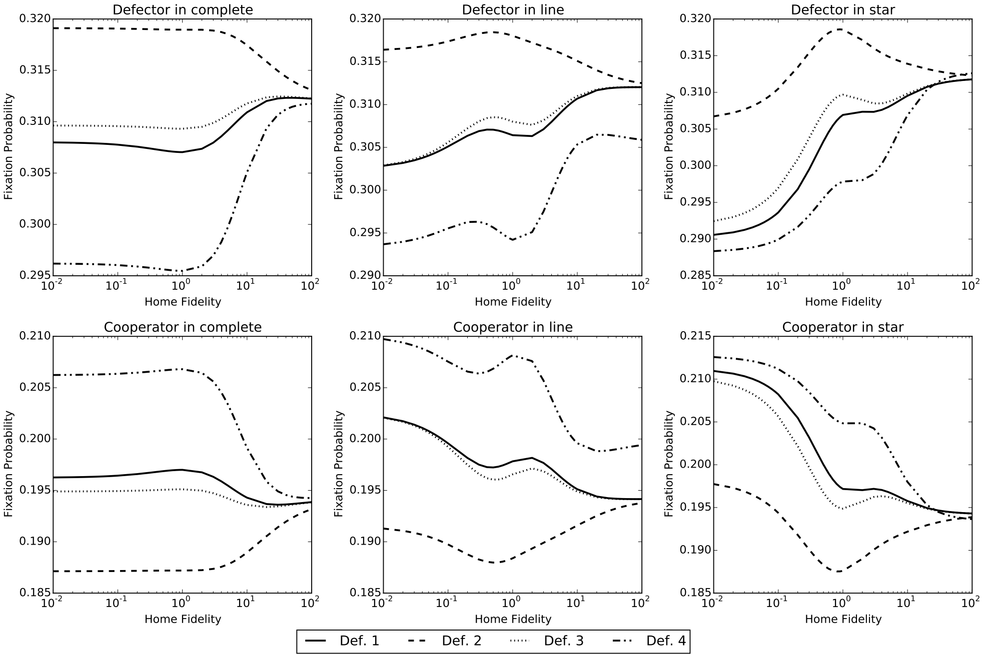


Figure 7.2: Comparison between Definitions 1, 2, 3 and 4 for DB dynamics. For the game $r = 10$ and $v = 2$. The selection bias is $x = 0.5$.

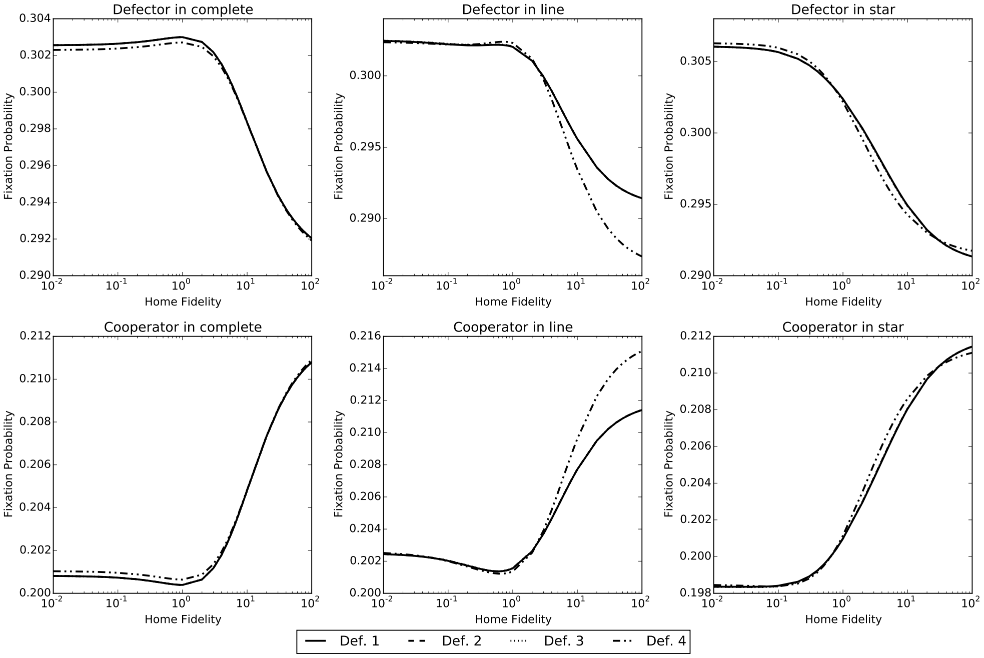


Figure 7.3: Comparison between Definitions 1, 2, 3 and 4 for Link dynamics. For the game $r = 10$ and $v = 2$. The selection bias is $x = 0.5$.

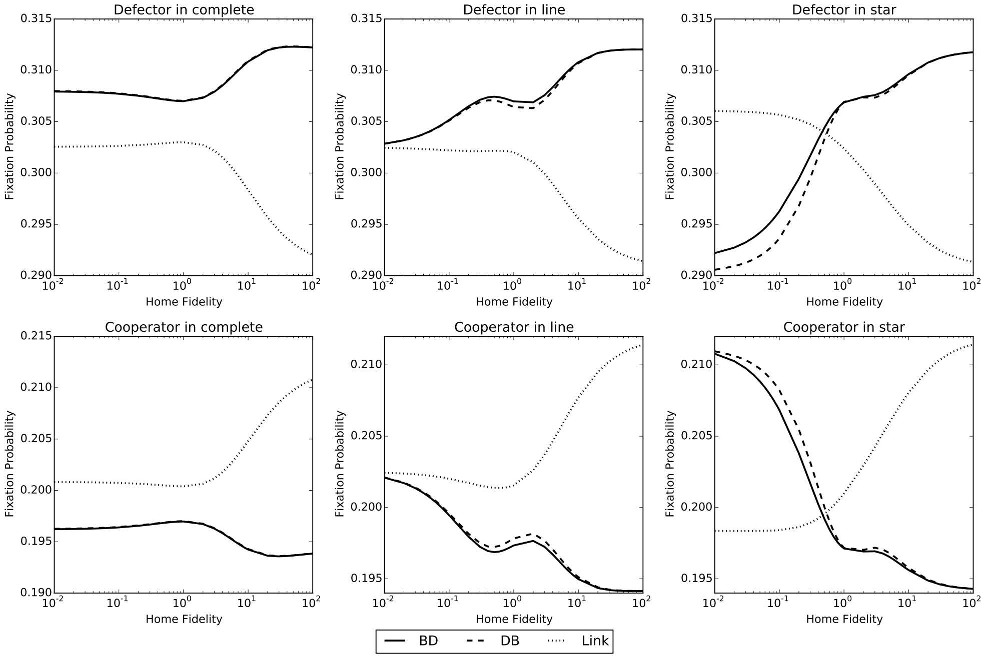


Figure 7.4: Comparison between BD, DB and Link dynamics for Def. 1. For the game $r = 10$ and $v = 2$. The selection bias is $x = 0.5$.

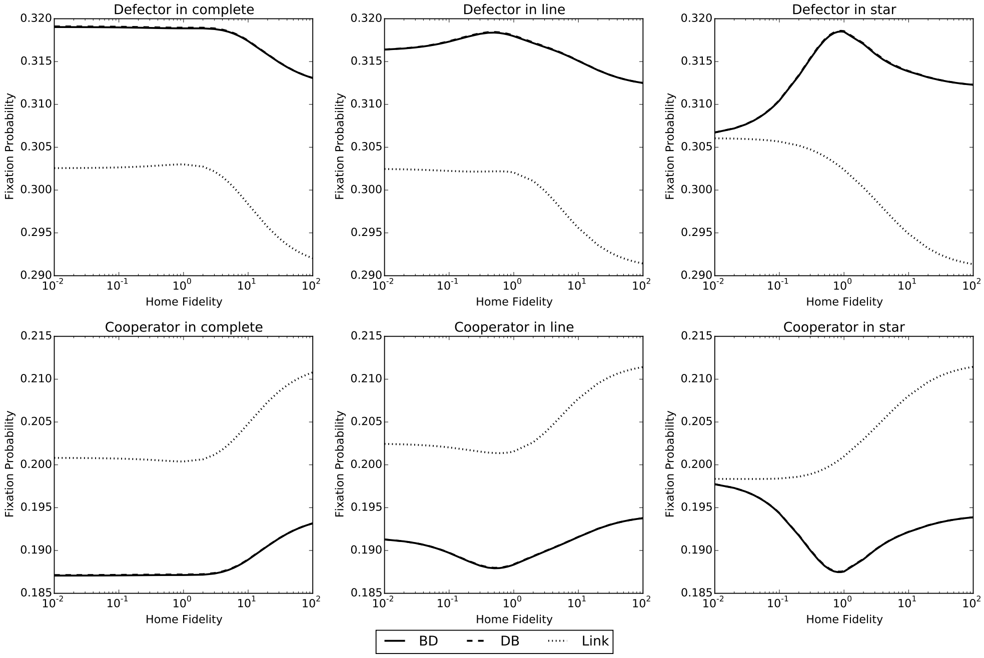


Figure 7.5: Comparison between BD, DB and Link dynamics for Def. 2. For the game $r = 10$ and $v = 2$. The selection bias is $x = 0.5$.

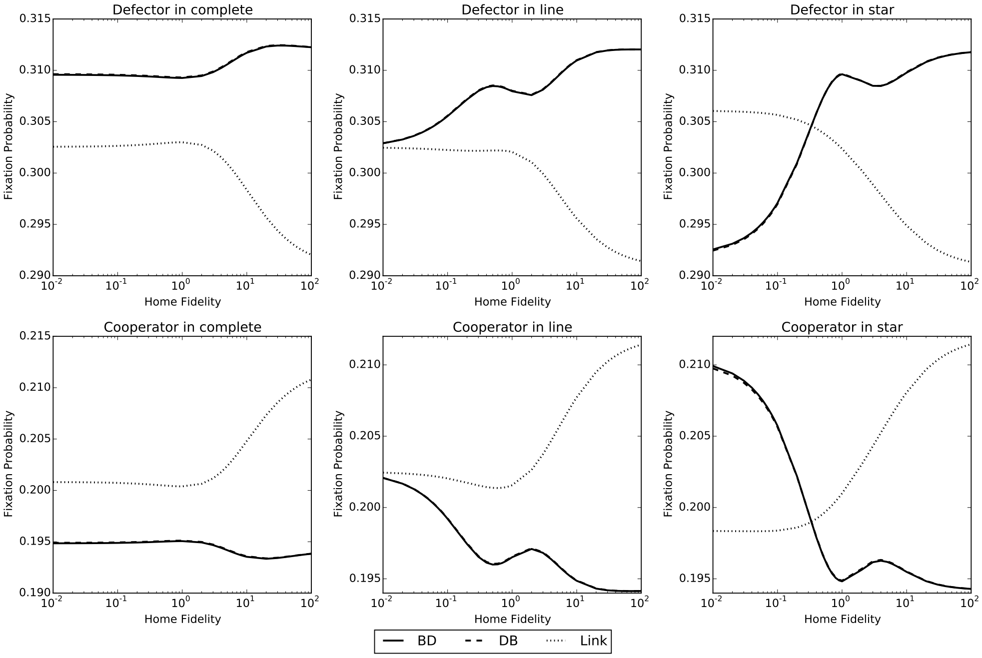


Figure 7.6: Comparison between BD, DB and Link dynamics for Def. 3. For the game $r = 10$ and $v = 2$. The selection bias is $x = 0.5$.

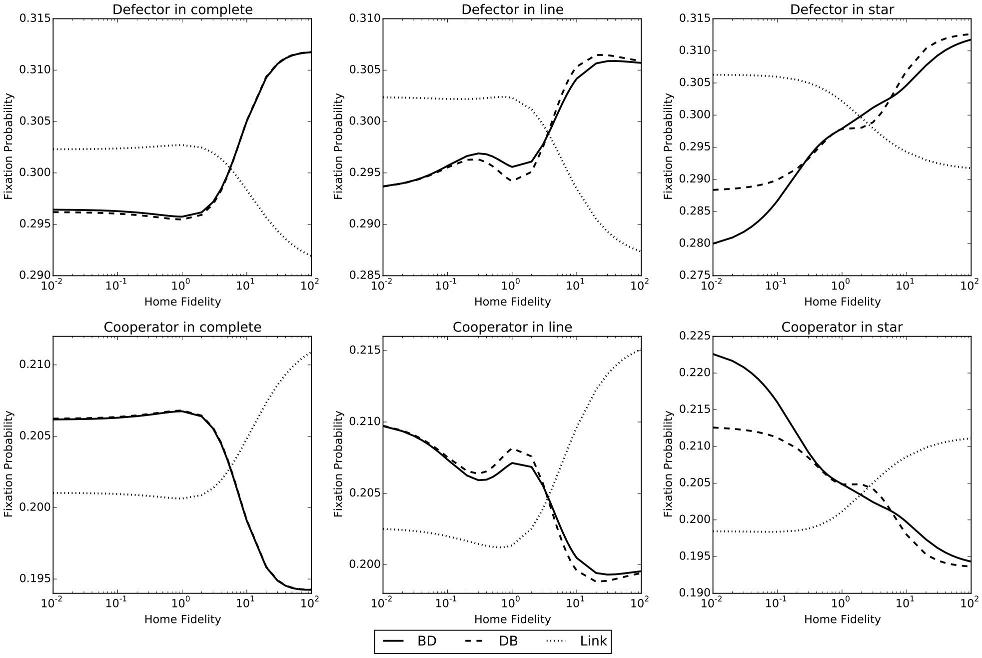


Figure 7.7: Comparison between BD, DB and Link dynamics for Def. 4. For the game $r = 10$ and $v = 2$. The selection bias is $x = 0.5$.

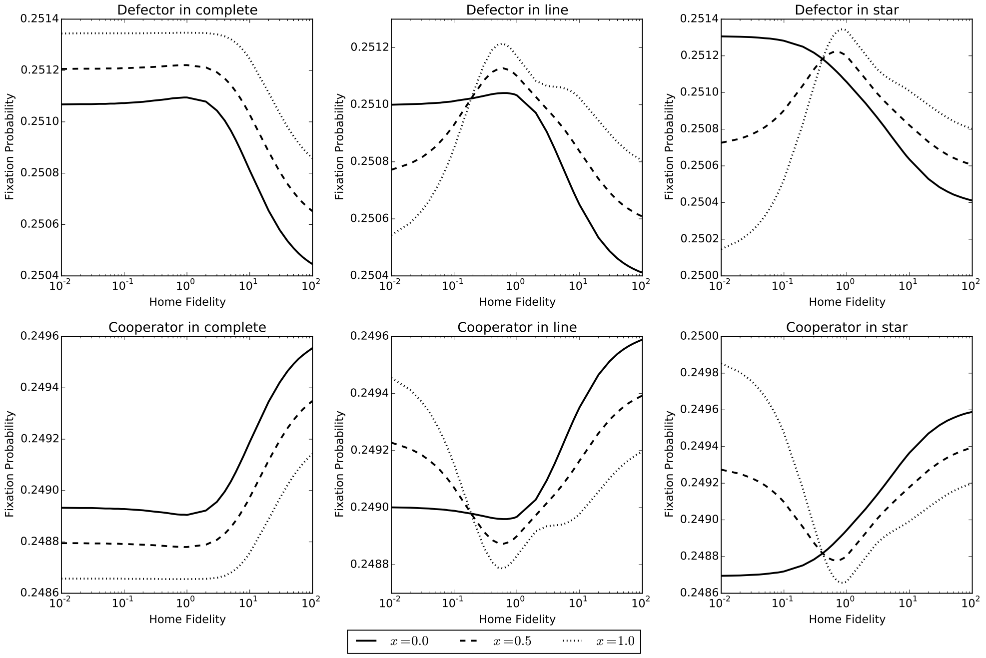


Figure 7.8: Comparing different values of the selection bias for BD Def. 3 dynamics. For the game $r = 10$ and $v = 2$.

change. Overall, this means that the replacement weights cannot be used with the standard definition of the dynamics.

7.4.1 Alternative Birth-Death (Alt. BD) Dynamics

These dynamics follow the same logic as the standard birth-death dynamics. In particular, with probability b_i an individual I_i is chosen for birth who then replaces individual I_j with probability $d_{i,j}$ so $\mathfrak{r}_{i,j} = b_i d_{i,j}$. The probability that individual I_i is chosen for birth is given by

$$b_i = \frac{F_i^{1-x}}{\sum_n F_n^{1-x}}. \tag{7.6}$$

The replacement weights $w_{i,j}$ will still be used to determine the probabilities $d_{i,j}$. The replacement weight contributions used to determine $w_{i,j}$ are an extension of Def. 3 above. In Def. 3, individual I_i is equally likely to replace each member of the group it is present with, excluding itself. Here, individual I_i is likely to replace a group member inversely proportional to their fitness. This takes into account the fact that I_i is most likely to replace the weakest individual it meets. The replacement weight contribution, for all $\mathcal{G}$ such that $i, j \in \mathcal{G}$, is then given by

$$u_{i,j}(m, \mathcal{G}, x) = \begin{cases} 0 & i = j \wedge |\mathcal{G}| > 1, \\ \chi(m, \mathcal{G}) & i = j \wedge |\mathcal{G}| = 1, \\ \dfrac{\chi(m, \mathcal{G}) F_j^{-x}}{\sum\limits_{n \in \mathcal{G} \setminus \{i\}} F_n^{-x}} & i \neq j. \end{cases} \tag{7.7}$$

Plugging the replacement weight contributions into equation (7.1) gives the replacement weights $w_{i,j}$. The probability $d_{i,j}$ is then set to $d_{i,j} = w_{i,j}$. Note that this is possible because $\mathbf{W} = (w_{i,j})$ is right-stochastic, i.e. the rows sum to 1. The selection bias parameter x is used in both the birth and death probabilities such that $x = 0$ ($x = 1$) implies that selection influences only the birth (death) event. Note that for $x = 0$, Alt. BD. is identical to the standard BD with Def. 3.

7.4.2 Alternative DB (Alt. DB) Dynamics

These dynamics are defined in a similar fashion to the standard death-birth dynamics where individual I_j is chosen for death with probability d_j and is then replaced by individual I_i with probability $b_{i,j}$. The death probability is given by

$$d_j = \frac{F_j^{-1+x}}{\sum\limits_{n=1}^{N} F_n^{-1+x}}. \tag{7.8}$$

The birth probability is function of the replacement weights, which are defined using the replacement contributions that are an extension of Def. 3 given above. Rather than using an equal weighting as in Def. 3, death individual I_j is most likely to be replaced by the fittest group member and, therefore, the birth individual I_i is chosen proportional to its fitness. The replacement weight contribution, for all groups $\mathcal{G}$ such that $i, j \in \mathcal{G}$, is then given by

$$u_{i,j}(m, \mathcal{G}) = \begin{cases} 0 & i = j \wedge |\mathcal{G}| > 1, \\ \chi(m, \mathcal{G}) & i = j \wedge |\mathcal{G}| = 1, \\ \dfrac{\chi(m, \mathcal{G}) F_i^{x}}{\sum\limits_{n \in \mathcal{G} \setminus \{j\}} F_n^{x}} & i \neq j. \end{cases} \tag{7.9}$$

The birth probability is then given by $b_{i,j} = w_{i,j}$ where this is possible because $\mathbf{W} = (w_{i,j})$ is left-stochastic, i.e. all columns sum to 1. The selection bias parameter x is once again used in both the birth and death probabilities. For $x = 0$, selection only influences the death event, which happens first, and Alt. DB is identical to standard DB with Def. 3. For $x = 1$, selection only influences the birth event, which happens second.

7.4.3 DB dynamics with no self-replacement (No self-rep. DB)

These dynamics are defined in the same way as Alt. DB with a slight adjustment replacement weight contribution to prevent self-replacement. The self-replacement weight contribution is set to zero, that is, $u_{j,j}(m, \mathcal{G}, x) = 0$ for $j = 1, \dots, N$. However, the probability that the death individual I_j is alone, $\chi(m, \{j\})$, still has to be accounted for. It is assumed that, whenever I_j is alone, I_i will replace I_j proportional to I_i, I_j meeting and the fitness of I_i, that is, $F_i^x \sum_m p_{i,m} p_{j,m}$. This simply means that resampling takes place when I_j is alone. The replacement weight contribution, for all $\mathcal{G}$ such that $j \in \mathcal{G}$, is then given by

$$u_{i,j}(m, \mathcal{G}, x) = \begin{cases} 0 & i = j, \\ \dfrac{\chi(m, \mathcal{G}) F_i^x \displaystyle\sum_{m=1}^{M} p_{i,m} p_{j,m}}{\displaystyle\sum_{\substack{n=1 \\ n \neq j}}^{N} F_n^x \sum_{m=1}^{M} p_{n,m} p_{j,m}} & i \neq j \wedge \mathcal{G} = \{j\}, \\ \dfrac{\chi(m, \mathcal{G}) F_i^x}{\displaystyle\sum_{\substack{n \in \mathcal{G} \\ n \neq j}} F_n^x} & \text{otherwise.} \end{cases} \tag{7.10}$$

7.4.4 Comparing the different dynamics

Figure 7.9 compares the Alt. BD and standard BD Def. 3 dynamics. For Alt. BD the difference between fixation probabilities converges even though its definition is derived from the standard BD Def. 3 dynamics, where the fixation probabilities diverge. In particular, it was previously mentioned that for the standard BD Def. 3 dynamics the fixation probabilities diverge because the selection bias is set to $x = 0.5$. This implies that the first event, birth, is influenced more by randomness with selection playing a smaller role. This gives the less fit cooperators a chance to replace a fitter defector, especially when home fidelity is low and individuals are in groups more often. The effect wears off as home fidelity increases, hence the divergence. However, for Alt. BD dynamics the overall effect of selection gets muted the larger the value of the selection bias gets. This is because, not only does selection take place in the second event, the effect of fitness is concentrated within the groups that form. Note the difference between the fixation probabilities is significantly narrower for Alt. BD than for standard BD Def. 3. However, when the groups on average are large, as is the case with the star graph for low home-fidelity where all individual converge to the center, it seems to match the standard BD Def. 3 dynamics.

Figure 7.9 compares the standard DB Def. 3 dynamics, Alt. DB and no self-rep. DB. Here, standard DB Def. 3 dynamics and Alt. DB essentially behave in the same way as their BD equivalents. The no self-rep. DB dynamics somewhat behaves like the Alt. DB dynamics since

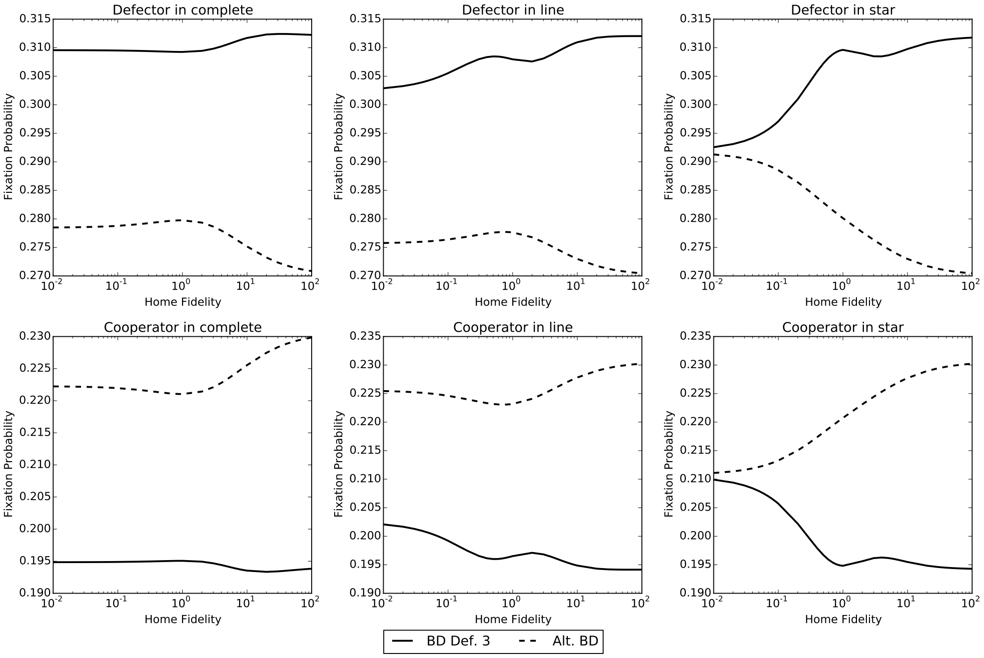


Figure 7.9: Comparison between Alt. BD and standard BD Def. 3. For the game $r = 10$ and $v = 2$. The selection bias is $x = 0.5$.

the difference between the fixation probabilities is also compressed. For the complete graph, it shows very little variability but for the star graph there is much more variation in its behaviour.

7.5 Discussion

In this chapter a generalised definition of the standard dynamics is given that uses a selection bias parameter, which controls the extent to which selection acts on birth or death in a replacement event. Several different definitions of the replacement weights that can be used with the fully independent model of the Broom-Rychtář framework are also given. Whilst only one of these definitions is used in the previous chapters, the objective is to demonstrate the flexibility with which different definitions can be accommodated within the framework.

The key difference between the definitions of the replacement weights is whether or not they can used with the standard dynamics. That is, whether the replacement weights can be plugged directly into the formula for the replacement probabilities given by the standard dynamics. Def. 1, 2, 3 and 4 are of this kind such that they are weights that associate each pair of individuals in terms of the likelihood of one replacing the other, and vice versa. Where as Alt. BD, Alt. DB and No self-rep. DB are nonstandard as they cannot be used with the standard dynamics, instead, a separate definition of the replacement probabilities needs to be given that

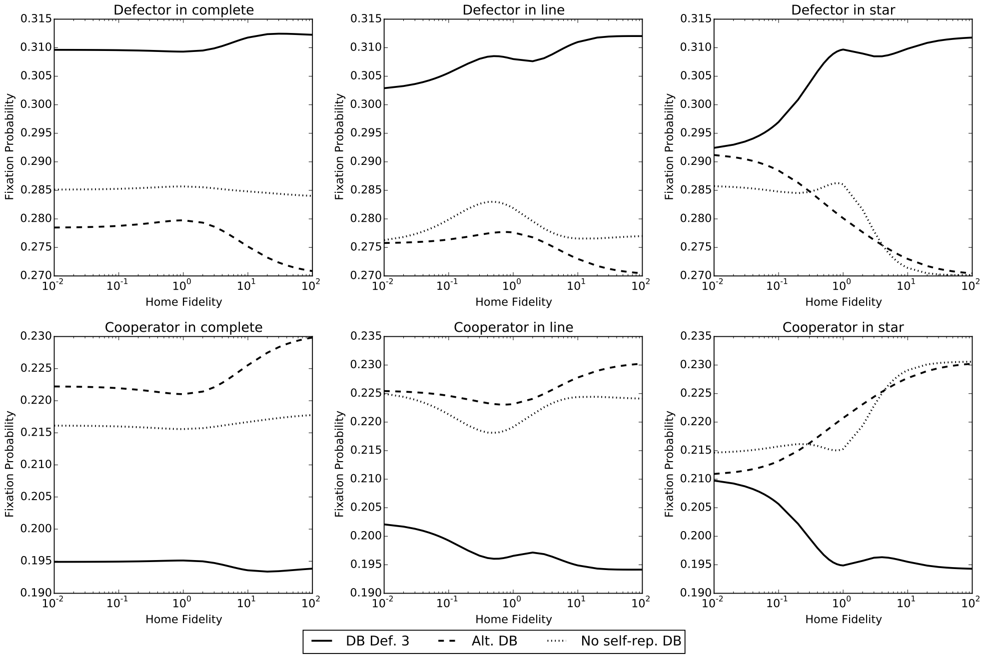


Figure 7.10: Comparison between standard DB Def. 3, Alt. DB and No self-rep. DB. For the game $r = 10$ and $v = 2$. The selection bias is $x = 0.5$.

can accommodate them. In particular, the replacement weights in these cases are probabilities, hence, they give the probability that one individual replaces another.

The nonstandard replacement weights compress the overall effect of selection. This is because with these dynamics the fitness of the individuals is accounted for within the groups they meet, therefore, if they meet less often, the fitness does not really play a major role. However, with the standard replacement weights, the fitness plays a more significant role as it is accounted for independently of the groups in which the individuals meet. This can therefore be used to argue that the standard replacement weights are more superior in that they are more effective at capturing the effect of selection. In particular, this is why Def. 3 was used in the previous chapters as, not only is it standard, but it is effective at accounting for the groups in which the individuals meet.

Chapter 8

Conclusions and Future Work

This research completes the development of the framework of Broom-Rychtář by implementing new evolutionary dynamics that can be used with this framework. The framework can now be used in its full capacity to model the evolution of a structured population consisting of mobile individuals who interact in groups. In order to implement the dynamics, a general understanding of evolutionary dynamics in a structured population was required that led to the study of evolutionary graph theory, which fits naturally in the case of structured populations. This culminated in a set of results that identify structured populations whose evolutionary process is a Moran process, which has homogeneous population structure, in the fixed fitness case for a set of standard evolutionary dynamics. A set of multiplayer interactions that can be used in the framework were then mathematically defined called social dilemmas, of which there are two kinds: public goods and commons dilemmas. Various models were then derived using the framework to illustrate its different applications, each of which give an insight into the evolutionary process. The territorial raider model showed that the mean temperature, i.e. the average likelihood an individual in a population is going to be replaced by another individual, is a better indicator of evolutionary success than the mean group size. Its extension, the generalized territorial raider model, included subpopulations to study the evolution of cooperation, where both the dynamics and structure were found to play a key role. Dynamics with selection second (DBB and BDD) and structures with, ideally, subpopulations of size two gave the cooperators a selective advantage. In this case, the subpopulation temperature was a better measure of the relative success of cooperators. The Markov movement model also studied the evolution of cooperation but, more importantly, made inroads into the development of history dependent models for added realism in modelling populations. It was found that slowing movement down using a movement cost and increasing the time allowed to interact helped cooperation evolve.

Some of the results provided were analytical in the cases where the evolutionary process was quite simple. However, once more complex evolutionary processes were considered, a state transition matrix was constructed and numerically solved. This meant that results could be obtained quickly and accurately but the size of the population that could be considered was restricted. This was purposely done to be aligned with with the project's main aim of developing the dynamics. Large population sizes was of lower priority and could be considered in future work. This would necessarily involve carrying out simulations as the number of states of the population would be very large. The results for larger population sizes can be checked for consistency using the results already available for the smaller population sizes.

A strength of these models is that they all consider multiplayer interactions in groups of variables sizes, thereby allowing more general group behaviours to be considered. Furthermore, rather than arbitrarily forming groups of various size, the group formations are dependent on the underlying movement parameters of the individuals. This results in the possibility of individuals being alone and not interacting with anyone, bringing into light the question what an individual should do when alone. The lone behaviour of an individual plays an important role as it could potentially give it an advantage or hinder it. Another benefit of using the underlying movement parameters is that the time spent interacting with each individual is accounted for. Individuals would interact with each other as often as they meet with these meetings being controlled by the movement parameters and, for the same topographical structure, the results could be different if this is changed. On the other hand, models that use pairwise interactions commonly assume that an equal amount of time is spent interacting with each individual and, even though this could be changed, there is no obvious underlying parameters with which to do this. An extension that can be considered in terms of generating a more varied multiplayer interaction between the individuals would be to allow each individual control over their own movement. Whilst this would be more complicated, it would be interesting to see if individuals with similar interactive strategies end up with similar movement strategies. Alternatively, instead of having individual movement, i.e. individuals move independently of others, movement that depends upon other individuals would be interesting to consider as, for example, some animals move in groups.

The models of population evolution considered do not take into account mutation during a replacement event. Instead, as is the case with many other models, it is assumed that mutation is a one of event in which a mutant type is introduced into a population. For very low mutation rates, the results presented here would hold because mutations would take a long time to appear, which is consistent with the assumptions made. For high mutation rates, the analytical results given would not hold. The way in which the results are presented would have to change as well since the population would now approach a stationary probability distribution that gives the amount of time the population stays in each state. For a highly beneficial mutation, it would be expected that the population spends a significant amount of time in the states where the number of mutant types exceed the resident type. High mutation rates can be incorporated into models in this research that numerically solve for the fixation probability using the state transition matrix. This is because the number of states would remain the same and all that is required is that the state transition matrix is recalculated to allow for mutations, which means that the number of transitions between the states would increase. The expected observation in the case of high mutation rates is that strategies that require continued synergy over a period of time would be adversely affected, as is the case with cooperative strategies.

A limiting feature in this research is that the replacement graphs considered remain constant throughout the evolutionary process. However, this is not a defining feature and the models can be altered to consider evolutionary graphs that evolve with the evolutionary process. For example, relaxing the time homogeneity assumption, implying that movement probabilities can change over time, allows the evolutionary graphs to evolve as they are a function of the individuals' movements. In this case it would be interesting to investigate the effect of individuals spending more or less time together on the evolutionary process. Certain strategies could potentially benefit if the amount of time spent together by certain groups of individuals increases, like cooperators.

Another limiting feature of the models considered is their theoretical nature, that is, the findings have not been checked against data collected in the field. In terms of developing the framework, this does not necessarily pose a major weakness because a lot of the development work revolved around mathematically describing the components of the framework. The models considered were simple illustrations of what can be achieved using the framework. By fully developing the framework and demonstrating how it can be applied, the foundation have been laid for future work using the framework. Furthermore, it is now more clear what kind of real-life scenarios the framework can be used to model. This in turn informs the modeller what kind of data will be required to support the results.

Overall, using the Broom-Rychtář framework, it has been shown how mathematics can be used to highlight the intricacies of an evolutionary process, by enabling the systematic construction of a population evolution model. This has led to an overall better understanding of population evolution with multiplayer interactions.

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