NETWORK FLUCTUATION
AS AN
EXPLANATORY FACTOR
IN THE
EVOLUTION OF COOPERATION

A THESIS SUBMITTED TO THE UNIVERSITY OF MANCHESTER
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Abstract

Network fluctuation as an explanatory factor in the evolution of cooperation

Steve Miller
A thesis submitted to the University of Manchester for the degree of Doctor of Philosophy, 2016

Network reciprocity describes the emergence of cooperative behaviour where interactions are constrained by incomplete network connectivity. It has been widely studied as an enabling mechanism for the emergence of cooperation and may be of particular interest in explaining cooperative behaviours amongst unrelated individuals or in organisms of lower cognitive abilities. Research in this area has been galvanised by the finding that heterogeneous topology promotes cooperation. Consequently there has been a strong focus on scale-free networks; however, such networks typically presuppose formative mechanisms based on preferential attachment, a process which has no general explanation. This assumption may give rise to models of cooperation that implicitly encode capabilities only generally found in more complex forms of life, thus constraining their relevance with regards to the real world.

By considering the connectivity of populations to be dynamic, rather than fixed, cooperation can exist at lower levels of heterogeneity. This thesis demonstrates that a model of network fluctuation, based on random rather than preferential growth, supports cooperative behaviour in simulated social networks of only moderate heterogeneity, thus overcoming difficulties associated with explanations based on scale-free networks. In addition to illustrating the emergence and persistence of cooperation in existing networks, we also demonstrate how cooperation may evolve in networks during their growth. In particular our model supports the emergence of cooperation in populations where it is originally absent. The combined impact of our findings increases the generality of reciprocity as an explanation for cooperation in networks.
Declaration

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Chapter 1

Introduction

The evolution of cooperation is a topic of interest that extends far beyond evolutionary biology. It is relevant to a large and diverse number of fields such as political science [Taylor, 1987], philosophy [Skyrms, 2014], psychology [Sober and Wilson, 1999], sociology [Bowles and Gintis, 2011], history [Ulloa and Froese, 2016], cultural evolution [Boyd and Richerson, 2009], ethics [Binmore, 2005], polemology [Choi and Bowles, 2007], anthropology [Tomasello, 2009], ethology [Dugatkin, 1997], ecology [Stacey and Koenig, 1990] and economics [Gintis, 2005]. In addition to being a widespread phenomenon within the natural world, cooperation is considered to be an important factor in evolutionary processes, particularly in situations where complexity increases, such as early evolutionary transitions, symbiogenesis, or the formation of multicellular organisms [Maynard Smith and Szathmary, 1997].

The existence of cooperative behaviour in nature had presented an ongoing challenge to scientific minds since long before the publication of The Origin of Species [Darwin, 1985, orig. 1859]. However, Darwin’s principle of natural selection transformed a topic of interest into a troubling paradox: why should cooperation exist if competition is the driving mechanism by which all creatures survive and breed? For 150 years, this apparent contradiction has focused the efforts of researchers attempting to explain the existence of cooperation in nature. Put simply, natural selection tells us that hereditary behaviours that increase the likelihood of survival (and hence reproduction), relative to other conspecific individuals, are those behaviours that will thus become more prevalent in subsequent generations. If, conversely, an individual exhibits a hereditary behaviour that increases the likelihood of others to reproduce, then in relative terms, it reduces its own evolutionary fitness. The demonstration of such a behaviour therefore reduces the likelihood of that behaviour appearing through evolution in subsequent
Hence given the simplest interpretation of natural selection, cooperative behaviour should not survive, yet in the real world, we see that cooperation is ubiquitous, at all scales of biological complexity, from bacteria through to humans. The rapid development of computing power has, in recent decades, allowed for the simulation of simplified artificial societies where we can implement abstracted representations of cooperative behaviour in evolving populations. Such approaches, when applied to well-mixed populations of individuals, demonstrate effects that tally with our reasoning based on natural selection, namely that cooperation does not survive. The same findings can also be reached by using a purely mathematical approach rather than by simulation.

After further research, and despite increasingly powerful mathematical and computational approaches to address the problem, the apparent paradox has persisted: the findings of various scientific approaches are contradicted by our empirical observations of real world phenomena. An answer to this apparent contradiction may be provided in the form of enabling mechanisms [Nowak, 2006b]. The work of this thesis focuses on the mechanism of network reciprocity, where rather than assuming that each member of a population has the same likelihood of interacting with any other member of the population, we instead implement simulated populations in the form of individuals interconnected within a network. In the former case—the well-mixed scenario—cooperation cannot survive in evolutionary simulations; whereas in models representing populations as networks, we see cooperation is possible.

We consider network reciprocity to be a particularly interesting explanation since it appears to have limited obvious constraints or assumptions, and as such it offers the potential for generality. In essence, the explanation for how cooperation evolves in networked populations arises from the fact that interactions only occur between connected individuals. This enables the emergence of self-assortativity (for cooperators) over generations. We can understand this effect by comparing with well-mixed populations. In this case, the likelihood of two individuals interacting repeatedly is low. Individuals who demonstrate cooperative behaviour within a well-mixed population will increase the fitness of others relative to themselves and will hence have fewer offspring. Those who take advantage of cooperators will conversely increase their own fitness and have more offspring. However, when a population exists in the form of a network, where individuals have permanent (or long-lasting) connections with neighbours, this creates the possibility for cooperative acts to be reciprocated. If reciprocated
cooperation boosts the fitnesses of the individuals involved, it therefore increases the likelihood of more copies of such behaviour in subsequent generations. Specifically, in the case of networked populations, more successful behaviours will displace the behaviours of less fit neighbours. In this way, cooperative communities can emerge.

From the above explanation, we can see that relationships matter, but what form should these relationships take? Or more specifically, what network topology serves cooperation best? An important part of the answer to this question is given by heterogeneity, by which we mean how diverse the range of connectivities is for different individuals within the network. Increased heterogeneity in these networks generally appears to correspond with increased cooperation. This observation has naturally driven many to investigate the emergence of cooperation in scale-free networks, given their extreme heterogeneity; however, the assumption of such a topology carries a number of challenges. Our work follows a different line of argument. Whilst the majority of research to date has focused on static networks, in this thesis we argue that cooperation can be supported by networks that are perturbed in some way during their existence—in particular we focus on population fluctuation. Such an approach overcomes several difficulties presented by the use of scale-free networks, and, as we shall see, it also offers a more viable explanation for the initial emergence of cooperation in originally non-cooperative societies.

1.1 Objectives and Contributions

The aim of this work is to explore and test the robustness of a mechanism, based on the principle of population fluctuation, that will support the emergence of cooperation within networks over a range of topological heterogeneity. Specifically, the model should support cooperation in networks, regardless of their stage of development or their initial degree distribution. Our thesis describes the following contributions:

- We initially show how introducing a mechanism for population fluctuation within a network can promote the emergence of cooperation within the population. In comparison to existing work, this approach offers an explanation for cooperation which is more robust for a variety of starting scenarios: i) we demonstrate the emergence of cooperation in both pre-existing networks and in networks grown from founders ii) we demonstrate the emergence of cooperation from originally non-cooperative populations.
• We show that the fluctuation model offers an approach that eliminates the requirement for scale-free network heterogeneity. Our model does not therefore assume networks that are likely to have been formed by preferential growth, nor does it imply higher cognitive abilities such as recognition, discrimination or memory.

• We broaden the model and demonstrate that the same principle of fluctuation serves as an explanation for the emergence of cooperation regardless of whether cooperation is viewed as a pair-wise or group-wise process.

• In support of the hypothesis that there may be alternative mechanisms to perturb a network and similarly promote cooperation, we demonstrate how the impact of a minority network of cooperators colliding with a non-cooperative population may precipitate the emergence of group-wise cooperation throughout the resultant population.

The thesis also serves to emphasise two important points which lack coverage in existing literature on models of cooperation:

i. that overly deterministic models, which may in addition be highly synchronous and lacking in noise, may unwittingly preclude the emergence of cooperation;

ii. whilst preferential attachment can have a positive effect on cooperation in societies where some cooperation is already present, it can also impede or even prevent its emergence in populations where cooperators are uncommon.

We emphasise within our work that a model designed to explain the emergence of cooperation should be predicated on it being originally absent from the population.

1.2 Outline of the Thesis

In Chapter 2 we provide historical background regarding scientific interest in cooperation from the field’s early origins, looking at more general questions that attempt to consider cooperation with regards to natural selection, up to more recent research where we focus in on specific work that relates to cooperation in networks.

Chapter 3 describes work involving the development of an existing model for the evolution of cooperation in growing networks. Here we introduced a mechanism that causes fluctuation in the population size. The aim of the this work was to carry out an
initial test of our hypothesis that fluctuation might lead to more consistently increased levels of cooperation as a result of escaping local optima.

Chapter 4 describes how, armed with the proof of concept from our previous work, we then developed a minimal model supporting the emergence of cooperation, which could be applied to both growing and established populations, and which supported the emergence of cooperation from populations that consisted initially of defectors. We refer to the model as minimal to reflect that it eliminates dependence on the assumptions of cognitive abilities. The model also supports the emergence of cooperation for a range of initial topologies of differing heterogeneity.

Chapter 5 explores the robustness of the developed model by testing it with respect to an alternative representation of the cooperative dilemma—the snowdrift game, and by assessing its performance in both the prisoner’s dilemma and the snowdrift game as connection density is increased.

Chapter 6 describes our attempts to extend our existing approach to a population interacting in a group-wise rather than the pair-wise approach we originally adopted. The aim of this was to test whether the same principal of fluctuation would generalise to other models of cooperative interaction.

Chapter 7 considers an idea that emerged during the previous investigations, that generally, perturbation of a network aids the emergence of cooperation. It also represents an attempt to use our model to address more specific questions regarding cooperation. Here we focus on the circumstances in which a small invading clique of cooperators may be able to transform the behaviour of an entire population.

Chapter 8 draws together the conclusions of the thesis. It also describes the impact of our work, limitations, and avenues for further research that the thesis has highlighted.

1.3 Publications Arising from the Thesis

Journal Papers

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Conference papers

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Chapter 2

Understanding Cooperation

In the previous chapter we introduced the apparent paradox that is presented by the existence of cooperative behaviour in the world. Such behaviour appears to contradict our expectations based on natural selection, our predictions from mathematical analysis and our observations of simple simulated artificial populations. In the following, we illustrate how natural selection results in this apparent contradiction, we provide some background of early thinking regarding social behaviour, and we subsequently consider how the appearance of Darwin’s theory of natural selection stimulated and focused questions around the emergence and persistence of cooperation in a competitive world.

With the foundation of an evolutionary perspective and the subsequent synthesis of Darwinian and Mendelian thinking, came the development of mathematically grounded theories attempting to explain the evolution of cooperation. Such theories opened up further possibilities for modelling and for experimental testing of hypotheses. We will describe briefly a number of enabling mechanisms, which have been posited in this way, as explanations for cooperation. In particular we will focus on the enabling mechanism referred to as ‘network reciprocity’ and the importance of heterogeneous network topology in realising this mechanism. This chapter will also consider in detail a number of key research works relating to network reciprocity, which serve as a foundation for the development of this thesis.

2.1 The Riddle of Cooperation

Cooperation among organisms is observed, both within and between species, throughout the natural world. It is necessary for the organization and functioning of societies,
from bacterial to human. Cooperation is also posited as essential to the evolutionary development of complex forms of life from simpler ones, such as the transition from prokaryotes to eukaryotes or the development of multicellular organisms [Maynard Smith and Szathmary, 1997]. A ubiquitous phenomenon in nature, cooperative behaviour has been studied in detail in a wide variety of situations and lifeforms: in viruses [Shirogane et al., 2013], bacteria [Crespi, 2001], insects [Wilson, 1971], fish [Milinski, 1987], birds [Stacey and Koenig, 1990], mammals [Clutton-Brock et al., 2001], primates [Mendres and de Waal, 2000] including of course humans [Axelrod and Hamilton, 1981], where the evolution of cooperation has been linked to the development of language [Nowak and Krakauer, 1999].

In situations where cooperative traits exist within a population, we view cooperating individuals as those paying the costs of cooperating whilst in return gaining benefits that arise when such behaviour is reciprocated by others. In such a scenario, we may pose the question: What happens to mutants that do not inherit such a trait and act entirely from selfish interests? Such individuals, typically referred to as ‘cheats’, ‘freeriders’ or ‘defectors’ will receive the benefits of cooperation without paying any cost. In evolutionary terms, such individuals would be fitter and thus more likely to survive to breeding age, and possibly also generate more offspring. The offspring of defectors would be likely to lack the cooperative trait, and they in turn would also demonstrate higher evolutionary fitness than cooperative offspring. Over generations then, we can see that the logical outcome of such an evolutionarily advantageous mutation would be that selfish behaviour will displace cooperation. In Fig. 2.1, we present an abstracted sketch of how a marginal gain in fitness, arising from a mutation to selfish behaviour, might affect the distribution of inherited behaviours in subsequent generations.

The above outcome, presented from the perspective of natural selection, can also be demonstrated mathematically, where the use of replicator equations [Hofbauer and Sigmund, 1998] to describe cooperation in evolutionary terms yields the same finding [Maynard Smith, 1982]. With the advent of increased computer power, we can simulate artificial populations of evolving individuals and again see the result that cooperation fails to survive.

The riddle of cooperation is hence a question of how to resolve the tension between the ubiquitous existence of cooperation in the natural world and the competitive struggle for survival between organisms (or other collective groups such as genes or cells), which is an essential ingredient of the Darwinian evolutionary perspective.
we need an explanation regarding the difference between empirical observations of cooperation in the real world and the findings obtained from experimental and analytical approaches.

Figure 2.1: Hereditary cheating behaviour dominates cooperation. In this illustration, cheats have a slightly higher fitness than cooperators. This results in: i) slightly increased numbers of viable offspring, and ii) slightly greater survival to breeding age. Offspring of cheats inherit the same cheat behaviour, and their elevated fitnesses translate to greater numbers surviving to breeding age, which in turn also have increased number of viable offspring. This repeats over generations, and hence the number of cheat offspring increases faster than the number of cooperator offspring. Once death is also factored in, the increasing number of cheats, within the constraint of a finite sized population and in the absence of other factors, would rapidly drive cooperators to extinction.

2.2 A ‘Pre-history’ of Cooperation

In the following, which is not intended to be a comprehensive history, we highlight some historical aspects that are relevant to later work on understanding cooperation. With regards to this preliminary material, we tend mainly to avoid use of the term
CHAPTER 2. UNDERSTANDING COOPERATION

‘cooperation’. This word is not typically used within the works discussed, and similarly, whilst the topics discussed may relate to cooperation, they are not specifically examples of it.

Early enquiries into morality, ethics, the social behaviour of humans, and how such behaviour impacts society, can be found in the work of philosophers, economists and political thinkers from at least as far back as the 15th century. Whilst early Greek philosophers such as Aristotle and Plato had considered moral and ethical issues, it was not until the English philosopher Thomas Hobbes’ masterpiece, *Leviathan* [Hobbes, 2008, orig. 1651], that the interdependence of individual behaviour and the nature of society was linked so explicitly. Hobbes argued that the natural state for humans, in the absence of a system of strong governance, was that of “perpetual warre of every man against his neighbour”. This view was undoubtedly influenced by events of the time: Hobbes wrote *Leviathan* during the tumultuous times of the English Civil War, whilst exiled in France, and the book’s publication in 1651 came only two years after the be-heading of England’s monarch, Charles I. Hobbes’ views on human nature were not by any means a universally held perspective; several decades later, writing from a calmer period in English history, John Locke [Locke, 1997, orig. 1689], the ‘Father of Liberal-ism’, argued from a very different position, namely that humans were born as a ‘*tabula rasa*’—a blank slate. The French enlightenment philosopher Jean-Jacques Rousseau was to continue and extend this argument in *A Discourse on the Moral Effects of the Arts and Sciences* [Rousseau, 1998, orig. 1750], explicitly criticising Hobbes, holding that the natural state of man was that of a morally uncorrupted savage whilst modern society was the corrupting influence. Here, on the one hand, we have a cynical view based on the premise that human nature is innately aggressive, violent and competitive; on the other, we have a view representing harmony within nature and cooperation with one’s fellow man. These contradictory views on the innate essence of human behaviour were to be paralleled a century later in the 19th century, by a disagreement between two prominent thinkers, Thomas Henry Huxley and Petr Kropotkin, each separately believing that the theory of natural selection clearly supported their own views.

Before moving on to address Darwin’s theory of evolution, it would be remiss not to mention Adam Smith, the father of modern economics: our understanding of cooperation, and the methods we use to investigate it, have both been informed by the field for which he laid the foundations. Smith, one of the most eminent of the Scottish enlightenment thinkers, is most famous for his work, *The Wealth of Nations* [Smith, 2012, orig. 1776], seen by many as a paean to competitive industrialisation. However,
Smith’s first book, the one he devoted the final stages of his life to rewriting and improving above all others, *The Theory of Moral Sentiments* [Smith, 2010, orig. 1759], appears to be of a rather different flavour; it presents arguments that morals are learned by emotional responses and, in particular, by means of sympathy in considering the circumstances of one’s fellow man. Much like the contrasting views of Rousseau and Hobbes with regards to human nature, here we appear to have a contrast within the key works of a single individual with, on the one hand, *The Wealth of Nations* arguing the economic benefits of selfish individualism whilst, on the other, *The Theory of Moral Sentiments* providing a framework and guidance for the development of virtues and moral behaviour.

It is wryly interesting to observe that the competing actions of many scientists and philosophers, who ultimately have a common goal of understanding how cooperation survives in a competitive world, demonstrate to this day precisely the tension between competition and cooperation that they seek to explain.

### 2.3 The Evolution of Cooperation

In this section, we consider increasingly explicit and more focused attempts to understand the existence of cooperative behaviour informed by, and in terms of, evolutionary thinking. Charles Darwin’s *The Origin of Species* [Darwin, 1985, orig. 1859] had a huge and fundamental impact on many areas of science following its publication, the effects of which continue to this day. In the case of understanding cooperation, the principles of natural selection provided a framework to guide and focus lines of enquiry. However, at the same time, cooperative behaviour created significant challenges to the theory itself. Natural selection also catalysed another interesting shift in thinking: it extended discussions of cooperative behaviour to organisms other than humans.

At the time of Darwin’s writing (ibid.), Victorian England was a nation fascinated with bees and bee-keeping. It was a necessity that Darwin should be able to explain the behaviour of social insects such as bees, which demonstrated apparently altruistic behaviour, both in the generally known example, where a bee’s sting used whilst defending a hive would result in the death of the bee, and also for the case of the selfless behaviour of celibate worker bees. The idea of an inherited adaptation, which was maintained through generations, yet with no method of being passed on through reproduction, clearly presented a challenge. These concerns are neatly reflected in a line
from *The Origin of Species* where Darwin refers in particular to sterile insect castes as being “one special difficulty, which at first appeared to me to be insuperable, and actually fatal to the whole theory”. Darwin was equally exercised over a second issue, this time in humans: altruistic behaviour was far more prevalent than his theory would lead us to expect.

These two concerns are considered in both *The Origin of Species* and in the subsequent *Descent of Man* [Darwin, 2004, orig. 1871] with explanations which have been argued to be precursors to both *kin selection* and *group selection*—two ideas which would go on to garner significant attention in the form of *enabling mechanisms* to support the emergence of cooperation. Within social insects, Darwin proposed an explanation based on blood kinship thus, “This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end.” Alternatively, in explaining altruistic behaviour in human groups, he offered an explanation couched in terms of individuals acting for ‘the good of the group’: “There can be no doubt that a tribe including many members who...were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection.” These two conjectures presaged later more comprehensive investigations regarding the existence of kin selection and group selection. Darwin’s initial forays into presenting these two mechanisms implicitly (but not necessarily deliberately) allowed for some degree of overlap between the two: family can of course also be viewed as a group. This overlap has been revisited in subsequent scientific disagreements regarding the evolution of cooperation and also in interpretations of Darwin’s original ideas.

With evolution reframed by Darwinian theory, the stage was set for the first of many arguments about the precise workings of natural selection; in this case, the argument related specifically to social behaviour. Whilst both were advocates of Darwin, the Victorian English physician, Thomas Huxley (‘Darwin’s Bulldog’), and the Russian former prince, turned anarchist-in-exile, Petr Kropotkin would vehemently disagree on the implications of natural selection for altruistic behaviour.

Huxley, a close friend of Darwin’s, was also an advocate of Thomas Malthus’ views [Malthus, 2008, orig. 1798] regarding the dangers of population growth, specifically that unchecked geometric population growth would outstrip arithmetic increases in the availability of food and other resources. Huxley’s views would undoubtedly also have been affected by his apprenticeship as a medical practitioner, working amidst the
squalor and poverty of the London poor in the mid 19th century. In 1888, shortly after the death of his daughter, and suffering from depression, he wrote an essay titled, “The Struggle for Existence in Human Society” [Huxley, 2006, orig. 1888]. In this essay, Huxley described how overpopulation combined with limited resources were likely to see the emergence of a barbaric ‘state of nature’, with individuals existing as little more than ruthless gladiators, thus setting the scene of nature as a bloodbath, the only respite from which would be provided via blood kinship. Kropotkin’s views, however, were clearly formed from very different experiences. Rather than overcrowding, his observations of nature reflected his expeditions travelling through Siberia, where underpopulation was much more of a pressing concern than overpopulation and Malthusian ideas were largely irrelevant. Similarly, Kropotkin witnessed how human societies cooperated to deal with food shortages and environmental hardship, findings which lead him to believe that authoritarian governance was detrimental to effective support within human societies, and hence further strengthened his belief in anarchy. Kropotkin would subsequently present his beliefs and experiences in his book *Mutual Aid: A Factor of Evolution* [Kropotkin, 2012, orig. 1902], a work which recognised the existence of competition in nature, but in contradiction to the beliefs expressed by Huxley, argued strongly that cooperation was also an important factor. In particular he emphasised its evolutionary role as a widespread survival mechanism in human societies and also amongst animals.

Thus, in the early 20th century, we have two generally opposed views (both politically and philosophically), that of nature exemplifying cooperation, versus that of ‘Nature, red in tooth and claw’ [Tennyson, 2013, orig. 1850]. These polarised positions are unsurprising, considering the authors’ backgrounds, and that at the time, scientific understanding in this field was largely based on subjective interpretation of empirical observations. The situation was improved in part with the rapidly increasing interest in ecology as a field of scientific study. It was also aided by the emergence of population genetics, established by the foundational works of Ronald Fisher, Sewall Wright and J.B.S. Haldane, all of whom were adept in developing scientific theories and using mathematical models to represent observed phenomena. Nevertheless, it would be another two decades before a mathematical model explaining the evolution of cooperation would eventually appear. In 1964, William D. Hamilton developed ideas originally presented by Haldane [Haldane, 1955] and also Fisher [Fisher, 1919], into a full mathematical model of kin selection [Hamilton, 1964] using an approach he labelled ‘inclusive fitness’. The development by these individuals of clearly formulated
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scientific theories, accompanied by mathematical models, set a precedent for others in the field to follow and also opened up possibilities for experimental and theoretical work to objectively assess hypotheses.

The combined work of Fisher, Wright and Haldane would form the basis for the modern evolutionary synthesis (neo-Darwinism), uniting Darwin’s theory of natural selection with the mathematical principles of Mendelian genetics. Research based on this neo-Darwinian perspective was to flourish subsequently, and the field was to gain significant attention with the publication of two highly influential books, *Sociobiology* [Wilson, 2000] in 1975 and *The Selfish Gene* [Dawkins, 1989] in 1976—both of which made current scientific understanding, on kin selection and group selection as explanations of cooperation, available to a much wider audience.

The final development we wish to introduce here extended the pioneering work of early ethologists such as Nikolaas Tinbergen, Konrad Lorenz and Karl von Frisch by bringing economic ideas into the study of hereditary animal behaviours. In an approach which would form the foundation for an entire field of work in evolutionary behaviour, with wider applications in areas such as cultural learning and behavioural economics, George Price and John Maynard Smith explicitly incorporated the relatively recent ideas of game theory [Von Neumann and Morgenstern, 1944] into evolutionary models. Their seminal 1973 publication, “The Logic of Animal Conflict” [Maynard Smith and Price, 1973], considered the question of why competition over resources in animal populations typically did not lead to the fight to the death that Darwinian ‘survival of the fittest’ [Spencer, 1896] would suggest. Maynard Smith and Price’s 1973 paper, and Maynard Smith’s subsequent book, *Evolution and the Theory of Games* [Maynard Smith, 1982], firmly established the field of evolutionary game theory, and also initiated a step change in research into the evolution of cooperation by means of this approach.

The brief history above describes how evolutionary thinking illuminated a pathway from initially philosophical ideas on prosocial behaviour, to the formation of well-defined scientific models seeking to explain cooperation. These foundational works would resolve over subsequent years into a number of discrete mechanisms which we will discuss in further detail in Section 2.6.
2.4 Clarification of Terminology

As attempts to understand social behaviour have progressed, historical work has used terms such as mutual aid, cooperation, altruism and prosociality, in a rather arbitrary manner. In our earlier summary of historical research (Sections 2.2 and 2.3), we have attempted to use terms consistent with those of the original authors’ works. We will now briefly provide clarification on how we use these terms within the context of the remainder of this thesis.

- It is useful to consider actions in terms of ‘cost’ and ‘benefit’, and also in terms of ‘donor’ and ‘recipient’. (Such an approach also sets the scene for the later discussions in this thesis relating to game theory.) The works of West et al. [West et al., 2007a, West et al., 2007b, West et al., 2008] provide further commentary on varying use of terms in this area.

- We use the term ‘cooperative’ to describe a hereditary behaviour or trait which provides a benefit to another individual. More specifically, we may say that cooperative behaviour is one that imposes a cost, $c$, on the donor and confers a benefit, $b$, on the recipient. It does not define which of $b$ and $c$ is the greater value.

- We use the term ‘defector’, as opposite to ‘cooperator’, to generally represent individuals that do not contribute, yet still receive benefits conferred by others (i.e. cooperators). Alternatively a defector may be described as an individual who receives benefits but (unlike cooperators) does not pay a cost. The literature variously uses terms such as ‘freerider’, ‘cheat’ and ‘non-reciprocator’ to refer to defectors.

- We use the term ‘prosocial’ in a very general sense, referring to behaviour by individuals that appears to benefit the group or population of which they are a part.

- Whilst historically the term ‘altruism’ has often been used synonymously with cooperation, outside of references to historical work we will avoid using this term which in general usage tends to denote selfless behaviour. Using the ideas of cost and benefit, altruism in such a sense would reflect hereditary behaviours that, after all factors are considered, provide a net benefit to the recipient that
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exceeds the cost to the donor \((b > c)\). We note that by this definition, an altruistic trait cannot survive in the face of evolution, since donors having this trait would have lower evolutionary fitness than recipients. An important related point here is that a behavioural trait which persists in the face of natural selection, and which may initially appear to be strictly altruistic \((b < c)\), will necessarily be supported by some mechanism which results in the relationship becoming \(b > c\). Ultimately, if a behavioural trait persists, there has to be a net benefit that supports those individuals carrying the trait to a greater extent than those who lack it. To quote Robert Trivers [Trivers, 1971]: “Models that attempt to explain altruistic behaviour in terms of natural selection are models designed to take the altruism out of altruism”.

2.5 Approaches to Investigating Cooperation

Before discussing proposed explanations for cooperation in any detail, we first need to discuss several overlapping approaches that are common in contemporary research on cooperation, and which we will be adopting within this thesis. As a general guide, our own work uses agent-based models, within the framework of evolutionary game theory, an approach which has become standard in investigations of cooperation in networks [Szabó and Fáth, 2007, Perc and Szolnoki, 2010].

2.5.1 Agent-based Modelling

As we mentioned briefly in Section 2.1, analytical (mathematical) approaches using replicator equations may be used to understand the evolution of cooperation; however, their use is constrained by the assumption of a mean field distribution. We commonly refer to a population with such a distribution as well-mixed, meaning that any given individual may interact with all other members of the population with equal probability. The introduction of relationships, or connectivity, between individuals in a population—specifically in the case where connectivity is heterogeneous for differing individuals—creates a mathematically intractable problem. Here we move to an agent-based modelling approach. In such an approach, the model is explicitly defined; namely each individual within the population acts to a clearly prescribed set of rules, within the context of a clearly specified environment. Assumptions within such
a model should be equally explicit. The use of modelling, in this way, is an intrinsically different approach to mathematical analysis. Here we are arguably less focused on solutions per se and the ability to explicitly predict numerical outcomes, and we are more interested in observation, predicting (emergent) phenomena and gaining general insights. Observations from agent-based models may aid in forming empirical explanations and may also help clarify further questions, regarding the phenomena under investigation. As a general guide, we embrace the maxim of George Box that, “All models are wrong; some models are useful” [Box et al., 2005].

2.5.2 Game Theory and Social Dilemma

“In football everything is complicated by the presence of the opposite team.”
—Jean-Paul Sartre

Game theory was pioneered by John von Neumann and Oskar Morgenstern in their ground-breaking work *Theory of Games and Economic Behavior* [Von Neumann and Morgenstern, 1944] as an approach for studying the outcomes of interactions between two or more individuals where each individual’s behaviour affects the others. The crucial assumption here is that the participants being studied are *economically rational*. That is, they make entirely rational decisions in order to maximise some *utility*. In the simplified arena of a game, the utility equates to a payoff. The aim of this approach, in thinking about decisions as a form of game, was to remove all extraneous and also emotive considerations, and thus strip interactions down to their fundamental components.

Of particular interest to those studying cooperation from a game theoretic perspective are those games that represent *social dilemmas*, or *social traps* [Platt, 1973]. Social dilemmas refer to situations where individual members within a group make entirely rational decisions with the explicit aim of maximising their utility, yet the net (collective) outcome is that of sub-optimal rewards for all. This phenomenon was famously outlined by Garrett Hardin, whilst game theory was in its relative infancy, in one of the most highly cited scientific papers ever published, “The Tragedy of the Commons” [Hardin, 1968].

The most well known game in this field, and one which also represents a social dilemma, is the *prisoner’s dilemma*. Originally formulated, in essence, by Merrill Flood and Melvin Dresher at the Rand Corporation in the early 1950s, this game was subsequently described in terms of two prisoners who have been arrested on suspicion
of committing some crime together. They are offered, by their captors, the lure of a reduced sentence in return for providing evidence against each other. Whilst keeping silent (cooperating) will allow them to walk free, rational analysis leads them to betray each other, and they both end up serving a longer jail sentence than if they had cooperated.

The dilemma is commonly represented in the form of a payoff matrix, as shown in Fig. 2.2. The two players shown here each pick one of two strategies: cooperate or defect. The players are not allowed to communicate with each other, and the choices are considered to be simultaneous (so that each player when making their decision is unaware of their opponent’s choice). Payoffs for the four possible strategy pairings are typically referred to by the parameters $T$, $R$, $P$ and $S$, which correspond to ‘Temptation to defect’, ‘Reward for mutual cooperation’, ‘Punishment for mutual defection’ and ‘Sucker’s payoff’ respectively. For the prisoner’s dilemma to exist, values for these parameters must satisfy the relationship $T > R > P > S$. A second condition exists, for those cases where the game is repeated between the same pair of players, namely that $2R > T + S$.

We consider cooperation in terms of costs and benefits between interacting individuals. We can present the original payoff matrix for the prisoner’s dilemma in such a way so as to make explicit how cost and benefit are involved in each of the four possible states for the game (see Fig. 2.2). Cooperation thus involves paying a cost to provide a benefit to another; this benefit may or may not be reciprocated dependent on the opponent. Defectors do not contribute; again, they may or may not receive a benefit depending on the opponent. The payoff matrix broken down in this way also highlights one of the key concepts of game theory: that an individual’s payoff is not just dependent on its own behaviour, it is also dependent on the opponent’s behaviour.

We can analyse the matrix in Fig. 2.3, where we have now replaced the parameters with typical values, and see that in the case where player Y chooses cooperate, player X would have achieved a higher score if they had chosen defect. Alternatively in the case where player Y chooses defect, player X’s highest score would be returned by choosing defect. Thus we see that whatever strategy player Y chooses, the best option for player X is to defect. The payoff matrix is symmetrical for the two players so a rational opponent will reach the same conclusion and will also always play defect. Thus by an entirely rational process, where each individual attempts to maximise their scores, they both end up defecting, whilst if they had both cooperated, they would have maximised their scores. The dilemma is clear.
Figure 2.2: Payoff matrix for the prisoner’s dilemma. (a) illustrates the payoffs in terms of the standard $T$, $R$, $P$ and $S$ parameters. (b) shows the payoffs represented in terms of cost, $c$, and benefit, $b$.

Figure 2.3: Payoff matrix for the prisoner’s dilemma illustrating typical payoff values, which satisfy the condition necessary for the dilemma to exist, $T > R > P > S$.

The prisoner’s dilemma represents an example of a two-player symmetric non-zero-sum game. In zero-sum games, the various players’ gains and losses (as opposed to their actual scores) will balance out. Classical examples are chess for two players or poker for more than two players. Non-zero-sum games offer a more diverse range of outcomes including win-win and lose-lose scenarios. Within game theory we talk in terms of ‘solution concepts’ or ‘equilibria’ to represent strategies that rational players will choose to maximise their utilities in playing a game. It is important to be clear that such solution concepts do not necessarily correspond to the globally optimal outcome, in which case a dilemma exists. Solution concepts instead refer to stable states. We can illustrate this by considering the prisoner’s dilemma payoff matrix values in Fig. 2.3b, which correspond to the globally optimal outcome based on both players cooperating. The global optimum is an unstable state since player X could have increased their score if they had chosen defect. The same applies to player Y. This principle is encapsulated
within the ‘Nash equilibrium’, which represents a solution state (a pair of strategies, in the current example), where no player can increase their score by changing their choice, assuming the other player’s strategy remains unchanged. (It can be useful to consider outcomes from the perspective of regret, for example, “Given the other player has chosen A, I would have been better off had I chosen B”.)

In game theory parlance we say that, for the prisoner’s dilemma, defect is a ‘strictly dominant’ strategy: it will provide a greater payoff for a player regardless of the opponent’s decision. Thus for the prisoner’s dilemma, the stable state defined by the Nash equilibrium is represented by both players choosing to defect.

There are a variety of other two-player games. For the purposes of this work our main interest is in the prisoner’s dilemma since it is the most commonly used representation of cooperation; however, a second game, the ‘snowdrift’ game (also known as ‘chicken’ or ‘hawk-dove’), is also used occasionally to represent cooperation. This game is described in terms of a car stuck in a snowdrift. In order to free the car, one or both of the participants need to dig the car out. If neither digs (both defect), then both will freeze. If one digs and the other does not, the car will still be freed, and both players will make it home. In the snowdrift game, the relative ordering of \( S \) and \( P \) values is reversed giving the following payoff relationship: \( T > R > S > P \) (see Fig. 2.4). Figure 2.5 shows the payoff matrix for the snowdrift game with parameters replaced by typical values. We can analyse this game as before.

If player Y cooperates (digs), the best choice for player X is to defect (refusing to dig is rational since they will still make it home if the other digs). Thus both players gain the benefit of getting home, but only Y pays the cost of digging the car out. If player Y defects (refuses to dig), the best choice for player X is to cooperate. (X pays the cost of digging; both players make it home.) When both players dig, sharing of the task means the cost is halved (see Fig. 2.4b). Thus, unlike the prisoner’s dilemma, there is no strictly dominant strategy. The best choice is to do the opposite of what the other player does. The game is thus termed an anti-coordination game and is sometimes referred to as brinksmanship.

We can also consider if Nash equilibria exist for this game. We can see that there are two such equilibria: the states cooperate:defect or defect:cooperate (bottom left and top right of Fig. 2.5). If we consider the state where both players cooperate, then either could have increased their score by defecting, assuming the other’s choice is unchanged. If we consider the state where both players defect, then either could
have increased their score by cooperating, again assuming the other’s choice is unchanged. It transpires that there are two Nash equilibria: the states cooperate: defect or defect: cooperate (bottom left and top right of Fig. 2.5) are both stable: neither can be improved by a player changing strategy.

In other words, the snowdrift game has Nash equilibria which support at least one individual cooperating, whereas the Nash equilibrium for the prisoner’s dilemma is that of mutual defection. The snowdrift game has thus been argued to be a more realistic representation of cooperation since it does not contradict empirical observations from the real world to the same extent [Hauert and Doebeli, 2004, Santos et al., 2006b].

Figure 2.4: Payoff matrix for the snowdrift game. (a) illustrates the payoffs in terms of the standard $T$, $R$, $P$ and $S$ parameters. (b) shows the payoffs represented in terms of cost, $c$, and benefit, $b$.

Figure 2.5: Payoff matrix for the snowdrift game illustrating typical payoff values which satisfy the condition necessary for the dilemma to exist, $T > R > S > P$. 
2.5.3 Evolutionary Game Theory

Game theory was reconsidered within an evolutionary perspective by George Price and John Maynard Smith [Maynard Smith and Price, 1973]. In evolutionary game theory, we dispense with the concept of rational actors, we relabel payoffs as ‘fitnesses’, and rather than thinking in terms of choices or decisions, we emphasise the word ‘strategies’ to represent hereditary behavioural traits. In this context, strategies that increase fitness will become more prevalent over evolutionary generations, whilst those that reduce fitness are likely to become less common or disappear from the population. Thus the effectiveness of a given strategy is now punished or rewarded by evolution rather than assessed by rational analysis.

The original approach used in evolutionary game theory was that of replicator equations [Taylor and Jonker, 1978, Schuster and Sigmund, 1983], a mathematical approach to represent the dynamics of evolutionary scenarios which allows the calculation of asymptotic frequencies—‘fixed points’, for a mixture of strategies in an evolving population without mutation. Such points are often referred to as ‘evolutionarily stable states’. As discussed in Section 2.5.1, the use of replicator equations is subject to the important constraint that the population is uniformly distributed (well-mixed). In the case of the prisoner’s dilemma, in large well-mixed populations (evolving without mutation), we can satisfy ourselves with regards to how the relationship of the game parameters will influence fitness-based outcomes for behaviours as follows:

Cooperating members of the population score $R$ when playing a cooperator and $S$ when playing a defector. Defector members of the population score $T$ when playing a cooperator and $P$ when playing a defector (see Fig. 2.2). Given random interactions between members of the population, average fitnesses for each strategy depend on the proportions of strategy types present and the values of the game parameters. If $x_C$ and $1 - x_C$ are the proportion of cooperators and defectors respectively present in a populations, then we can see that the average fitness for these two behaviours, $f_C$ and $f_D$ are as follows:

$$f_C = R \cdot x_C + S \cdot (1 - x_C) ,$$

(2.1)

$$f_D = T \cdot x_C + P \cdot (1 - x_C) .$$

(2.2)

Whilst the values of the parameters satisfy the requirements for the dilemma to exist ($T > R > P > S$), we can see that for well-mixed populations, the average fitness
for defectors will be greater than that for cooperators. Since strategies associated with higher fitness values will be found in increased proportions in subsequent generations, the proportion of defectors will increase with evolution. We should note, however, that the ability of individuals to increase their fitness will be impacted by the frequencies of the various hereditary strategies in the population; for example, if strategy A maximises the fitness of its carriers by freeriding on the back of benefits offered by carriers of strategy B, then strategy A can only increase in frequency if there are sufficient carriers of strategy B for it to gain benefits from. Should strategy B become extinct, then carriers of A will see their fitnesses reduce.

The above equations illustrate a general approach for considering long-term evolutionary outcomes for evolutionary strategies. The thinking here parallels the use of Nash equilibria in classical theory. Much like Nash equilibria are used to describe stable solution concepts (strategies) in standard game theory, in evolutionary game theory we use the concept of an ‘evolutionary stable strategy’ (ESS) [Maynard Smith and Price, 1973]. The general idea of such a strategy is that when adopted throughout a population, it cannot be displaced by an invading (initially rare) mutant carrying a different strategy. For many games, the game theoretic concept of Nash equilibria translates to the evolutionary game theoretic concept of the ESS (note that in the former we define a set of strategies, one for each player, whereas in the latter we define one solution for the population). In the prisoner’s dilemma, defect: defect is the strategy set corresponding to the Nash equilibrium and defect is the ESS. In the snowdrift game, however, neither of the Nash equilibria translate to an ESS.1 In the snowdrift game an ESS does, nevertheless, exist: it is based on what is called a ‘mixed strategy’, where we can consider one of two interpretations, either that the population is ‘monomorphic’, hence each individual will choose strategies according to a probability (e.g. cooperate 60% of the time and defect 40% of the time), or that the population is ‘polymorphic’. In this way, subsets of the population are playing different pure strategies. (We use the term ‘pure strategy’ in referring to individuals demonstrating strategies that are deterministically, rather than probabilistically, defined.)

In those cases where we wish to move beyond the idea of a well-mixed population, we may use the concept of a ‘social network’ which describes populations where interactions can only occur between connected individuals. These networks of connections can be represented using agent-based models which can then be implemented as

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1Except in the special case described as ‘uncorrelated asymmetry’ [Maynard Smith, 1982]. This term refers to symmetry breaking of the game, arising from the players actually being aware of which strategy they have inherited.
computer simulations. In such models, we have a starting population of networked individuals containing various strategies and a game which defines network interactions that are conditional on agents’ strategies. With the interactions and the population fully defined, we then wrap these within the context of an evolutionary simulation. In running such simulations, we can then investigate the long-term success for different strategies. Success, in this case, depends on how a strategy performs against other strategies, *in conjunction with* how it fares when faced with other individuals having the same strategy.

In a typical agent-based model of an evolutionary game theoretic scenario, there are generally two fundamental processes that occur within each single time-step or generation (additional processes may also be present, depending on the nature of the model):

i. **Game playing.** Individuals within the population play a specified game against other members of the population. The game that is specified will represent the phenomenon under investigation; for example, whilst prisoner’s dilemma may be used to represent cooperation, the ‘stag hunt’ game is often used to investigate coordination. This game-playing component is an abstracted representation of the behavioural experience of an individual within a population. How an individual fares against the rest of the population depends on its inherited strategy and the strategies of the other individuals it interacts with.

ii. **Strategy updating:** The strategies of higher-scoring individuals probabilistically displace strategies of lower-scoring individuals. This is an abstracted representation of the evolution of heritable traits by natural (genetic) selection. It may also be used to represent the spread of ideas or learning by cultural selection.

This general outline is the basis for many studies investigating the emergence of cooperation in non-homogeneous populations and is the basis for our approach in this work. Further information around evolutionary game theory can be found in the earlier mentioned textbook by Maynard Smith [Maynard Smith, 1982] and in the texts by Hofbauer [Hofbauer and Sigmund, 1998], Gintis [Gintis, 2000] and also Nowak [Nowak, 2006a]. The field of evolutionary game theory that has emerged from the body of work looking specifically at networks is at times referred to as ‘evolutionary graph theory’ [Lieberman et al., 2005].
2.6 Enabling Mechanisms

In the previous sections we have described how cooperation appears to contradict natural selection. An explanation of this apparent paradox is offered in the form of enabling mechanisms [Nowak, 2006b]. Such mechanisms are able to catalyse the emergence of cooperation by modifying the cost-benefit relationship for cooperators and defectors, so as to make cooperation more attractive.

Nowak presents a framework (ibid.), focusing on five of these mechanisms, to explain the existence of cooperation under a range of differing scenarios. The framework consists of: kin selection, direct and indirect reciprocity, group selection and network reciprocity. These five mechanisms have been developed and much studied within the flourishing area of evolutionary game theory, and to a lesser extent in the simulated evolution and artificial life areas (in computer science). We now provide a brief summary of these mechanisms, focusing where necessary on issues relevant to this thesis.

2.6.1 Group Selection or Multi-level Selection

The fundamental idea of group or multi-level selection is that groups that contain altruists may be more successful than groups that do not. Thus natural selection may favour groups containing altruists and therefore (indirectly) favour altruism.

The idea of group selection was hinted at a number of times by Darwin [Darwin, 1859, orig. 1859, Darwin, 2004, orig. 1871], and evolutionary ideas loosely referring to “the good of the species” existed until the publication of Vero Copner Wynne-Edwards’ 1962 book, Animal Dispersion [Wynne-Edwards, 1962], which argued strongly for group selection as an explanation for altruistic behaviour. This work drew fire from ethologists and evolutionary biologists. John Maynard Smith argued that group selection was a weak evolutionary force that could only act under a narrow set of prescribed circumstances [Maynard Smith, 1964], and a damning response was delivered via George C. Williams’ book, Adaptation and Natural Selection: a Critique of Some Current Evolutionary Thought [Williams, 1966], which strongly reinforced gene-centric views of selection. Group selection, as a theory, spent many years in the wilderness before re-emerging in the mid-1970s [Wilson, 1975, Cohen and Eshel, 1976, Matessi and Jayakar, 1976, Wade, 1977] with the support of mathematical models demonstrating that selection may occur at multiple levels and for a wider range of scenarios than had previously been assumed (see also [Wilson and Sober, 1994, Sober and Wilson, 1999, Wilson and Wilson, 2008]). The term multi-level selection is now used
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rather than *group selection*, to reflect recent developments and highlight the model’s applicability throughout a hierarchy of levels.

A model of group selection has been proposed [Traulsen and Nowak, 2006] in the form of a population that is subdivided into smaller groups, each containing cooperators and defectors, which will reproduce according to their fitness scores (payoffs). The groups grow in size depending on the rate at which individuals reproduce. On reaching a certain size, a group will split into two. When one group splits, another becomes extinct to constrain the overall population size. Competition arises between groups since some groups grow faster than others. In particular, groups containing cooperators will grow faster than groups of defectors (defectors playing against defectors result in low or zero payoffs and hence have low reproduction rates). Thus whilst defectors are selected for *within* groups, *at the level of the individual*, groups containing cooperators are favoured and consequently selection occurs *at the level of the group*. The model proposes that, under the assumptions of weak selection and rare group splitting, cooperation may evolve by group selection given the condition:

$$\frac{b}{c} > 1 + \frac{n}{m} ,$$  \hspace{1cm} (2.3)

where $b$ is the benefit gained by being the recipient of a cooperative act, $c$ is the cost of performing a cooperative act, $n$ is the maximum group size and $m$ is the number of groups.

### 2.6.2 Kin Selection

At around the time of the demise of group selection as an explanation for altruistic behaviour, an alternative theory based on selection of related individuals was emerging. Kin selection is used to describe how a tendency to apparently altruistic behaviour is more likely amongst closely related individuals. This was a concept hinted at by the early population geneticists in Haldane’s famous quip, “I would lay down my life for two brothers or eight cousins”, and in Fisher’s tables of relatedness [Fisher, 1919]. A theory was not clearly formulated, however, until Hamilton’s seminal publications in 1964 [Hamilton, 1964] in which he established the relationship (Hamilton’s rule) stating that for altruism to occur, the cost-to-benefit ratio must be less than the *coefficient of relatedness* (the probability of sharing a gene), thus:

$$r > \frac{c}{b} .$$  \hspace{1cm} (2.4)
Simply, it makes sense for an individual to sacrifice themselves to save others if such an action increases the likelihood that genes which the altruist carries will be expressed in greater frequencies in subsequent generations. Clearly one option where this may happen is amongst closely related individuals. From a gene-centric perspective, a gene that causes its host to behave altruistically to other closely related individuals may thus be able to increase the number of copies of itself in subsequent generations, even if that involves the death of the altruist. In other words, rearranging the above equation, \( c < b * r \), an altruistic act will only be performed if the cost of the act is outweighed by the benefits multiplied by the relatedness. Hence increased population relatedness will correspond to increased likelihood of altruistic behaviour, and, similarly, low cost altruistic acts are more likely to occur than high cost ones.

It is clear that for such a mechanism to exist, individuals must be able to discriminate kin from non-kin, or alternatively, they must live in communities where the majority of members are closely related. In ecology, the term ‘population viscosity’ [Goodhart, 1962] is a useful descriptor in referring to groups where membership is ‘sticky’ i.e. where individuals (in the case of kin selection we are specifically considering related offspring) tend to disperse less readily, such as in insect societies [Wilson, 1971] and in naked mole-rats [Jarvis, 1981].

Kin selection is viewed by many as an important mechanism to explain cooperative behaviour for the specific scenario where individuals are closely related. Yet, despite widespread acceptance, the mechanism is not without its detractors. As mentioned in Section 2.3, Darwin alluded to the idea that a community of closely related individuals may also be viewed as a group [Darwin, 2004, orig. 1859]. There has been considerable disagreement over whether examples of kin selection (specifically in the case of those using inclusive fitness) are mathematically equivalent to multi-level selection (‘new group selection’) [Grafen, 1984, Queller, 1992, Frank, 1998, West et al., 2007b, Lehmann et al., 2007, Marshall, 2011]. Of particular note is that the highly respected Edward O. Wilson, formerly one of kin selection’s most passionate exponents, has significantly revised his position and now, as an advocate of David Sloan Wilson’s trait group (multi-level selection) model, relegates the kin selection mechanism to one having a minor evolutionary effect in eusocial behaviour (as found in insect colonies) [Wilson and Wilson, 2007, Wilson and Wilson, 2008]. In 2010, (Edward) Wilson co-authored a paper with Nowak and Tarnita [Nowak et al., 2010] arguing that the inclusive fitness accounting mechanism for kin selection is redundant. This claim has been met with staunch criticism from very many scientists [Abbot et al.,
2.6.3 Direct Reciprocity

Whilst kin selection is arguably of value in explaining cooperation amongst related individuals, and group selection may explain cooperation given certain constraints or assumptions of how sub-groups may form part of a larger population, these two mechanisms are insufficient to form a comprehensive explanation for all examples of cooperative behaviour. How do we explain cooperation that does not fall into such cases?

This was the question that motivated Robert Trivers’ 1971 work, “The Evolution of Reciprocal Altruism” [Trivers, 1971]. In this work Trivers describes (mathematically) a mechanism where the possibility of repeated (iterated) interactions between pairs of individuals increases the likelihood of individuals choosing a costly altruistic behaviour. Such behaviour is demonstrated by one individual to another in the hope of becoming the recipient of future reciprocated beneficial acts in subsequent repeat interactions with the same individual. The extent to which an altruistic behaviour may be chosen over a non-altruistic one is governed by the parameter, \( w \), which represents the probability of the same two individuals meeting again, also referred to as ‘the discounting parameter’ or ‘the shadow of the future’. Direct reciprocity may emerge when the cost-to-benefit ratio of the altruistic behaviour is less than the probability of a further encounter thus:

\[
    w > \frac{c}{b} .
\]  

(2.5)

We emphasise that the term ‘altruistic’ is used by Trivers to describe a behaviour as it appears in the short term. In actuality, this model “take[s] the altruism out of altruism” (ibid.). Trivers demonstrated that apparently discrete altruistic acts actually represented long-term cooperation, which through iterated reciprocity can emerge without any requirement for relatedness and can even arise between different species, such as symbiotic cleaner relationships in fish [Limbaugh, 1961]. Trivers’ paper is also notable for introducing game theoretic elements to the study of cooperative behaviour in evolution: the iterated prisoner’s dilemma is used as an analogue for cooperation. Unlike one-shot prisoner’s dilemma, this iterated version of the game defines repeated interactions between the same pair of individuals.

The criterion for repeated interactions between the same two individuals requires either that individuals are permanently paired which does not typically correspond to
real world scenarios, or that the probability of the same two individuals interacting again is high. This probability can be increased by individuals having the ability to recognise and remember those individuals that have cooperated with them previously. The likely requirement for both recognition and memory, in order to be able to conditionally choose to cooperate or not with another individual, based on their previous behaviour, suggests that direct reciprocity will be confined to species having higher cognitive abilities. In nature, we find that this mechanism is confined primarily to humans and other primates, birds, and a limited number of additional examples such as cleaner fish [Limbaugh, 1961] and vampire bats [Wilkinson, 1984, Wilkinson, 1988].

No summary regarding the evolution of cooperation, and particularly the role of direct reciprocity, would be complete without mentioning the work of Axelrod and Hamilton [Axelrod and Hamilton, 1981]. Trivers had highlighted that in societies where individuals could chose altruistic behaviour or not, reciprocity would support cooperation given repeated interactions. Axelrod focused on the conditionality within this model, considering how one individual should react to another’s behaviour to maximise their own utility? Framed more specifically, this becomes the question: What is the best strategy for playing iterated prisoner’s dilemma? To provide an answer to this, Axelrod ran two computer-simulated tournaments using conditional strategies supplied by members of the scientific community and beyond. The challenge here was for a strategy to perform well, not only against all other strategies, but also when paired against itself. The winner in both tournaments was one of the simplest strategies, ‘tit-for-tat’ (TFT), submitted by Anatol Rapoport. TFT was a straightforward implementation of reciprocity: its overwhelming success arose from simply responding to cooperation with cooperation and defection with defection.

2.6.4 Indirect Reciprocity

Whilst direct reciprocity is generally confined to individuals with higher cognitive abilities such as higher mammals and birds, indirect reciprocity [Alexander, 1987, Nowak and Sigmund, 1998] is almost exclusively restricted to humans. This mechanism expands on the idea of direct reciprocity to describe how one individual may be induced to cooperate with another on the basis of knowledge of the other’s reputation. An obvious example is feedback scoring on eBay. The evolutionary biologist David Haig is quoted as saying, “For direct reciprocity you need a face, for indirect reciprocity you need a name.” [Nowak and Highfield, 2011], highlighting the likelihood that some form of language is required to support the record-keeping and identification needed
for this mechanism. It has been proposed that indirect reciprocity may support cooperation when the probability of knowing someone’s reputation, \( q \), is greater than the cost-to-benefit ratio for cooperative behaviour, thus:

\[ q > c/b . \]  

(2.6)

### 2.6.5 Network Reciprocity

Network reciprocity can be thought of as a case of direct reciprocity where the parameter \( w \) is elevated due to a form of population viscosity. By thus increasing the probability of future encounters, this removes the constraint that recognition is necessary in order to support cooperation. More simply, we can say that a population that has some form of spatial structure is more likely to support cooperation. ‘Spatial structure’, in this sense, should not be considered too literally (as meaning explicitly geospatial). It should be interpreted generally to describe that there are established connections between certain individuals in a population. Here we are thinking of a social network. This connectivity ensures that interactions occur in a repeated manner with the same neighbours, rather than as one-shot incidents between randomly paired individuals.

This mechanism has its origins in a key paper of 1992 by Martin Nowak and Robert May [Nowak and May, 1992]. It is known that in a well-mixed population, cooperation does not survive. With this premise, Nowak and May located the individual members of their population at nodes in a lattice. In evolutionary simulations with populations structured in this way, cooperation was able to survive, due to the ability of cooperators to self-assort\(^2\) over generations. Such clusters allowed cooperators to maintain higher benefits (fitness scores) by excluding non-contributing defectors. In later work [Ohtsuki et al., 2006] it was proposed that network reciprocity (on topologically static graphs) could support cooperation where the benefit-to-cost ratio for cooperation exceeded the average number of neighbours, \( z \), for an individual, thus:

\[ b/c > z . \]  

(2.7)

In subsequent work [Konno, 2011], an alternative relationship was proposed reframing

---

\(^2\)We use ‘assortativity’ throughout this thesis as a term referring to self-similar grouping by strategy, as opposed to ‘assortative mixing by degree’—a measure often found in ecology, physics and network science literature.
the relationship with regards to the mean nearest-neighbour degree value, \( k_{nn} \):

\[
b/c > k_{nn}.
\] (2.8)

The precise nature of the expression is also affected by the choice of update rule used (conditions are shown for death-birth updating [Nowak and Sigmund, 2004]).

We will discuss further aspects of network reciprocity in greater detail in the following sections. For now we highlight an important point about its potential role in explaining cooperation as follows: We have seen how the common enabling mechanisms described above all carry constraints or assumptions that bind them to specific scenarios. This is a less than satisfying state of affairs in the search to explain a phenomenon that is ubiquitous throughout nature, at all levels of complexity. The mechanism of network reciprocity, at present, does not appear to have such specific or restrictive constraints and may thus offer a more general explanation for the emergence of cooperation. Even taking into account species which tend to have solitary lives, it is hard to conceive of organisms which do not exist in some form of social network.

### 2.7 Network Reciprocity and Heterogeneity

We devote this section to a more detailed discussion of the development of scientific work around understanding reciprocity in networks, focusing in particular on the impact of heterogeneity upon cooperation. The works discussed here are core to the content of this thesis. The aim in this section is simply to review, with emphasis on the key elements that our relevant to our work. Additional comments regarding implications and issues are dealt with collectively in Section 2.8.

#### 2.7.1 Effect of Spatial Structure

The classical finding, using the prisoner’s dilemma to model cooperation in an evolutionary game theoretic framework with replicator equations, is that selection on the basis of fitness extinguishes cooperation. In such a model, given an initial mixture of strategies (cooperate and defect) within a population, the population will eventually be overrun by defectors. This result corresponds to our understanding of natural selection (in the absence of any form of enabling mechanism) and, as mentioned earlier, clearly does not correspond with our observations of cooperative behaviour in nature.
In their pivotal 1992 work, Nowak and May [Nowak and May, 1992] laid the foundation for a large field of subsequent research into the impact of spatial structure in evolutionary game theory. Within this work, the authors moved away from the concept of well-mixed populations and instead described a population where agents were located at the nodes of a lattice. In this representation, agents could only interact with those individuals they were directly connected to. Implementing an evolutionary game theoretic model, using the prisoner’s dilemma to represent the social dilemma of cooperation, the authors observed a marked difference to findings obtained on the basis of well-mixed populations: they observed that the effect of spatial structure allowed for the asymptotic persistence of cooperation over generations.

As we have mentioned, the explanation for this marked change in outcome is often considered in terms of population viscosity. Rather than being able to move and interact freely with other members of the population, there is a stickiness due to spatial relationships between members of the population which means that the probability of a pair of adjacent individuals interacting again in the future increases. In other words, the presence of spatial structure eliminates random interactions and results in the same individuals playing each other repeatedly. Thus we have reciprocity simply as a result of spatial adjacency, rather than as a result of individuals using recognition and memory, as is the case for direct reciprocity.

Within an evolutionary context, where we use strategy updating to represent natural selection of fitter strategies, spatial connectivity creates the opportunity for strategies to self-assort. This is because strategy updating results in the displacement of strategies from less fit nodes, by the strategies of fitter neighbours. Strategies located on high fitness nodes are thus unlikely to be displaced and will persist at their location. As updating continues, the strategies of high scoring nodes are likely to displace the strategies of lower scoring nodes. In this way, strategies that cause high fitness can spread and create clusters of nodes all of the same strategy. Whilst this selection process is clearly able to drive self-assortment, there is no mechanism to create other-assortativity: successful strategies only generate copies of themselves.

This understanding raises an important question: In spatial reciprocity models, fitness-based selection drives self-assortativity; but why should self-assortativity benefit cooperators more than defectors? The answer is that cooperators achieve higher fitness when playing other cooperators; however, the same is not true for defectors (see Table 2.1 which shows the prisoner’s dilemma payoffs tabulated). Defectors achieve higher fitness scores by playing against cooperators. Strategy updating can benefit
**Table 2.1:** Table illustrating payoffs for strategy pairings in single parameter weak prisoner’s dilemma. C and D represent *cooperate* and *defect* respectively.

<table>
<thead>
<tr>
<th>Strategy pairing</th>
<th>Scores</th>
</tr>
</thead>
<tbody>
<tr>
<td>C : C</td>
<td>1 : 1</td>
</tr>
<tr>
<td>C : D</td>
<td>1 : b</td>
</tr>
<tr>
<td>D : D</td>
<td>0 : 0</td>
</tr>
</tbody>
</table>

successful cooperators by increasing the numbers of cooperators in their immediate vicinity; whereas if defectors are successful and create copies of themselves (i.e. more defectors in the vicinity), this will reduce their fitness in subsequent prisoner’s dilemma games—*defect:defect* pairings score 0:0, and consequently they will be likely to be displaced. We illustrate this principle in Fig. 2.6. The figure shows how self-similar clustering around a cooperator can increases its fitness, its potential to invade a group of defectors, and hence its ability to promote self-assortativity. There is thus the possibility of a feedback process to drive further self-assortativity. By contrast, we see that if we add self-similar strategies to a defector, this does not increase the defector’s score, nor does it increase its ability to invade adjacent cooperators, or its potential to promote self-assortativity. Self-similar clustering for defectors does not therefore increase the likelihood of further defector self-assortativity.

The above work (ibid.) is notably the first use of the weak prisoner’s dilemma. This is a reformulation of the original game which allows it to be varied by means of a single parameter, $b$, which represents the *temptation to defect*. We show this parameterisation in Fig. 2.7. We refer to the game as weak since, whilst player X is still better to defect when player Y cooperates, in the case where player Y defects, player X achieves the same score regardless of their choice. The drive to defect is therefore somewhat weakened in comparison to the traditional version of the game.

By increasing the temptation to defect, $b$, for a particular model we make it harder for cooperation to emerge within the population. This parameter therefore allows us to characterise models, for comparative purposes, by assessing final levels of cooperation in simulations (after sufficient generations for equilibrium to occur) for a range of $b$ values. An illustration of such a characterisation is shown in Fig. 2.8.

### 2.7.2 Network Heterogeneity and Cooperation

The original findings of Nowak and May with regards to spatial reciprocity were subsequently generalised to networks by Santos and Pacheco [Santos and Pacheco,
Figure 2.6: Diagram to illustrate how self-similar connectivity (arising from self-assortativity) has different effects on cooperators versus defectors whilst attempting to invade a group which has the opposite strategy. The four plots show how connectivity to self-similar strategies can change outcomes for cooperators but not defectors. (a) A cooperator connecting to two defectors (via dotted lines) in a defector dominated population achieves a fitness score of \( f_C = 0 \) and is vulnerable to being displaced by the higher scoring defectors (\( f_D = 1.5 \)). But when it is connected to 2 cooperators (b), outcomes are changed. The backup provided by the self-similar nodes results in an elevated fitness score of \( f_C = 2 \), and the cooperator, hence, now has a higher fitness than either of the defectors it has connected to. Invasion is possible. (c) A defector connecting to two cooperators (via dotted lines) in a cooperator dominated population achieves a fitness score, \( f_D = 3 \). In (d), we can see that when the defector is connected to two other defectors, this offers it no advantage. Fitness scores remain the same as they were in (c).

2005, Santos and Pacheco, 2006]. Here, the authors considered agents located at the nodes of networks, and thus, the term ‘network reciprocity’ was born. In this work the authors examined the effect of networks of varying topology and observed that networks of increasing degree heterogeneity were correlated with increasing levels of cooperation.
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Figure 2.7: Payoff matrix for single parameter weak prisoner’s dilemma. The parameter \( b \) represents the variable temptation to defect. (See Section 2.7.1 for explanation of this parameter’s role in the weak prisoner’s dilemma.)

As described earlier, evolutionary game theoretic models contain both a game playing step and a selection step within a single generation, thus within this work (ibid.) we have:

i. **Play prisoner’s dilemma:** Each agent plays one-shot prisoner’s dilemma, in a ‘round robin’ fashion, with all connected individuals (neighbours) and achieves a fitness score that is the sum of all individual game payoffs.

ii. **Update strategies:** Strategies that achieve low scores are replaced on a probabilistic basis by the strategies of randomly selected neighbours which have higher fitness scores.

We expand further on how these steps are implemented:

**Play prisoner’s dilemma**

The game used is the weak prisoner’s dilemma with payoff values for the actions, referred to as \( T, R, P \) and \( S \), which in the weak game become \( b, 1, 0 \) and \( 0 \) (see Fig. 2.7). The \( b \) parameter represents the temptation to defect and is set at a value greater than 1 for the dilemma to exist. Reconsidering Equations 2.1 and 2.2, we see that asymptotic outcomes for well-mixed populations remain unchanged by this modification. Given the relationship \( T > R \), in the form of \( b > 1 \), defectors will achieve higher fitness scores and will displace cooperation.

From the accumulated prisoner’s dilemma interaction payoffs, an agent (node), \( i \), will achieve a fitness score as follows:

\[
\begin{align*}
T & > R > P = S \\
b & > 1 > 0 = 0
\end{align*}
\]
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\[ f_i = \sum_{j=1}^{k_i} \pi_{i,j} \]  

(2.9)

where \( k_i \) is the number of neighbours that node \( i \) has, \( j \) represents a connected neighbour, and \( \pi_{i,j} \) represents the payoff achieved by node \( i \) from playing prisoner’s dilemma with node \( j \).

**Update strategies**

Each node \( i \) selects a neighbour \( j \) at random. If the fitness of node \( i \), \( f_i \), is greater or equal to the neighbour’s fitness, \( f_j \), then \( i \)'s strategy is unchanged. If the fitness of node \( i \), is less than the neighbour’s fitness, then \( i \)'s strategy is replaced by a copy of the neighbour \( j \)'s strategy, according to a probability proportional to the difference between their fitness values. Thus poor scoring nodes have strategies displaced by those of more successful neighbours.

Hence, at generation \( t \), if \( f_i(t) < f_j(t) \) then \( i \)'s strategy is replaced with that of the neighbour \( j \) with the following probability:

\[ \Pi_{S_i \rightarrow S_i}(t) = \frac{f_j(t) - f_i(t)}{b \cdot \max(k_i(t), k_j(t))} \]  

(2.10)

where \( k_i \) and \( k_j \) are degrees of node \( i \) and its neighbour \( j \) respectively. The purpose of the denominator is to normalise the difference between the two nodes. The expression \( b \cdot \max[k_i(t), k_j(t)] \) represents the largest achievable fitness difference between the two nodes given their respective degrees. (The highest payoff value in the prisoner’s dilemma is \( T \), equivalent to \( b \) in the single-parameter version of the game used here. The maximum possible score for a node of degree \( k \) is therefore \( k \cdot b \). The lowest payoff value is \( P \) or \( S \), both equal to zero, giving \( k \cdot b = 0 \). Thus the maximum possible difference between two nodes is simply the maximum possible score of the fitter node.)

In Fig. 2.9, we illustrate the general findings of this work upon applying the above model to a variety of networks having known topologies. In essence, it is observed that a correlation exists between the extent to which cooperation arises and the degree heterogeneity of the network. The degree of a node is the number of neighbours that node has, and we use heterogeneity to describe how wide the range of observed degree values is. In a lattice, (disregarding edge effects) each node has the same number of neighbours. In a small world network, we see a limited distribution of degree values around a mean. In a random network (a particular case of small-world networks), we
Figure 2.8: Example behaviour profile, used to characterise models of cooperation. Plot shows final fraction of cooperators at end of simulation vs. a variable representing cost-to-benefit (or benefit-to-cost) relationship. In the case of the weak prisoner’s dilemma (as shown in this example), this variable becomes the reward for defection: the temptation to defect \( (b) \). It is thus, effectively, a cost to cooperation. Hence the relationship between cooperation and this variable takes the form of a negative sigmoid. In reporting simulation results for a model, typically each data point would be the average value from a number of replicates.

see a Poisson distribution. In the case of scale-free networks, we see a distribution that corresponds to a power-law. In the latter case, whilst the majority of individuals have 1 or 2 neighbours, a few nodes will have very high degree values; these nodes may be referred to as hubs. We can see then that scale-free networks have a very high range of degree values. In keeping with Santos and Pacheco (ibid.), we refer to this as extreme heterogeneity (although noting that star-like structures can offer even higher heterogeneity).

With regards to the work contained in this thesis, we highlight that the research of Santos and Pacheco, discussed above [Santos and Pacheco, 2005, Santos and Pacheco, 2006], refers specifically and only to fully-formed networks, that is to say the networks are topologically static during the course of evolutionary simulations. We now introduce a piece of work that extends understanding of cooperation beyond purely static networks.

### 2.7.3 Linking Network Growth to Agent Behaviour

In the innovative work of Poncela et al. [Poncela et al., 2008], the authors investigated dynamic networks—those that grew from founding populations of just 3 nodes.
Figure 2.9: The correlation of degree heterogeneity and network-reciprocal cooperation for common network types. The figure illustrates how topologies of increasing heterogeneity may typically be considered to support cooperation. The plots to the right hand side give example degree distributions (on linear plots) for each of the four categories.

Further, they took the ingenious approach of linking agent strategies to the network topology in a manner that connected individual behaviour with the population’s environment. In essence this was a development of the previously discussed works [Santos and Pacheco, 2005, Santos and Pacheco, 2006] with a third step added to the evolutionary process whereby new nodes were added to the network in a manner which preferentially connected them to fitter members of the existing population.

The evolutionary process for a single generation is thus extended from the original model of Santos and Pacheco (ibid.) and becomes:

i. Play prisoner’s dilemma

ii. Update strategies

iii. Grow network

In this additional third step, 10 new nodes with randomly allocated strategies are added per generation (7 on the first generation). Each new node uses $m$ edges to connect to existing nodes. Duplicate edges and self-edges are not allowed. The probability $\Pi(t)$ that an existing node $i$ receives one of the $m$ new edges is as follows:
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\[ \Pi_{\text{edge}}(t) = \frac{1 - \epsilon + \epsilon f_i(t)}{\sum_{j=1}^{N(t)}(1 - \epsilon + \epsilon f_j(t))} , \tag{2.11} \]

where \( f_i(t) \) is the fitness of an existing node \( i \) and \( N(t) \) is the number of nodes available to connect to at time \( t \) in the existing network. Given that each new node extends \( m = 2 \) new edges, and multiple edges are not allowed, \( N \) is therefore determined without replacement. The parameter \( \epsilon \in [0, 1) \) is used to adjust selection pressure. Using a value of \( \epsilon = 0.99 \) represents strong selection thus focusing growth on preferential rather than random attachment.

Using this model of evolutionary preferential attachment (EPA), the authors found that for simulations grown from 3 cooperator founder nodes, cooperation developed alongside the growth of complex (scale-free) networks.

2.8 Comments on Topics of Interest Relating to Existing Research

We now present a series of notes recording topics of interest from our observations regarding the existing research. This section generally underpins the motivations for work described later in the thesis.

2.8.1 The Emergence of Cooperation in Initially Non-cooperative Populations

As indicated earlier, whilst we can intuit how higher organisms may rationalise the benefits of cooperation, we require broader explanations to consider scenarios beyond those that involve mechanisms such as direct reciprocity or kin selection. Our work is motivated by an interest in understanding the origins of cooperation, particularly in the context of early evolutionary transitions [Szathmary and Maynard Smith, 1995].

With this perspective, given that the aim of the work is to model the evolution or emergence of cooperation, we take as our basis for such work the predicate that cooperative behaviour is originally absent from a population. Generally, work to date has considered the persistence of cooperation within populations where it is initially present. We are therefore motivated to consider how cooperation fares when it enters a population that is composed of defectors. The initial appearance of cooperation may be in the form of (genetic) mutations, learning, or invasions from other populations.
of conspecifics. We are reminded here of Axelrod and Hamilton’s 1981 paper, “The Evolution of Cooperation” [Axelrod and Hamilton, 1981], where the authors posed the question: “Initial viability: Even if a strategy is robust and stable, how can it ever get a foothold in an environment which is pre-dominantly noncooperative?”

### 2.8.2 The Emergence of Non-intelligent Cooperative Behaviour

Having briefly summarised the role of enabling mechanisms in explaining cooperation, it is worth expanding on the relevance of the constraints we have outlined for these mechanisms. In doing so, we focus on an issue that is central to the motivations of this thesis: the explanation of cooperation beyond intelligent creatures such as humans. We have mentioned the presence of cooperation throughout the natural world in organisms of varying complexity (see Section 2.1). It is relatively easy to appreciate how, for example, chimpanzees and monkeys might be able to rationalise tit-for-tat cooperative behaviour (direct reciprocity) [Axelrod and Hamilton, 1981]. Intelligent individuals may be able to fathom or learn from experience that the upfront costs, for example, of removing parasites from a fellow individual (in grooming) will offer longer-term benefits in terms of having the favour reciprocated. Such behaviour appears to presuppose, at least, memory, recognition and some form of reasoning ability. Assumptions such as these clearly limit our ability to apply this explanation more widely. We cannot reasonably extend the same line of reasoning to bacteria where we have examples of individuals cooperating to hunt, forage or build shelters. Simply, if you cannot remember who has previously done you a favour, or you can’t differentiate between (recognise) individuals, you cannot return favours. Within this work we are looking for explanations of cooperation that do not pre-suppose higher cognitive abilities. The absence of such abilities precludes tit-for-tat type (direct) reciprocity and also indirect reciprocity, however, network reciprocity may serve as a viable alternative explanation.

In light of the considerations above, we return to the interesting and novel model of evolutionary preferential attachment proposed by Poncela et al. [Poncela et al., 2008] (discussed in Section 2.7.3). We highlight Equation 2.11 of the model which represents the attachment of newcomers to existing nodes in the network. Clearly this equation describes a mechanism which relies on agents joining the network to have some form of global knowledge, in the form of \( N(t) \), the number of individuals in the population and \( f_j \), the individual fitnesses of all other members of the population. The equation also appears to define some form of cognitive ability in summing the fitness of all
individuals. The model clearly supports cooperation, however, its role in explaining the evolution of cooperation would appear to be constrained by the assumptions implicit within the model. In the interests of pursuing a more general model to explain network reciprocal cooperation without intelligence, it would be interesting to test whether such constraints might be eliminated.

### 2.8.3 The Emergence of Cooperation in Static, Fluctuating and Growing Populations

The majority of research into cooperation in networks has been based on fully-formed or pre-existing networks and has generally considered static structures (both [Szabó and Fáth, 2007] and [Perc and Szolnoki, 2010] feature reviews of the literature). A smaller subset of work exists investigating dynamic networks; but these are still based around a nominally constant size, and the fluctuations tend to be focused on rewiring of edges between a constant set of individuals [Zimmermann and Eguíluz, 2005, Santos et al., 2006a, Pacheco et al., 2006a, Traulsen et al., 2009]. Only a few studies look at actually deleting and adding individual members of a network [Perc, 2009, Szolnoki et al., 2009, Ichinose et al., 2013]. We consider that it is important that explanations addressing the emergence of cooperation can accommodate changes in social networks and will be robust in the face of such changes. We also believe that such explanations should be able to demonstrate the emergence of cooperation as a population grows from its origins.

### 2.8.4 The Emergence of Cooperation in the Absence of Scale-free Network Topology

The highly cited works of Santos and Pacheco [Santos and Pacheco, 2005, Santos and Pacheco, 2006] and also Poncela et al. [Poncela et al., 2008] focus on scale-free networks, with the latter paper by Santos and Pacheco specifically illustrating a correspondence between network degree heterogeneity and levels of cooperation observed. Such findings have naturally encouraged much activity investigating the emergence of cooperation with particular regard to scale-free networks. It is not the purpose of our work to in any way refute these clear findings; we do, however, ask the question as to whether there are alternative paths to the emergence of network-reciprocal cooperation which avoid dependency on scale-free networks as a prerequisite. Our reasoning here follows two trajectories:
Explaining the Development of Scale-free Social Networks by Preferential Attachment

The nature of our research, and indeed much research into the evolution of cooperation, relates to social networks—populations of individuals whose interactions are determined on the basis of whether they are connected by an edge or not. Whilst accepting that there other mechanisms by which scale-free networks can emerge [Miller, 1957, Mitzenmacher, 2004], in the context of social networks, and our understanding of how such networks might form, it is more than likely that the emergence of any social network found to have a scale-free structure is the result of a preferential attachment (PA) mechanism [Newman, 2001]. Indeed, within simulations of scale-free social networks, it is almost certainly the case that a preferential mechanism will be explicitly defined [Poncela et al., 2008].

There is no general explanation for the process of preferential attachment [Perc, 2014]. For each scenario where it is posited, an explanation is required specific to that situation. How, for example, would a human entering a social network identify the most well-connected member of the existing network, or the wealthiest, or the most powerful? Even in such a simple example, featuring an organism with advanced cognitive abilities, clearly one explanation cannot satisfy all 3 scenarios. Similar questions become even more challenging when considering less advanced creatures. The assumption of scale-free network structure may aid our understanding of cooperation in simulated networks, but it also creates questions and dependencies regarding the mechanisms by which such networked populations develop.

Challenges to Claims Regarding Scale-free Structure in Real World Scale-free Networks

Initial publications regarding the presence of apparently scale-free networks in real-world phenomena made claims such as: “A common property of many large networks is that the vertex connectivities follow a scale-free power-law distribution.” [Barabási and Albert, 1999], and “Recently, it has been demonstrated that most large networks for which topological information is available display scale-free features” [Barabási et al., 1999]. Following these fairly bold claims, and initial excitement regarding the possible potential of scale-free structure as a unifying factor for complex real world networks, subsequent publications have been critical of original claims of generality [Amaral et al., 2000, Fox Keller, 2005], and further investigations have reported a
range of different distributions for real world networks [Jin et al., 2001, Dorogovtsev and Mendes, 2002]. There have also been critical publications regarding difficulties and failings in attempts to accurately characterise scale-free structure and power-law distributions [Mitzenmacher, 2004, Li et al., 2005, Clauset et al., 2009, Willinger et al., 2009, Stumpf and Porter, 2012].

In some theoretical scenarios, it may be possible to investigate networks with very large orders of magnitude. Such large ranges allow for the ready characterisation of power-law distributions (which define scale-free networks). In contrast, when considering real world networks where sizes are constrained by an upper limit, orders of magnitude are limited [Stumpf and Porter, 2012] thus making reliable characterisation more difficult. In addition, noise and variability are likely to present further confounding factors. The simplest assessment of a power-law distribution is by visual inspection of straight-line behaviour on a log-log plot of a network’s degree distribution. However, given limited orders of magnitude combined with the presence of noise, there is a limit to how effectively a visual inspection can differentiate between, for example, exponential, stretched exponential, log-normal, power-law and power-law with cutoff distributions.

The comments above relate to the characterisation of real-world networks, yet such issues also have relevance within the field of computer-simulated populations. For reasons of computing power/time, evolutionary game theoretic simulations may have similar limitations to those seen for real world networks. Many simulations take place on relatively limited populations of, for example, 1,000 individuals. Clearly the concerns we have described earlier regarding the difficulty of accurately characterising real-world degree distributions, are also pertinent to simulations of networked populations.

Two quotes (from [Clauset et al., 2009]) neatly capture the concerns around characterising scale-free network structures which we attempt to highlight here:

- “In practice, we can rarely, if ever, be certain that an observed quantity is drawn from a power-law distribution.”
- “...in many cases hypothesized distributions are not tested rigorously against the data. This naturally leaves open the possibility that apparent power-law behaviour is, in some cases at least, the result of wishful thinking.”

In summary, whilst scale-free networks clearly can promote cooperation in models of simulated populations, dependence on this topology may be incorporating an
assumption that cannot be met by real world networks.

In the following chapters of this thesis, we report on research we have carried out regarding the evolution of cooperation by means of network reciprocity. We initially start by building on published work that has investigated the role of heterogeneity, and scale-free networks in particular, in the form of a coevolutionary model which supports the evolution of cooperation, alongside that of simulated social networks. In subsequent chapters we adapt and develop this approach in a number of ways so as to explore and address some of the specific observations and issues we have highlighted in this section.
Chapter 3

Evolutionary Preferential Attachment with Fluctuation

In this chapter, we present work in the form of a proof of concept: we investigate whether a mechanism, based on repeated perturbation, will aid the emergence of cooperation in dynamic network-structured populations. Our work here builds on that of Poncela et al. [Poncela, 2012], which demonstrates how cooperation in the one-shot (non-iterated) prisoner’s dilemma game is supported in initially growing populations by an evolutionary preferential attachment (EPA) model. Our motivations arise from two observations after implementing EPA ourselves, namely: i) the model quickly results in a topologically static network, and ii) it is less effective in promoting cooperation when applied to initially non-cooperative networks. These observations raise the questions of whether cooperation levels within the population may be settling at local optima and whether such optima may be escaped by extending the dynamic aspects of the model. We thus propose a model to introduce continuous network topology fluctuation and we investigate the effect of this mechanism on population behaviour for a variety of initial network scenarios.¹

3.1 Introduction

This chapter describes the first of our investigations into network reciprocity. We use agent-based models which feature simulated evolving populations represented in the form of a network, with individuals existing at the nodes of the network and connections represented by edges. The term ‘degree’, in referring to such models, represents

¹Much of the material presented in this chapter has been presented in [Miller and Knowles, 2015b].
the number of neighbour nodes to which an individual is connected. The term ‘heterogeneity’ is used to describe the range of degree values present in the population. Previous research adopting an agent-based approach, using the prisoner’s dilemma game as a metaphor for cooperation, has investigated the behaviour of spatially structured populations of evolving individuals [Nowak and May, 1992]. Within such models, agents may only interact with other agents (nodes) that they are connected to by edges. In well-mixed populations, where interactions are not confined to connected neighbours, cooperators are eliminated. In contrast, in the spatially structured populations described here, the ability of cooperators to self-assort (cluster) over generations allows for the emergence and persistence of cooperation. The subsequent work of Santos and Pacheco using this approach [Santos and Pacheco, 2005] in networks of varying topology, found that heterogeneously structured populations could support cooperation and that increasing heterogeneity (range of degree values) corresponded to greater levels of cooperation.

As with the work referred to above, the majority of studies investigating cooperation with regards to network structure have focused on static networks and hence consider the behaviour of agents distinct from the networks within which they exist (see [Szabó and Fáth, 2007] for a review). Specifically in these works, the behaviour of the individuals within the network has no effect on their environment. In the more recent works of Poncela et al. (see [Poncela, 2012] which collates much of the research), behaviour has been linked to environment by connecting network growth to fitness values arising from individual interactions. The evolutionary preferential attachment (EPA) model developed by Poncela et al. (ibid.) proposes a novel fitness-based coevolutionary mechanism where scale-free networks, which are supportive of cooperation, emerge in a manner that is influenced by the behaviour of agents connecting to the network.

There is a large body of work devoted to coevolutionary investigations of cooperation (see [Perc and Szolnoki, 2010] for a review) of which a subset focuses on coevolutionary studies within networks [Ebel and Bornholdt, 2002, Pacheco et al., 2006b, Szolnoki et al., 2008, Cardillo et al., 2010]. However, the EPA approach of Poncela, which we investigate further in this chapter, is notable in that it addresses an area that seems to have received very little attention: specifically it explores how environment affects the behaviour of individuals simultaneously with how such individuals, in return, affect their developing environment. In typical models of cooperation in networks, population behaviour is affected by environment. The EPA model adds a further causal
relationship in the reverse direction: agent behaviour impacts network structure, thus offering the possibility of some form of feedback.

A typical preferential attachment (PA) system for network growth involves attachment of newcomers preferentially to those existing individuals that have more network connections. The EPA model differs from such an approach in that it describes a process whereby newcomers are more likely to attach to fitter members of the existing population. Here, fitness scores are the sums of accumulated payoffs, gained by agents located on nodes within the network, playing one-shot prisoner’s dilemma with their neighbours. Agents’ game strategies are subsequently updated on a probabilistic basis by comparison with the relative fitness of a randomly-selected neighbour.

The linking of evolutionary agent behaviours to their environment in this way has been shown to promote cooperation, and by using fitness as a basis for preferential attachment, rather than degree, the model may offer a more natural representation of attachment [Nguyen and Tran, 2012] with respect to evolution. The EPA model is an interesting and novel development in the exploration of scale-free networks’ role in the evolution of cooperation. It implements one-shot rather than iterated prisoner’s dilemma and it utilises agents having unconditional (fixed) strategies; hence it potentially presents a very simple model for the co-emergence of cooperation and scale-free networks.

## 3.2 Proposed Model

Our investigations here are driven by two observations regarding the EPA model. First, we note that the model achieves a fixed network structure very early within simulations, from which point onwards agent behaviour has no effect on network structure. It has been highlighted by Poncela [Poncela et al., 2008] that cooperation continues to increase after the network has become topologically static. There is thus a lag phase between the final nodes being added and the level of cooperation reaching a maximum. Within this lag phase, self-assortment continues. Accepting that levels of cooperation are a result of the combined effects of both self-assortment and network topology, we may then ask whether the observed final levels of cooperation represent either global or local maxima. If the latter is the case, then continued structural change might allow for greater exploration of optima, which may then be exploited by self-assortment.

Secondly, whilst the EPA model is shown to support the growth of cooperation in networks from a founder population consisting solely of cooperators (ibid.), it is
not clear how the model functions for networks grown from defectors. Given that we are unable to assume the initial presence of cooperators in nature, we suggest that the broad question of how cooperation emerges requires an answer which generalises to include the case of populations that are not initially cooperative.

Within this work, we introduce a modification to the EPA model which we consider an abstraction common to most, if not all, real populations—that of population size fluctuation. We investigate whether the resulting opportunity for the agents to continually drive the network structure leads to increased levels of cooperation in the population. We achieve this fluctuation effect by pruning the evolving population whenever it reaches a specified maximum size. Here we borrow the term ‘carrying capacity’ from ecology to denote the nominal maximum population size our simulated ecosystem supports. On population size reaching the carrying capacity of the system, agents are selected for deletion on the basis of fitness. Those least fit are removed from the network. The networked population is then grown again, using the EPA mechanism. Fluctuation by means of growth (EPA-based) and attrition (least fitness-based) continues repeatedly until the simulation is ceased. To summarise, our conjecture here is that whilst the original EPA model offered a limited period of time for agents to initially affect the structure of their network, our proposed modification will make this ‘window of opportunity’ repeatedly available.

Whilst a small number of interesting studies have explored the effect on cooperation of deleting network links [Zimmermann and Eguíluz, 2005, Santos et al., 2006a, Pacheco et al., 2006a, Traulsen et al., 2009], or to a much lesser extent, nodes [Perc, 2009, Szolnoki et al., 2009, Ichinose et al., 2013], the process we have implemented here differs to that of existing work, in that it specifically targets individuals (nodes) on the basis of least-fitness. As such it has a ready analogue in nature, in terms of natural selection.

To summarise, our model implements the following steps for each generation:

i. *Play prisoner's dilemma.* Fitnesses are established: each agent plays a single one-shot prisoner’s dilemma game with each of its neighbours and achieves a fitness score that is the sum of all the payoffs.

ii. *Update strategies.* Selection occurs: agents with low scores will have their strategies replaced, on a probabilistic basis, by comparison with the fitness scores of randomly selected neighbours.

iii. *Grow network.* New nodes attach: a specified number of new nodes are added to
the network, each extending \( m \) edges to preferentially selected distinct existing nodes.

iv. **Remove nodes (only in the case of fluctuation models).** Node deletion: if the network size has reached the carrying capacity, it is pruned by removal of least fit agents.

The construction of our model thus incorporates three processes which are dependent on fitness: i) new nodes are connected to the existing population by EPA, ii) updating is based on relative fitness between two competing individuals, iii) nodes are deleted on the basis of least fitness. Whilst all of these processes may be argued to be evolutionary in the sense that they are fitness dependent, we only consider the updating and the deletion mechanisms as being readily comparable with natural selection as it operates in the real world (we return to this issue in Chapter 4).

Finally, with regards to the simulations of networked populations we investigate here, we consider that the question, “How does cooperation emerge?” may be considered from two extreme perspectives: first, the scenario where cooperation develops within a network from its very earliest origins, and secondly, in terms of its emergence within a pre-existing non-cooperative network. In reality, cooperation may occur in scenarios anywhere along a continuum bounded by these two extrema, at varying times, depending on events and circumstances. Hence a network-based model to explain cooperation should be able to deal with either extreme and positions in between. In assessing our proposed model, we investigate scenarios where cooperation may develop as a population grows from its founder members and we also test the model against pre-existing randomly structured networks.

### 3.3 Methods

Our models and simulations are adapted from those described by Poncela et al. [Poncela et al., 2008], with the addition of a pruning mechanism which deletes nodes from the network. We here give a full description of the approach for completeness.

#### 3.3.1 Overview of Approach

The models consist of networks (i.e. graphs) with agents situated at the nodes. Edges between nodes represent interactions between agents. Interactions are *behaviours* of
CHAPTER 3. EPA WITH FLUCTUATION

agents playing the one-shot prisoner’s dilemma game. These behaviours are encoded by strategy variables, one associated with each agent, which take one of two values: cooperate or defect. The game is played in a round robin fashion, with each agent playing its strategy against all its connected neighbours in turn. Each agent accumulates a fitness score which is the sum of all its individual game payoffs.

Within an evolutionary simulation, starting from a founding population, this process is repeated over generations. The evolutionary process assesses agents at each generation on the basis of their fitness scores. Fitter agents’ strategies remain unchanged; less fit agents are more likely to have strategies displaced by those of fitter neighbours. The EPA process [Poncela et al., 2008] connects strategy dynamics to network growth: starting from a small founding population, new nodes are added which preferentially connect to fitter agents within the network.

Our adaptation of the EPA model adds a further component which repeatedly prunes the network: whenever the population reaches a maximum size, a specified percentage of nodes in the network are removed. Nodes are ranked on the basis of fitness and the ranked population is truncated by removal of a set percentage of the least fit individuals. After truncation the network grows again.

3.3.2 Implementation of the Evolutionary Model

As described earlier, the general evolutionary process we implement is as follows:

i. Play prisoner's dilemma
ii. Update strategies
iii. Grow network
iv. Remove nodes (only in the case of fluctuation model)

In the following, we provide more detail on the implementation of each of the four steps:

Play prisoner's dilemma

We use the single parameter representation of the one-shot prisoner's dilemma as formulated by Nowak and May [Nowak and May, 1992]. In this form, commonly known as the weak prisoner’s dilemma, the payoff parameters $T, R, P$ and $S$, become $b$, 1, 0 and 0 respectively (see Fig. 2.7). The $b$ parameter represents the temptation to defect
and is set at \( b > 1 \) for the dilemma to exist.

From the accumulated prisoner’s dilemma interactions, each agent achieves a fitness score, \( f \), as follows:

\[
f_i = \sum_{j=1}^{k_i} \pi_{i,j},
\]

(3.1)

where \( k_i \) is the number of neighbours that node \( i \) has, \( j \) represents a connected neighbour and \( \pi_{i,j} \) represents the payoff achieved by node \( i \) from playing prisoner’s dilemma with node \( j \).

**Update strategies**

Each node \( i \) selects a neighbour \( j \) at random. If the fitness of node \( i \), \( f_i \), is greater or equal to the neighbour’s fitness, \( f_j \), then \( i \)'s strategy is unchanged. If \( f_i \) is less than \( f_j \), then node \( i \)'s strategy is replaced by a copy of the neighbour \( j \)'s strategy, according to a probability proportional to the difference between their fitness values. Thus poor scoring nodes have their strategies displaced by the strategies of more successful neighbours.

More precisely, at generation \( t \), if \( f_i(t) \geq f_j(t) \) then \( i \)'s strategy remains unchanged. If \( f_i(t) < f_j(t) \) then \( i \)'s strategy is replaced with that of the neighbour \( j \), with the following probability:

\[
\Pi_{S_j \rightarrow S_i}(t) = \frac{f_j(t) - f_i(t)}{b \cdot \max[k_i(t), k_j(t)]},
\]

(3.2)

where \( k_i \) and \( k_j \) are the degree values for node \( i \) and its neighbour \( j \) respectively, \( S_i \) and \( S_j \) being their corresponding strategies. The purpose of the denominator is to normalise the difference between the two nodes. The term \( b \cdot \max[k_i(t), k_j(t)] \) represents the largest achievable fitness difference between the two nodes given their respective degrees. (The highest payoff value in the prisoner’s dilemma is \( T \), equivalent to \( b \) in the single-parameter version of the game used here. The maximum possible score for a node of degree \( k \) is therefore \( k \cdot b \). The lowest payoff value is \( P \) or \( S \), both equal to zero, giving \( k \cdot b = 0 \). Thus the maximum possible difference between two nodes is simply the maximum possible score of whichever is the fitter node.)
CHAPTER 3. EPA WITH FLUCTUATION

Grow network

New nodes are added, to achieve a total of 10 at each generation. (On the first generation only 7 new nodes are added to the 3 founders.) Each new node uses \( m \) edges to connect to existing nodes. In all our simulations, we use \( m = 2 \) edges. Duplicate edges and self-loops are not allowed. The probability that an existing node \( i \) receives one of the \( m \) new edges is as follows:

\[
\Pi_{edge_i}(t) = \frac{1 - \varepsilon + \varepsilon f_i(t)}{\sum_{j=1}^{N(t)} \left( 1 - \varepsilon + \varepsilon f_j(t) \right)},
\]

where \( f_i(t) \) is the fitness of an existing node \( i \) and \( N(t) \) is the number of nodes available to connect to at time \( t \) in the existing population. Given that in our model each new node extends \( m = 2 \) new edges, and multiple edges are not allowed, \( N \) is therefore sampled without replacement. The parameter \( \varepsilon \in [0, 1) \) is used to adjust the strength of the attachment mechanism. For all of our simulations \( \varepsilon = 0.99 \), hence focusing our model on selection occurring directly as a result of the preferential attachment process. Strategy types of added nodes (cooperate, defect) are allocated independently, uniformly, at random.

Remove nodes (only in the case of fluctuation model)

On achieving a specified size, the network is pruned based on a set percentage, \( X \), of the population size. We truncate the network by ranking all nodes in order of current fitness scores from minimum to maximum. The \( X \) least fit nodes are then deleted from the network. All edges from deleted nodes are removed from the network. Any nodes that become disconnected from the network as a result of this process are also deleted. (Failure to do this would result in small numbers of single, disconnected, non-playing nodes, having static strategies, whose zero fitness values would result in continual isolation from the network.) When there are multiple nodes of equivalent low fitness value, the earliest (oldest) nodes are deleted first. Where \( X = 0 \), no truncation occurs and the fluctuation model becomes the EPA model.

3.3.3 Applying the Fluctuation Model in Networks Grown from Founder Populations

We investigated networks grown from an initial complete network with size, \( N_0 = 3 \) agents at generation \( t_0 \). Founding populations were either entirely cooperators or
entirely defectors. We tested a range of different sized truncation values from 0.1% to 50% starting from each of the two founder populations (cooperators or defectors). Networks were grown to a maximum size of $N = 1,000$ nodes with an overall average degree of approximately $z = 4$. Simulations were run for 2,000 generations.

### 3.3.4 Applying the Fluctuation Model Applied to Pre-existing Random Networks

Random networks were generated by random connection of edges between a specified number of nodes, corresponding to the required size of network, using the approach of Erdős and Rényi [Erdős and Rényi, 1959]. We used a probability of edge creation given by $\frac{z}{N}$ where $z = 4$, the required average degree for our networks, and $N$ is the size of the population. Simulation parameters were as described for founder population investigations except, i) we focused on a single truncation value of $X = 2.5\%$ and ii) longer run times (e.g. 20,000 generations) were generally required for replicate simulations to stabilise, when looking at pre-existing networks (in particular those initially populated entirely with defectors).

In applying the fluctuation model to pre-existing networks, the model simply ‘sees’ a pre-existing network as a network grown from founders, which has reached the point where it requires truncation. The fluctuation model is thus the same model when it is applied to pre-existing networks as it is when applied to networks grown from founders.

### 3.3.5 General Simulation Conditions

The final fraction of cooperators values we use are means, averaged over the last 20 generations of each simulation (to compensate for variability that might occur if just using final generation values). Simulation data is recorded after step 4 (Remove nodes). Each of the data points on the behaviour profile plots (Figs. 3.1, 3.2, and 3.7) is the mean of 25 simulations. Simulations run solely for the purpose of visually illustrating time plots or degree distributions were limited to 10 replicates in the interests of clarity. Where parameters were modified from those described in this methods section (e.g. longer simulations), this is made clear in the results.
CHAPTER 3. EPA WITH FLUCTUATION

3.4 Results

We present results here for simulations based on two different network starting scenarios: i) networks growing from a complete network of founder nodes, either 3 cooperators or 3 defectors, ii) pre-existing (i.e. fully formed) networks of 1,000 nodes, where nodes have a probability = 0.5 of being occupied by a cooperator (or defector) strategy.

3.4.1 Results for Networks Grown from Founder Populations

We investigate the effect of population fluctuation in networks growing from founder populations consisting of three nodes. We identify several key findings which we describe below.

**Low levels of truncation result in increased levels of cooperation.** For simulations starting from founder networks consisting solely of cooperators (see Fig. 3.1a), we achieved similar profiles to those from the EPA model; however, when lower levels of truncation (less than 20%) were used, we observed consistently higher levels of cooperation than the EPA model, for values of $b$ (the temptation to defect) greater than 1.6. Highest levels of cooperation were achieved using as little as 2.5% and 5% truncation. We observed that cooperation does not reduce to the levels seen for EPA until truncation values are reduced to as little as 0.1% (not shown). Whilst large percentage truncations risk deleting some of the higher fitness nodes which drive (by EPA) the development of the network’s heterogeneous degree distribution and hence aid cooperation, small truncation percentages will focus on lower fitness, likely to be lower connectivity nodes, the deletion of which is unlikely to have such a detrimental effect. Smaller truncation values, occurring at higher frequencies, will maintain a population size closer to the nominally defined carrying capacity with a steady drip-feed of new nodes.

The reason that the EPA model can achieve higher levels of cooperation, for $1 < b \leq 1.6$, than the fluctuation model is because in the (non-fluctuating) EPA model it is possible for the population to be overrun by cooperators, whilst in the fluctuation model repeated truncation prevents such a situation occurring. The fluctuation effect means that new defectors are being added to the population continually, between truncation events. At the other end of the $b$ range, a similar effect occurs. Here, a population overrun with defectors, will be supplied with a steady influx of cooperators.
Figure 3.1: Effect of truncation value on cooperation. Simulations were run for 2,000 generations using the EPA and fluctuation models at a range of temptation to defect ($b$) values. The graphs show the final fraction of cooperators in the population, against $b$ values. Each point on the graph represents an average of 25 replicate results. Each of the individual results is an average over the last 20 generations of a simulation. Plots are shown from fluctuation model simulations using truncation values from 2.5 to 50% of the population. An EPA simulation is also shown which does not feature any truncation. (a) illustrates results grown from founder populations of 3 cooperators. (b) illustrates results grown from founder populations of 3 defectors. (See Figs. 3.3 and 3.4, and accompanying text for more detailed discussion of within-simulation data variability.)

Cooperation occurs even for populations that are founded entirely with defectors. Our results starting from founder populations that consist solely of defectors (see Fig. 3.1b) show a marked increase compared with levels of cooperation achieved by the EPA model. Further, we note that final levels of cooperation arising from the fluctuation model for networks founded from cooperator and from defector strategies were almost indistinguishable statistically: we tested the dependence of the final cooperation levels observed as a function of $b$, the temptation to defect, and the founding strategy type (C or D), using a nonparametric sign test [Conover, 1999] (see Table 3.1).

Fluctuation using random selection can still improve cooperation for defector-founded populations. As a control to the effect seen in the fluctuation model, we repeated the above simulations, deleting nodes randomly rather than on the basis of lowest fitness. Results are illustrated in Fig. 3.2. By comparing with Fig. 3.1, it can be seen that there is a clear difference in outcomes. First, for random deletion (Fig. 3.2), fractions of cooperators present are reduced compared to least-fitness deletion (Fig. 3.1).
Table 3.1: Results of a nonparametric sign test (using a two-tailed exact binomial calculation), comparing the final level of cooperation observed in networks founded with cooperators and networks founded with defectors. For each level of truncation, the 240 * 2 independent samples were paired by the value of b, the temptation to defect. The column n is the number of non-tied sample pairs. The column k is the number of times the cooperator-founded population had a larger final cooperation level than the defector-founded population. With the standard EPA model there is strong statistical evidence that the cooperator-founded and defector-founded networks differ. For the fluctuation model, the evidence is much less clear. Given the power of the test is high here due to the relatively large number of samples used, we can tentatively conclude that there is little or no effect of the type of network founding strategy (cooperator or defector) in those fluctuation models having above 2.5% truncation.

<table>
<thead>
<tr>
<th>Model</th>
<th>n</th>
<th>k</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>EPA</td>
<td>178</td>
<td>151</td>
<td>&lt; 2.20 * 10^{-16}</td>
</tr>
<tr>
<td>T 2.5%</td>
<td>240</td>
<td>143</td>
<td>0.003587</td>
</tr>
<tr>
<td>T 5%</td>
<td>240</td>
<td>129</td>
<td>0.2724</td>
</tr>
<tr>
<td>T 10%</td>
<td>240</td>
<td>126</td>
<td>0.4778</td>
</tr>
<tr>
<td>T 20%</td>
<td>240</td>
<td>137</td>
<td>0.03294</td>
</tr>
<tr>
<td>T 30%</td>
<td>240</td>
<td>131</td>
<td>0.1751</td>
</tr>
<tr>
<td>T 40%</td>
<td>239</td>
<td>136</td>
<td>0.03820</td>
</tr>
<tr>
<td>T 50%</td>
<td>239</td>
<td>129</td>
<td>0.2442</td>
</tr>
</tbody>
</table>

although we note that levels of cooperation achieved still appear to be independent of the founder population strategy (Figs. 3.2a and 3.2b are approximately equivalent for fluctuation model simulations). Secondly, the percentage truncation parameter no longer appears to have anything like the same effect on cooperation as observed for least-fitness deletion (all graphs in Fig. 3.2 look approximately equivalent regardless of % truncation values).

Focusing solely on Fig. 3.2, we now consider the fluctuation model compared to the EPA model. In the case of networks grown from cooperator founders (Fig. 3.2a), EPA demonstrates higher levels of cooperation than the fluctuation simulations. Truncating the network by a method that simply deletes nodes at random is, unsurprisingly, less effective at promoting cooperation than the EPA model which has been shown to be effective for cooperator-founded networks. In the case of networks grown from defector founders (Fig. 3.2b), the fluctuation model achieves the same results as it did for cooperator founders (in Fig. 3.2a). Even with random deletion of nodes though, and given defector-founded populations, the fluctuation model still achieves higher levels
Figure 3.2: Effect of random, rather than least fitness-based, selection of nodes for network truncation. Simulations were run as described for Fig. 3.1, but in the fluctuation model, least-fitness based node deletion was replaced with random deletion. Plots are shown from fluctuation model simulations using truncation values from 2.5 to 50\% of the population. For reference, an EPA simulation is also shown (which does not feature any truncation). (a) illustrates results grown from founder populations of 3 cooperators. (b) illustrates results grown from founder populations of 3 defectors.

of cooperation than those seen for EPA. This result is consistent with similar observations for ranked deletion (see Fig. 3.1b). Thus generally, we see that EPA is less effective at promoting cooperation when networks are grown from defector founders.

How is the fluctuation model with random node deletion still able to promote cooperation, albeit at reduced levels compared to targeted deletion? The random deletion process will inevitably disrupt the formation of the heterogeneous network since it will delete fewer less fit nodes, and more of the higher fitness, higher degree nodes that are important to the scale-free structure. However, this disruption will be countered by the preferential process for addition of nodes which is still fitness-based, i.e. new nodes added will still be preferentially attached to existing nodes of higher fitness. Thus heterogeneity of degree (which supports cooperation) still arises, albeit at a reduced level to that seen in the case of ranked deletion. In final degree distributions, at $b = 1.3$ with $X = 2.5\%$, fluctuation using targeted deletion results in typical degree ranges from 1 to $\approx 100$ with maximum frequencies seen of $> 400$ for $k = 2$, whilst random deletion results in a degree range from 1 to $\approx 50$ with a slight reduction in maximum frequencies for $k = 2$. Whilst there is some reduction in the range of degree values, these values indicate that high heterogeneity is still present. We can hence see that the preferential attachment process enables the fluctuation model to still have a positive (albeit
Fluctuation in population size reduces variability within simulation results and increases cooperation. In Fig. 3.3, we show time plots from the EPA and fluctuation models respectively (starting from cooperator founders, $b = 2.2$). The EPA model (Fig. 3.3a) results in high variability between different simulation replicates with one replicate remaining primarily defectors. The fluctuation model (Fig. 3.3b) demonstrates clear transitions with far less variability in terms of transition time and levels of cooperation achieved. We note that for the fluctuation model, most replicates achieved transitions to a consistent level of cooperation which was equivalent to, or greater than, the highest level observed from amongst all simulations in comparable EPA models.

We considered the possibility that the EPA model may simply require longer for convergence, so ran extended simulations up to 200,000 generations (not shown). We did not see any consistent convergence over later generations: whilst some replicates achieved higher levels of cooperation beyond 2,000 generations, others did not, and some oscillated continually.

**Figure 3.3:** Simulation time plots for EPA and fluctuation models starting from cooperator founders. Figures show 10 replicates using a $b$ value of 2.2. (a) shows the EPA model. (b) shows the fluctuation model operating with $X = 2.5\%$ truncation. Generation 100 is marked in both figures by a vertical black line. This is the point at which the EPA model reaches a fixed network structure, after which no further nodes are added.

Fluctuation results in dramatic increases in cooperation for networks grown from defectors. Figure 3.4 shows replicate simulations for populations grown from defector founders, using the EPA and fluctuation models respectively. In the EPA model
(Fig. 3.4a), all replicates are overrun by defectors. In the fluctuation model (Fig. 3.4b), all replicates transition to cooperation.

Figure 3.4: Simulation time plots for EPA and fluctuation models starting from defector founders. Figures show 10 replicates using a $b$ value of 2.2. (a) shows the EPA model with network fixation occurring at generation 100. (b) shows the fluctuation model operating with $X = 2.5\%$ truncation. Generation 100 is marked in both figures by a vertical black line. This is the point at which the EPA model reaches a fixed network structure, after which no further nodes are added.

Ultimately, the levels of cooperation achieved are similar for the fluctuation model regardless of whether the founder network is cooperators or defectors. We have, however, noticed that whilst final outcomes are typically similar for both types of founding strategy, defector-founded simulations tend to result in later times to transitions and greater variation in such times (comparison of Figs. 3.3b and 3.4b illustrates this difference). Generally, for cooperator-founded populations, with $b$ values where cooperation was able to emerge, we observed transition of the majority ($> 95\%$) of replicates within our typical simulation period of 2,000 generations, with delayed transitions becoming more common given increasing $b$ values. For defector-founded populations, delayed transitions occurred more frequently and to achieve consistent results ($> 95\%$ transitioned) generally required 20,000 generations.

Figure 3.5 shows replicate time plots, along with their corresponding final network degree distributions, for simulations grown from cooperator founders using the fluctuation model. We see that the fluctuation model enables all replicates to consistently reach an apparent power-law degree distribution, as previously reported for the EPA model [Poncela et al., 2012]. We also observe the same final distribution (not shown) for the fluctuation model operating on networks grown from defector-founded
populations. In addition, the replicate data makes clear that, when cooperation arises, variability in transition times (Fig. 3.5a) does not have any bearing on final degree distribution (Fig. 3.5b).

Figure 3.5: Time plots and corresponding final degree distributions for networks grown from cooperator founders using the fluctuation model. (a) shows the time plot for a simulation consisting of 10 replicates with a $b$ value of 2.2. The fluctuation model pruned networks using $X = 2.5\%$ truncation. (b) shows the final degree distributions (at generation 2,000) for each of the 10 simulation replicates.

The presence of a small number of nodes with degree $k = 1$ is an artefact caused by our implementation of the attrition process. The fluctuation model grows the network in the same way as EPA (with each new node extending $m = 2$ connections), but the node deletion component of the fluctuation model can leave residual nodes of degree $k = 1$ (at low frequencies) due to the deletion of connections from removed nodes.

**Cooperation has a characteristic degree distribution.** Whilst in the majority of cases, the fluctuation model supported a transition of networks to a higher level of cooperation, we observed that as $b$ values increased, the transition was not guaranteed. Figure 3.6 captures an example of this, for 1 replicate out of 10 (for $b = 2.2$). The replicate data demonstrates clearly the difference in degree distributions between networks that transition to cooperation and those that do not (the red lines in Figs. 3.6a and 3.6b refer to the same replicate). This result highlights an interesting point; there is a consensus within published literature that increased heterogeneity corresponds with
increased cooperation. The degree distribution shown by the red line in Fig. 3.6 indicates a *star-like* topology\(^2\), which represents maximal heterogeneity, greater than that observed for a scale-free topology, yet this replicate has failed to transition to cooperation. The likely explanation for this is that a defector is occupying the hub node and given the huge influence it exerts due to its position, as long as new cooperators continue joining the network, it will readily maintain a score that is higher than other existing defectors (or newcomer cooperators). Regardless of the explanation, this observation serves as an indication that we should exercise some caution in assuming an overly simplistic relationship between heterogeneity and cooperation. It is also interesting to note that if nodes attached randomly, rather than preferentially, the fitness of a defector on a hub would be reduced since newcomers (which, if they were cooperators, would boost its score) would no longer be driven straight to the defector hub. The resultant reduction in fitness would increase the likelihood of such a defector hub being displaced by a cooperator. Hence whilst preferential attachment may generate heterogeneity, which generally aids cooperation, we cannot assume that it will *always* serve in the interests of cooperators.

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\(^2\) In our simulations, each new node introduces \(m = 2\) edges thus creating an average degree of \(z = 4\). It is therefore not possible to achieve a true star structure for our population (such networks have average degree, \(z = 2(N-1)/N \approx 2\)), hence we use the term ‘star-like’, to describe a network approaching this topology.
3.4.2 Results for Pre-existing Random Networks

The following results look at the effect of the fluctuation model when applied to pre-existing random networks.

**Fluctuation drives non-cooperative pre-existing networks to cooperation.** Figure 3.7 shows final levels of cooperation achieved in simulations which started from randomly structured networks (random graphs). Nodes within these networks were allocated cooperator strategies according to probability $P$ (and hence $1 - P$ for defectors). Simulations were run for 20,000 generations during which time the majority ($> 95\%$) of replicates transitioned to cooperation (for those simulations using $b$ values where cooperation was typically seen to emerge). Three pre-existing networks were tested, consisting of i) $P = 1$, all cooperators, ii) $P = 0.5$, cooperators and defectors in approximately equal amounts, and iii) $P = 0$, all defectors. The curves for these three networks are almost entirely coincident, again illustrating the emergence of cooperation in the fluctuation model, regardless of starting criteria (as seen previously in networks grown from founder populations). A static network where structural changes were disallowed (i.e. strategy updating only) is shown for comparison and clearly illustrates the contribution of the fluctuation mechanism.

![Figure 3.7](image_url)

**Figure 3.7:** Effect of fluctuation model on pre-existing random networks. The plot shows temptation to defect plotted against final fraction of cooperators. Each data point represents an average of 25 replicate simulations. Simulations were run for 20,000 generations. The fluctuation model used $X = 2.5\%$ truncation. The pre-existing networks were in the form of random graphs with each node in the network being populated by cooperators according to probabilities, $P_C = 0, 0.5$ and $1.0$. For reference, simulations involving a topologically static network are also shown. For the static network, nodes were populated with cooperators or defectors randomly, with equal probability.
Fluctuation transforms pre-existing network structure from random to scale-free. In Fig. 3.8 we show the effect of the fluctuation model on degree distribution, for pre-existing random networks, initially composed entirely of defectors. Figure 3.8a, using linear axes, highlights the initial Poisson degree distribution for the pre-existing random network, and Fig. 3.8b highlights, for the final degree distribution, an apparent log-log linearity characteristic of a power-law distribution and hence indicating scale-free topology.

![Figure 3.8](image)

Figure 3.8: Degree distributions for *pre-existing initially random networks* at start and end of fluctuation model simulations. The plots present aggregate data from fluctuation model simulations of 25 replicates and illustrate the starting and finishing degree distributions, after 20,000 generations. The simulations used a $b$ value of 2.2 and truncation used $X = 2.5\%$. The starting networks were in the form of random graphs populated entirely by defectors. The same data are represented on linear plots (a) and log-log plots (b) in order to clearly illustrate the apparent initial Poisson and final power-law distributions. In the interests of visualising both curves, the linear graph only includes degree values up to $k = 20$. The error bars shown represent 95% confidence intervals for the data.

**Cooperation appears to be permanent.** In several thousands of simulations, excluding the small fluctuations visible in asymptotic states (see Figs. 3.3, 3.4 and 3.5), whilst we have observed failures to transition to cooperation, we have not observed a single instance of widespread reversion to defection once cooperation has been achieved within a population. It would appear that once cooperation is established by means of this model, it does not collapse.
CHAPTER 3. EPA WITH FLUCTUATION

3.5 Discussion

The main findings of the work described in this chapter are that:

i. fluctuation of networks leads to an increase in levels of cooperation compared with the EPA model,

ii. that the levels of cooperation achieved thus are largely independent of whether the populations were founded from defectors or cooperators,

iii. that the fluctuation model supports the emergence of cooperation both in networks grown from founder populations and also in pre-existing random networks.

The simulation time plots we have provided in our results give an indication as to how the fluctuation model is able to reach the increased levels of cooperation we observe. Whilst the EPA model results in a high degree of variability, the fluctuation model produces consistent transitions. The EPA model has two interacting dynamic components: preferential attachment and strategy updating. The attachment process generates structure. Strategy updating, which represents selection, allows for assortativity. Structural organisation within the EPA model therefore only occurs until the network reaches its defined size limit. Changes in levels of cooperation continue to occur after this point. Given that the network structure is fixed, these latter changes can only occur by means of the remaining active component of the EPA model: strategy updating. Close examination of EPA simulation time plots (such as are shown in Fig. 3.3) reveals a noteworthy observation when we look at $b$ values greater than 1.6: at the time point where network structure becomes fixed (shown by vertical line in the figure), those replicates having higher levels of cooperation at this point often finish with higher levels of cooperation than those replicates experiencing lower levels of cooperation at the network fixation point. Whilst we do not yet have a detailed understanding of how cooperative structure develops within our networks, this observation suggests that prior to the network fixation point, some structural precedent is set which gives a probabilistic indication of how a network will profit, in cooperative terms, from the strategy updating that occurs subsequent to structure fixation.

Based on the work of Poncela et al. [Poncela et al., 2012] which describes the connection between scale-free network structure and cooperation, a plausible explanation for how such a structural precedent may impact EPA simulation outcomes is as
follows: Whilst new nodes are preferentially attached to a growing network in a way that may generate hubs and hence a scale-free structure, there is no guarantee that the early clusters of nodes appearing in the network will be cooperators (cooperator and defector strategies are assigned to newly added nodes with equal probability). If the first hubs appearing in the network are largely occupied by cooperators who in turn have cooperative neighbours, then these agents are likely to accumulate high fitness scores. This would potentially set the foundation for cooperation since such a group is likely to have a hub which would then draw further connections from newcomer nodes and so promote scale-free structure. On the other hand, if early groupings of cooperators are interspersed with large numbers of defectors, this is likely to result in defectors predating cooperators and (initially) accumulating higher fitness values than the cooperators. Strategy updating within such groups is likely to result in the conversion of any lower-scoring cooperators present to defection. Eventually larger groups of defectors will emerge, resulting in generally lower fitness values.

Where defectors predominate, there will generally exist a sea of zero fitness values (defect:defect interactions score 0:0), however, as long as preferential attachment continues supplying new nodes of which approximately half are cooperators, there are opportunities for a few of the existing defectors to gain positive scores. We can see from Equation 3.2, which defines EPA node addition, that given $\varepsilon = 0.99$, any rare defector(s) that achieves a positive score will end up with the majority of newcomers connecting to them. Given that half of the newcomers will be cooperators, such a defector can then continue to maintain a positive score. Thus, rather than having a distribution of nodes presenting a range of attachment probabilities (the rich-get-richer effect), in the scenario where a population is mostly defectors EPA can bring about a runaway effect where one node becomes winner-take-all as long as new cooperators continue to be provided. It is this very strong draw from a single node that creates a star-like rather than a scale-free structure.

After network fixation, strategies can be updated, but network structure cannot change. A network that initially tends to a star-like structure will present a topology that is less than ideal in terms of providing the clustering of nodes necessary for cooperators to self-assort by the process of strategy updating. Further, structures that are of this topology or are tending towards it at the time of network fixation are likely to delay or permanently obstruct the emergence of more heterogeneous topologies which will better support cooperation.
The fluctuation model effectively allows a network to ‘go back in time’ to fix structures that may have caused such a poor start. The model targets low fitness nodes (and their edges) for deletion. Such nodes are more likely to be defectors surrounded by other defectors (a defect:defect interaction results in a payoff of zero for both parties) since any low degree defect:cooperate pairings that do occur are likely to result in rapid conversion of a cooperator to defector during strategy updating. New nodes do not serve as replacements for those deleted, i.e. they do not inherit the deleted node’s connections. Instead, newcomers are preferentially attached (by EPA) to higher fitness nodes. In this way, networks that have a poor start are no longer permanently fixed, they have repeated opportunities to address the poorest performing elements of their structure. When considered in this way, it is no longer surprising that similar levels of cooperation are ultimately achieved regardless of starting strategies. In the same way that this process of continual readjustment allows the network to deal with a particularly sub-optimal initial structure, it similarly allows the network to deal with less than favourable initial strategy distributions. If nodes perform poorly, then sooner or later there is a likelihood they will be deleted (and should subsequent newcomers also perform poorly, there is a similar likelihood that they too will be deleted).

It is this ability to continually eliminate poorer performing network nodes and their positions in the network (their connections) that supports the fluctuation model’s ability to convert pre-existing random networks, initially populated entirely by defectors, to highly cooperative networks with a power-law distribution.

The fluctuation model as described in this chapter is of highly abstracted form and is not intended to be an accurate representation of specific real world examples of the evolution of cooperation; it is unlikely to readily map onto any such examples. Nevertheless, the model, and its component parts, may be interpreted in several ways as loosely analogous to natural phenomena. Equally, aspects of the model might be criticised as being inaccurate or misleading representations of real world effects. Indeed, some aspects of the model serve as a convenience: they are incorporated to establish a functional model, rather than because they accurately represent real world effects or well-defined elements of evolution. We now briefly highlight a few specific points regarding components of the model:

- Strategy updating: Our model is in essence intended to be one of (Darwinian) evolution, and the aim of the strategy updating process is as an analogue of natural selection. However, it does not seem unreasonable to consider that whilst this
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updating process was initially considered to be representative of genetic evolution, it could also represent transmission of ideas by selection, for example, cultural evolution or social learning [Campbell, 1965, Cavalli-Sforza and Feldman, 1981, Boyd and Richerson, 1988a, Richerson and Boyd, 2005]. It is also worth highlighting that unlike the attachment process for newcomers, in strategy updating, the new strategy ‘inherits’ a set of connections forged by its ancestors, along with the advantages or disadvantages that those connections confer.

• Newcomer node attachment: In the EPA model, new nodes joining the network could be considered as being ‘newly born into the network’ or alternatively as ‘newcomers from outside the network’. In either case, they are positioned (given connections to existing nodes) by fitness-based preferential attachment and the connections to these existing nodes may prove advantageous or disadvantageous to the newcomers. Arguably, this mechanism could be criticised on the basis that an individual ‘born’ into a network is likely to inherit some connectivity to existing members, and also that preferential attachment as a mechanism for forming connections, might be ‘unrealistic’. We will return to the topic of newcomer attachment in the following chapter (see Section 4.2.1).

• Deletion: Whilst deletion in combination with node attachment may be viewed as a kind of death-birth process, it is important to note that in our model, when individuals are deleted we remove their connections and, as stated above, newcomers form new connections. Deletion thus eliminates not only the least fit agents, but also the relationships established over generations by successive offspring. (For some scenarios this may be realistic, for others, not.) The deletion mechanism we have chosen thus serves to introduce some form of flux into the actual network topology itself rather than just its members’ behaviour. This is therefore a different, more general, and perhaps more disruptive process to that described by strategy updating which simply represents two individuals competing to pass on their strategies. Deleting both nodes and connections simultaneously is a simple option to incorporate a broad-based fitness effect in the network structure, perhaps akin to real world scenarios where external environmental effects may have wider consequences for an entire population (or group) rather than for just specific individuals.

Each of these processes is open to alternative interpretations. However, we suspect based on our results from this work, that it is not necessarily the exact process that
is critical, it is merely that, much like most ecological systems in nature, a network continues to be perturbed in some way and is hence unable to achieve a permanently fixed structure: it thus continues to adapt. The investigations described here show evidence of fluctuation promoting cooperation, but in a manner that may be dependent on the specifics of EPA. In the next chapter we investigate this idea further whilst removing dependency on the preferential mechanism.

### 3.6 Conclusion

Natural selection acts as a culling process that maintains diversity. In this chapter we have attempted to represent such a process, within a model of networked individuals, by implementing a mechanism that enables the network to adapt in response to such culls. Essentially we have introduced a relatively simple modification to the original EPA model that symbolises an effect elemental to the behaviour of populations in the real world—effectively some form of flux in the environment or ecosystem that in turn impacts selection. Our incorporation of *fitness-based node deletion* into the EPA model enhances the opportunities for a networked population to continue to adapt in response to selective pressures from the environment. We have shown that such a mechanism generally promotes the evolution of cooperation beyond that of the well-mixed scenario and markedly so in the case of networks grown from defector-founded populations. We have also shown that this mechanism results in levels of cooperation that are generally independent of starting behaviour. We thus have a model that supports cooperation in both growing and pre-existing networks, regardless of whether they are initially cooperative or not.

It is important that models which seek to explain the origins of cooperation are general and also robust to starting conditions. The work reported in this chapter, based on incorporating fluctuation within EPA, suggests the possibility of a model that has the potential to achieve both of these requirements. Our findings here thus form the precursor to work in the following chapter(s) where we describe the development of more natural and minimal models of network fluctuation.
Chapter 4

A Minimal Model for the Emergence of Pair-wise Cooperation in Randomly Growing Networks

In the wake of Santos and Pacheco’s finding [Santos and Pacheco, 2006] that heterogeneous connectivity promotes cooperation in networks (in particular scale-free heterogeneity [Santos and Pacheco, 2005]), much research has been published describing further investigations into the role of network topology in the evolution of cooperation by means of network reciprocity [Abramson and Kuperman, 2001, Hauert, 2002, Hauert and Doebeli, 2004, Lieberman et al., 2005, Ohtsuki et al., 2006]. Such research is commonly conducted using agent-based models of social networks, where we describe populations with regards to the microscopic behaviours of their members (agents) and the connectivity between those agents. Within such models, the assumption of scale-free topology almost certainly implies a network that has been formed by a process of preferential attachment (PA) [Newman, 2001]. Further, given the absence of a general explanation for preferential attachment, there is a requirement for individual, case-specific explanations. In the case of social networks, such explanations likely imply higher cognitive abilities, thus potentially limiting the generality of such models.

Continuing within an evolutionary game theoretic context, using the weak prisoner’s dilemma as a metaphor for cooperation, in this chapter we present a minimal model for cooperation in networks.¹ The model describes network growth by chronological random addition of new nodes, combined with regular attrition of less fit members of the population. Our aim is that this model will demonstrate an alternative

¹Some of the material presented in this chapter has been presented in [Miller and Knowles, 2015a].
explanation for network-reciprocal cooperation which specifically meets two further requirements:

i. Dependence on scale-free network structure (and preferential attachment) should be eliminated—thus allowing for a model which makes minimal demands regarding the abilities of agents within it.

ii. Cooperation should be promoted regardless of initial population behaviour—a model that supports cooperation in populations that are initially dominated by defectors may be of value in helping to explain the emergence of cooperation in early evolutionary transitions [Maynard Smith and Szathmary, 1997].

4.1 Introduction

In the previous chapter, we demonstrated how a model of evolutionary preferential attachment (EPA) featuring network fluctuation was able to support cooperation. We showed that such an approach was robust with regards to network starting scenarios and types of strategies initially present. Specifically the model enabled the emergence of cooperation in initially non-cooperative founder networks. We observed that the use of a preferential attachment process within the model typically resulted in apparently scale-free network topology (as expected).

We have highlighted in Chapter 2 that applicability of models based on scale-free networks, in serving as a possible explanation for the evolution of cooperation, would be limited to networks featuring such extreme heterogeneity. We also highlighted that no general explanation exists for preferential attachment and that consequently explanation for scale-free social networks is required on a case-by-case basis. For example, we may ask questions such as, “By what process would a newcomer about to join a network, identify the fittest/most wealthy/most well connected/most sexually prolific members of a population?” In considering such questions, it is difficult to provide answers explaining such preferential attachment processes that do not require or imply the higher cognitive abilities typically seen in humans. Here, for example, we are thinking of capabilities such as memory and recognition (or at the least discrimination). Outside of the human sphere, offering answers to such questions becomes far more challenging.

In the following work, we develop the findings of the previous chapter to propose
and investigate a minimal model for the evolution of cooperation, by network reciprocity, in growing networks. The aim here is to minimise assumptions required of the model, in order to increase its generality. Specifically, the model should be supportive of cooperation regardless of initial population behaviour and it should not explicitly or implicitly assume any significant cognitive abilities for agents within the model. Whilst accepting the finding that network degree heterogeneity promotes cooperation and that increased heterogeneity has been found to correspond to increased cooperation [Santos and Pacheco, 2005], we are asking here whether similar levels of cooperation may arise from alternative models. We are further motivated by the specific observation that EPA is less able to promote cooperation in networks predicated upon defection. We therefore question whether under certain circumstances preferential attachment may actually be deleterious to cooperative behaviour and explore why this may be the case. The key to the alternative approach we present here involves shifting the evolutionary focus from the network growth process of the model to the node deletion process.

In the following two sections, we explain why such a shift may offer advantages to cooperation, how it aids in the construction of a minimal model, and why we believe it is a plausible approach. To make this explanation we will discuss the role of assortativity relative to degree heterogeneity in the evolution of cooperation (Section 4.1.1), before focusing on considerations relevant to constructing our minimal model (Section 4.1.2).

### 4.1.1 Two Elements of Network Reciprocity: Degree Heterogeneity and Strategy Assortativity

The emergence of cooperation by network reciprocity is often explained with reference to a network’s degree heterogeneity. However, the promotion of cooperation originally observed in the foundational work of Nowak and May [Nowak and May, 1992] is due to assortativity of agent strategies, resulting in grouping of cooperators. Connectivity in that work was in the form of a homogeneous lattice structure. The contemporary focus on degree heterogeneity in explaining the evolution of cooperation, subsequent to the findings of Santos and Pacheco [Santos and Pacheco, 2005], and given high scientific interest in complex (scale-free) networks, has tended to leave strategy assortativity as a somewhat marginalised topic (although we highlight the recent work of Iyer and
Killingback, 2016] as an exception to this observation). We emphasise that whilst network reciprocal models of cooperation are always dependent on assortativity, they are not necessarily dependent on degree heterogeneity. Regardless of the heterogeneity (or lack of) in the network topology, cooperation cannot evolve without some form of redistribution process that supports grouping of cooperators: assortativity remains the essential underpinning requirement for spatially structured reciprocity. The model we propose here focuses on the importance of maintaining long-term assortativity over that of primarily increasing degree heterogeneity.

Figure 4.1 illustrates how differing spatial distributions of strategies contribute to the emergence of cooperation on networks that have homogeneous degree distributions. It thus shows how assortativity may promote or suppress cooperation, in the absence of degree heterogeneity. The figure presents samples from three larger topologically identical homogeneously structured networks, where every node has degree, \( k = 4 \).

Figure 4.1a represents a homogeneous, regular spatial distribution of strategies, where each node connects to two defectors and two cooperators. From the mean scores for each of the two strategies, we can see that defectors out-compete cooperators in this distribution. Figure 4.1b shows a non-homogeneous, disassortative strategy distribution where each agent connects to non-self-similar strategies. In this case the mean population score is greater than in Fig. 4.1a; however, this strategy distribution results in scores of zero for all cooperators, and positive scores for defectors. Figure 4.1c illustrates a non-homogeneous, assortative strategy distribution which shows how self-similar grouping benefits cooperators but not defectors.

It is useful to consider each of these three scenarios from the perspective of Nash equilibria, as specific time-points in isolation, hence considering the agents as if they were rational actors. In classical prisoner’s dilemma, the Nash equilibrium is to defect, but this is based on the principle that each member of the population interacts with another with equal probability. The constraints imposed by spatial relationships, however, can affect the outcomes arising from certain strategy choices, as we now illustrate.

- **Figure 4.1a** illustrates regular mixing of strategies. Any individual defector here, acting rationally (rather than evolutionarily), cannot improve its score by

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2Here we are using *homogeneous* to refer to the spatial distribution of strategies rather than the mathematical distribution of degree values for the network. Homogeneous, in this sense, means that in a network containing equal numbers of cooperate and defect strategies, an individual node will connect to an equal number of cooperators and defectors.
Figure 4.1: Samples of larger networks illustrating how three identical homogeneous network topologies can support cooperation to differing extents given differing spatial distribution of strategies. Blue circles represent nodes having cooperator (C) strategies. Red triangles represent nodes having defector (D) strategies. Black lines represent edges (interactions) between nodes. The values within the nodes represent scores, which are the sum of individual payoffs achieved from the games played along each edge. For illustrative purposes we have selected an arbitrary value of $b = 1.5$ to calculate values for the scores. In the mean scores shown above the networks, we have assumed large populations ($N = 1,000$) and disregarded edge effects.

choosing to cooperate instead. A cooperator on the other hand will improve its score by switching to defect. This observation fits with the classical game theory finding for well-mixed populations. (Our regularly mixed strategy distribution here is actually analogous to a well-mixed population.) Extrapolating this observation to an evolutionary scenario, where strategies will increase or decrease in frequency based on how they impact individual fitness, it seems that a regular spatial distribution of strategies like this, cannot be evolutionarily stable, since
cooperators can improve their scores by becoming defectors.\footnote{We are referring here to the evolutionarily stability of a \textit{spatial distribution of strategies}, as opposed to an \textit{evolutionarily stable strategy} [Maynard Smith, 1982].} We can confirm this by considering the selection effect of the strategy updating component of an evolutionary game theory model (see Equation 2.10), applied to this example. We can now see that during updating, defector strategies, since they have higher scores, will displace lower-scoring cooperators.

- **Figure 4.1b** illustrates a population where disassortative (or non-self-assortative) mixing has occurred. If a rational defector had the option to change strategy here, it would not do so since that would reduce its payoff. Similarly any individual cooperator would not improve its score by changing to defector; given that it would be entirely surrounded by defectors, its score would be reduced to zero. This distribution of strategies appears to present a Nash equilibrium, although the equilibrium is only a \textit{weak} one because payoffs of cooperators would not be reduced if they became defectors. Thus, if we extrapolate to an evolutionary scenario, it seems possible that some cooperators will be displaced by defectors. If, as previously, we now consider strategy updating, we gain a clearer impression of likely evolutionary outcomes: during updating the large disparity between cooperator and defector scores will drive displacement of cooperator strategies by defectors, \textit{even though this does not create any increase in scores for affected individuals}. Clearly the extreme of disassortative mixing that we have shown here does not represent an evolutionarily stable spatial distribution of strategies.

- **Figure 4.1c** illustrates a population where assortative mixing has occurred. We first consider the scenario for the majority of defectors in the population, namely being surrounded by a sea of defectors. If a rational defector could choose to change to cooperation, it would not do so since this would not increase its score. If we consider the majority scenario for cooperators, namely being surrounded by other cooperators, we can see that such individuals if given the choice would not change strategies. It seems that for individuals not at \textquote{the frontier}, this spatial distribution of strategies appears to offer stability. If we now extrapolate to the evolutionary scenario, and consider strategy updating \textit{away from the frontier}, our findings hold.Updating only defines displacement of \textit{adjacent} strategies, so changes may only occur \textit{at the frontier}—and where neighbouring individuals have non-self-similar strategies. Given the simple scenario illustrated here,
strategy updating at the frontier is likely to lead to displacement of defectors by cooperators. After displacement in this way, the new cooperators would find themselves surrounded on three sides by defectors; they would not have the same backup as other cooperators and would be vulnerable to being converted back to defectors. It is easy to see how the frontier could hence consist of agents whose strategies are constantly fluctuating, and indeed previous research exists which reports such findings [Gómez-Gardeñes et al., 2007].

From the highly simplified and extreme scenarios shown above, we gain some impression of how the spatial distribution of strategies might affect outcomes for cooperation in a population, and also how strategy updating is impacted by the nature of the strategy distribution. Of the three examples, regular mixing and disassortative mixing are not evolutionarily stable spatial distributions of strategies. Further, it seems that strategy updating based on these two cases is likely to increase the proportion of defectors. Only self-assortativity appears to hold any promise of stability; it is also the only distribution that does not drive an immediate reduction in numbers of cooperators and demonstrates some potential to convert defectors to cooperators. We can see that the role of the frontier (i.e. its shape) will be of particular importance, although the microscopic details of this will be complex and far less tractable.

From these examples, we see that in networks having homogeneous topology, given an ability of strategies to redistribute themselves, it is possible for cooperators to improve their lot as a result of self-assorting. If cooperators are able to self-assort, they can survive. Specifically we should note that whilst cooperators benefit by self-assortativity, defectors benefit from non-self-assortativity. In other words: everyone wants to play with cooperators. We also reiterate the point made in Section 2.7.1 that, given population viscosity, (natural) selection drives the self-assortativity of successful (fitness-enhancing) behaviours.

Whilst we have offered an explanation of how self-assortativity can benefit cooperators, this does still leave an unanswered question regarding how the first clusters of cooperators may originally emerge in a growing or topologically changing network. The answer is simply that small cooperator clumps could simply arise by random activity. Strategy updating and node addition can both support such a possibility. The strategy updating process involves probabilistic elements (in terms of which neighbour to compare with and also the probability of displacement) and as a result, it is not a certainty that low fitness cooperators will be immediately displaced from a population, they may thus persist for several generations. Such low fitness cooperators may then
find themselves connected to newcomer cooperators added during subsequent network growth (node addition) steps. The addition of newcomer cooperators to existing cooperators may result in very small clusters of cooperators which are then able to spread further via strategy updating. One important point regarding the possible emergence of cooperative clusters in this way is that EPA will drive newcomers to connect to a highly limited subset of the population, namely the highest fitness nodes; these are likely to be hubs. In scenarios where such hub nodes are occupied by defectors, cooperative newcomers are very likely to be rapidly converted to defectors, thus making the emergence of cooperation unlikely. In contrast, random attachment offers the potential for cooperative clusters to emerge in such a scenario.

In the work by Santos and Pacheco [Santos and Pacheco, 2006] which looks at the effect of heterogeneously (rather than homogeneously) structured networks, the process of assortativity supports the formation of groups of cooperators whilst the greater connectivity that can be found between some individuals in heterogeneous networks offers further rewards to cooperators which distribute themselves so as to take advantage of such connectivity. In summary, models of network reciprocity typically support cooperation by combining the two elements discussed in this section: degree heterogeneity thus further increases the potential gains that are achieved by self-assortativity.

Our proposed model makes fewer demands regarding the specifics of network structure (and associated mechanisms of network formation), and focuses more on promoting assortativity. We explore further the rationale to produce such a model in the following section.

### 4.1.2 Considerations for the Minimal Model

The EPA model [Poncela et al., 2008] introduced earlier has been proposed as a possible explanation for the evolutionary origins of cooperation. The model uses a mechanism for network growth whereby new agents (nodes) added to a network preferentially attach to fitter nodes. The probability that an existing node $i$ receives one of the $m$ new edges is as follows:

$$\Pi_{\text{edge}_i}(t) = \frac{1 - \varepsilon + \varepsilon f_i(t)}{\sum_{j=1}^{N(t)} (1 - \varepsilon + \varepsilon f_j(t))},$$

where $f_i(t)$ is the fitness of an existing node $i$ and $N(t)$ is the number of nodes available to connect to at time $t$ in the existing population. The parameter $\varepsilon \in [0, 1)$ is used to adjust the strength of the preferential mechanism. (A fuller explanation of the details
of the EPA implementation is provided in the methods section.) On inspection, Equation 4.1 appears to imply that a newcomer connecting to an existing network has access to *global* knowledge regarding i) the fitness of all other individuals in the population \((f_j)\), and ii) the size of the population \((N(t))\), both of which are unlikely to be satisfiable in real world examples. The sigma term also implies some form of reasoning ability in summing these elements. (We accept that the equation could be interpreted to represent a process that is implemented either by the environment or by the network, rather than individuals, but neither of these assumptions leads to easier general explanations of how such functionality could arise in real world situations).

Given its preferential attachment mechanism, the EPA model seems likely to generate scale-free networks. Visual assessment of degree distribution appears to confirm this hypothesis for certain implementations i.e. for those \(b\) values where cooperators form the majority strategy and hence most individuals have positive fitness scores. We have commented in detail on the role of scale-free networks in the evolution of cooperation in Section 2.8.4. Relevant to the current chapter we highlight a few key points with regards to scale-free topology and explanations of cooperation:

- The scale-free property observed in models of preferential attachment is claimed to parallel many empirical findings for real networks [Barabási and Bonabeau, 2003]; however, some claims of scale-free characteristics in real networks have subsequently been challenged [Amaral et al., 2000, Fox Keller, 2005, Willinger et al., 2009].

- Whilst many real networks have been proposed to be scale-free (on the basis of apparent power-law degree distributions), it has been highlighted that such claims are often hypothesised rather than demonstrated [Clauset et al., 2009].

- Complex networks are difficult to characterise with certainty (accurately distinguishing between e.g. power-law and stretched exponential distributions is a non-trivial problem) and claims based on visual assessment of log-log linearity, over limited orders of magnitude, with real world (or even simulated) data featuring variability and/or noise should be treated with caution [Stumpf and Porter, 2012].

- A claim that a network is scale-free is clearly plausible if a preferential attachment process is known to have generated the network (e.g. in the case of the EPA model as discussed in the previous chapter, PA is explicitly defined), but
in the absence of such knowledge, assumptions of scale-free topology may be unreliable.

- Finally, we acknowledge the important point that whilst preferential attachment models are likely (but not guaranteed) to generate scale-free networks with corresponding power-law distributions, the converse is not necessarily certain, i.e. while power-law distributions may arise as the result of preferential attachment, other approaches can also generate such distributions [Miller, 1957, Albert and Barabási, 2002, Caldarelli et al., 2002, Dorogovtsev and Mendes, 2002]. However, in the case of those social networks where it is found to exist, scale-free connectivity is likely to have arisen by preferential attachment [Newman, 2001].

Models that assume scale-free heterogeneity in order to explain cooperation in social networks are potentially constrained by such an assumption, both regarding the network topology itself, and also regarding the likely requirement for preferential attachment in order to generate such topology. In the latter case, the suitability of preferential processes in modelling real world phenomena is potentially impacted by the absence of a general explanation for preferential attachment. Each novel situation where preferential attachment is proposed requires its own explanation to address the underlying mechanism. We consider, in particular, that cooperation is thought to have had a key role in the development of organisms of increasing complexity in early evolutionary transitions [Maynard Smith and Szathmary, 1997]. In such situations involving primitive life forms, which might be, for example, immobile, carried by currents or interacting at random, it is unclear whether a mechanism may have existed by which preferential attachment occurred. It therefore seems questionable to assume, in our models, the existence of an ability or process whereby more well-connected (or in the case of EPA, fitter) individuals will preferentially influence social structure (and hence drive the formation of scale-free networks).

## 4.2 Proposed Minimal Model

We propose a minimal model for cooperation in fluctuating networks that does not require agents have access to global knowledge, does not depend on preferential attachment, and does not require scale-free network structure. For purposes of comparison, our model is based as closely as possible on the EPA model [Poncela et al., 2008]. Where possible we use similar parameters to the original work. Strategy updating rules
are identical. The network growth process is an adaptation; the node deletion process we implement is new. Fluctuation within the networks arises from the combined network growth and attrition processes.

### 4.2.1 Proposed Growth Mechanism

We propose a growth mechanism which functions in the absence of any form of preferential attachment. This proposal is not based on a rejection of the existing findings regarding the positive role of heterogeneity in promoting cooperation. It represents our intention to establish a model for cooperation which serves in the absence of any mechanisms which require additional explanation or assumption. (Should such mechanisms transpire to be present for particular scenarios they may further enhance cooperation). The resulting model therefore does not depend on high degree heterogeneity.

We implement the connection of new nodes to the existing network as an entirely random process. The network grows by chronological random attachment (CRA) of newcomers to existing nodes within the network. Such a mechanism does not cause the development of a simple Poisson degree distribution as would be seen in the case of a random network; instead the chronological nature of the additions results in an exponential degree distribution [Dorogovtsev and Mendes, 2002], with ‘older’ nodes being more highly connected. In the absence of other influences, the exponential distribution corresponds to network structure with heterogeneity somewhere between that of random and scale-free.

### 4.2.2 Proposed Attrition Mechanism

In the EPA model, strategy updating between adjacent individuals forms the primary evolutionary component, with selection acting on relative fitnesses which arise from agent-agent interactions. However, EPA also incorporates a secondary evolutionary mechanism into the growth processes of the social network. Within our model, we shift this secondary evolutionary component over to shrinkage of the network. Specifically, this global effect causes death of less fit individual agents. We consider that this revision offers a model more analogous to the processes of selection in real world evolutionary situations. Such a shift separates evolutionary effects from the attachment processes responsible for network growth, and represents evolution more realistically as a process which calls less fit members of a population. As described in Chapter 3, we implement such a culling mechanism by means of a nominal maximum population
size, analogous to the population biology concept of *carrying capacity*. In this sense, the size of a population reduces in response to extrinsic factors which are the result of environmental effects (such as predation, disease, food availability—many of which may be seasonal variations).

### 4.2.3 Summary: A Model of Population Fluctuation in Social Networks

The earlier EPA+fluctuation model, described in Chapter 3, featured three evolutionary components describing network growth, strategy updating and node deletion. We commented that the evolutionary mechanism of network growth seemed to have no obvious analogue in the real world. The model presented in this chapter is reduced to two evolutionary components which we see as being representative of *intrinsic* and *extrinsic* effects:

- **Intrinsic evolutionary effect**: *Strategy updating*. This corresponds to competition directly between (co-located) individuals within a population, e.g. two individuals competing to breed. In our model, fitter strategies will displace those of less fit neighbours.

  This process enables strategy assortment but it does not affect the network topology.

  (This is the evolutionary mechanism, present in [Santos and Pacheco, 2005], common to the majority of evolutionary game theoretic models used to investigate cooperation in networks.)

- **Extrinsic evolutionary effect**: *Node deletion on reaching carrying capacity*. This corresponds to broad acting *disruptive* effects arising from outside the population, i.e. those arising from the environment and which impact a whole population or sub-population (real world examples being drought, disease, predation, food shortages, many of which are likely to be periodic). In our model, less fit individuals are repeatedly killed off, along with the positions they occupied within the network due to their connections.

  This process enables changes in the network topology, but it does not implement the spread of strategies from one individual to another.

  (This additional evolutionary mechanism was presented previously in Chapter 3.)
The combination of growth by random attachment which is limited by carrying capacity, and featuring attrition which is based on least fitness, results in a model of fluctuating social networks which describes the growth of a population from founder members. The model avoids assumptions of either higher cognitive abilities or underlying mechanisms for the formation of highly heterogeneous network topologies.

4.3 Methods

Our models and simulations are based on the work described in Chapter 3, but with growth by random attachment, and deletion (in the case of fluctuation implementations) by a tournament selection step that removes nodes from the network. We will recap, with a brief overview, on items described previously in Section 3.3 whilst covering novel elements of the model in more detail.

4.3.1 Overview of Approach

The models describe networks (i.e. graphs) with agents situated at the nodes. Edges between nodes represent interactions between agents. Interactions are behaviours of agents playing the one-shot prisoner’s dilemma game. Behaviours are encoded by a strategy variable which takes one of two values: cooperate or defect. The game is played in a round robin fashion, with each agent playing its strategy against all its connected neighbours in turn. Each agent accumulates a fitness score which is the sum of all the individual game payoffs. Strategy updating between adjacent individuals, as an analogue of natural selection, results in the displacement of less fit strategies by fitter ones.

The evolutionary simulations in this chapter consider social networks in the form of pre-existing networks and also those grown from founder populations consisting of \( N_0 = 3 \) completely connected nodes. Founder population simulations were initialised with either all cooperators or all defectors. For pre-existing networks we investigated the effects of our model when applied to a range of initial topologies: regular, random and scale-free. We considered two scenarios for initial strategy distribution in such networks: i) where nodes are initially allocated cooperate or defect strategies with equal probability (see Sections 3.3.3 and 3.3.4 for further detail), and ii) where the networks are initialised with all nodes being allocated defect strategies. The latter obviously presents a greater challenge for the emergence of cooperation.
The EPA model connects strategy dynamics to network growth: starting from a small founding population, newcomer nodes are added which preferentially connect to fitter agents within the network. Our chronological random attachment (CRA) model uses the same founding population structures as EPA but adds newcomer nodes to randomly selected existing nodes.

4.3.2 Implementation of the Evolutionary Model

Unless stated otherwise in the text, the general outline of the evolutionary process we use is described, for one generation, as follows:

i. Play prisoner’s dilemma: Each agent plays one-shot prisoner’s dilemma with all neighbours and achieves a fitness score that is the sum of all the payoffs.

ii. Update strategies: Selection occurs. Those agents that achieve low scores may have their strategies replaced on a probabilistic basis with the strategies of randomly selected (fitter) neighbours.

iii. Grow network: A specified number of new nodes are added to the network, connecting to $m$ distinct existing nodes via $m$ edges using either EPA or CRA.

iv. Remove nodes (only in the case of fluctuation models): If the network has reached maximum size, it is pruned by a tournament selection process that removes less fit agents.

In the following, we provide more detail on the implementation of the growth and attrition steps, and also general simulation conditions.

Grow Network

New nodes are added to achieve a total of 10 at each generation. Duplicate edges and self loops are not allowed. EPA and CRA mechanisms are described below. Strategy types of added nodes (cooperate, defect) are allocated independently, uniformly, at random.
EPA implementation: New nodes connect to existing nodes preferentially, based on fitness. The probability that an existing node, $i$, receives one of the $m$ new edges is shown in Equation 4.2. Each new node uses $m$ edges to connect to existing nodes. In all our simulations, we use $m = 2$ edges.

$$
\Pi_{\text{edge}}(t) = \frac{1 - \varepsilon + \varepsilon f_i(t)}{\sum_{j=1}^{N(t)} (1 - \varepsilon + \varepsilon f_j(t))}.
$$

(4.2)

The parameter $\varepsilon \in [0, 1]$ is used to adjust the strength of the preferential mechanism. For all of our EPA simulations $\varepsilon = 0.99$, hence focusing on selection occurring directly as a result of the preferential attachment process.

CRA implementation: New nodes connect to existing nodes randomly. The probability that an existing node, $i$, receives one of the $m$ new edges becomes:

$$
\Pi_{\text{edge}}(t) = \frac{1}{N(t)}.
$$

(4.3)

In both growth mechanisms, given that each new node extends $m = 2$ new edges, and multiple edges are not allowed, the population of existing nodes, $N$, is therefore sampled without replacement.

Remove Nodes (in the Case of Fluctuation Models)

On achieving a specified size, the network is pruned by a shrinkage value of $X\%$ of the total population size. This is achieved by tournament selection using a tournament size equivalent to 1% of the population. The tournament members are selected randomly from the population. The tournament member having the least fitness is the ‘winner’. The remaining nodes are returned to the population. By this method, a shortlist of $X\%$ nodes is established for removal from the network. All edges from deleted nodes are also removed from the network. Any singleton nodes that become disconnected from the network as a result of this process are also deleted. (Failure to do this would result in small numbers of disconnected, non-playing nodes, having immutable strategies. In the case of EPA simulations, the zero fitness of such nodes would result in continual isolation from the network.) When there are multiple nodes of equivalent low fitness value, the selection is effectively random (on the basis that the members were originally picked from the population randomly). Where the shrinkage value, $X = 0$, no attrition occurs. Tournament selection is used (in comparison to ranked truncation in
CHAPTER 4. A MINIMAL MODEL FOR PAIR-WISE COOPERATION

the previous chapter) to introduce a more probabilistic (less deterministic) mechanism for attrition.

4.3.3 Network Generation for Pre-existing Networks

We used networks based on regular, random and scale-free undirected graph topologies. Duplicate edges and self-loops are prevented. We maintained an average degree of \( z \approx 4 \) for all networks. Details for topologies are as follows:

**Regular networks:** Each node connects to \( z = 4 \) neighbours. We use a network (population size) of \( N \) nodes in the form of a ring structure to exclude edge effects.

**Random networks:** These are Erdős-Rényi graphs [Erdős and Rényi, 1959] generated with a probability of edge creation given by \( z/N \) where \( z \) is the required average degree of the network and \( N \) is the size of the population.

**Scale-free networks:** These were generated using the Barabási-Albert (BA) preferential attachment model [Barabási et al., 1999], with each new node extending \( m = z/2 \) edges to existing nodes of the network. The probability of an existing node, \( i \), receiving an edge from a new node is given by \( k_i/\sum_{j=1}^{N} (k_j) \), where \( k_i \) is the degree of the existing node.

4.3.4 Growth of Networks from Founder Populations

We investigated networks grown from initially complete networks with \( N_0 = 3 \) agents at generation \( t_0 \). Founding populations were either entirely cooperators or entirely defectors. Networks were grown to a maximum size of \( N = 1,000 \) nodes, with an overall average degree of approximately \( z = 4 \). For models featuring fluctuation, the same mechanism used to grow networks to maximum size (either EPA or CRA) continued to be used thereafter (as part of the fluctuation process) for adding new nodes following node deletions.

4.3.5 General Simulation Conditions

Simulations were run until 20,000 generations. The final fraction of cooperators values we use are means, averaged over the last 20 generations of each simulation, in
order to compensate for variability that might occur if just using values from the final generation. Each simulation consisted of 25 replicates. We pruned the network using a shrinkage value of $X = 2.5\%$ for all fluctuation simulations. Simulation data is recorded after step 2 (Update strategies).

4.4 Results and Discussion

We initially compare static and fluctuating (‘+’) models in pre-existing networks, where we consider two different cases: networks initially populated with equal numbers of cooperators and defectors, versus networks initialised only with defectors. We report results for three different types of initial network topology: regular, random and scale-free networks. In all cases we compare results achieved using the CRA model with those from the EPA model.

We subsequently compare non-fluctuating\(^4\) versus fluctuating (‘+’) models in networks grown from founders, where we consider the two cases of cooperator, and defector, founders. ‘Non-fluctuating’ refers to models where the network, having grown, becomes topologically static on reaching maximum size. ‘Fluctuating’ refers to models where the processes of growth and attrition allow the network to fluctuate, relative to a nominal maximum size, continually until the simulation is stopped. Again, we report results achieved using the CRA model and compare these with results from the EPA model.

4.4.1 Performance of Models Applied to Pre-existing Networks

We consider two approaches to implementing fluctuation, EPA+fluctuation and CRA+fluctuation. Node deletion is the same mechanism in both and is fitness-based. Node addition, however, is either by preferential attachment or random attachment respectively. We investigate the performance of each of the two fluctuation models when applied to pre-existing networks of regular, random, and scale-free topologies.

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\(^4\)In the case of pre-existing networks we have correctly used the term ‘static’ to apply to the topology of the non-fluctuation network. In the case of networks grown from founders, the term ‘static’ is misleading (the network grows initially); we hence use the term ‘non-fluctuating’ to refer to those simulations where fluctuation is not enabled.
Evolutionary Preferential Attachment

In Fig. 4.2a we show behaviour profiles for the EPA model when applied to networks initialised with an approximately equal number of cooperators and defectors. The solid lines represent simulations implemented on static networks. The only processes active in this case are game-playing and strategy updating. As expected from existing research, we see greater levels of cooperation for networks of greater heterogeneity. When the fluctuation mechanism (growth and attrition of nodes) is applied (see dashed lines), final levels of cooperation are very similar for all initial network topologies: profiles for regular and random networks appear to coincide, whilst slightly higher levels of cooperation are seen for initially scale-free networks at higher temptation to defect values.

Figure 4.2: The effect of initial network topology on the emergence of cooperation in pre-existing networks using the EPA+fluctuation model. (a) shows results for networks initially populated with approximately equal numbers of cooperators and defectors. (b) shows results for networks initially populated entirely with defectors (in this case the profiles for all three static network types lie on the x-axis). Final fraction of cooperators is determined from the average of 25 replicate simulations. Simulations featured 1,000 nodes and were run for 20,000 generations. Fluctuation implementations are represented with dashed lines.

In Fig. 4.2b we show the EPA model applied to the more challenging case of networks initially populated entirely with defectors. The static networks naturally follow the x-axis. (In the absence of mutation or noise, there is no mechanism for cooperation to appear.) When the fluctuation mechanism is applied, highly consistent outcomes are observed. Regardless of the initial network topology, the fluctuation mechanism enables all networks to reach similar final levels of cooperation.
The form of the final degree distributions, for networks subject to the EPA+fluctuation model, appears to be dependent on the $b$ value. Figure 4.3a illustrates degree distributions for low, medium and high $b$ values. We can see that exponential-type distributions indicating moderate heterogeneity arise in the case of lower temptation to defect values ($1.0 < b \leq 1.6$); apparent power-law distributions indicating scale-free heterogeneity are seen for intermediate values ($1.9 \leq b \leq 2.2$); and extreme heterogeneity suggesting star-like topology is observed for high values ($b \geq 2.5$). The distributions appear to be largely independent of initial network topology; we see similar distributions, for any given $b$ value, regardless of whether the initial network is regular, random or scale-free. Similar distributions also arise regardless of initial population strategy composition (whether we start from equal numbers of cooperators and defectors or whether we start from all defectors). The consistency of final degree distribution (and therefore heterogeneity) for given values of $b$, regardless of initial population and network conditions, explains the similarity in behaviour profiles that we see for the EPA+fluctuation model.

A possible explanation for the relationship between the resultant network topology and $b$ value may be offered from inspection of Equation 4.1 which defines the addition of new nodes for EPA. We can see that in a population consisting of entirely cooperators, given that cooperate:cooperate interactions give payoffs of $1:1$ (see Table 2.1), an individual’s fitness score will simply correspond to its degree value. In this case, EPA becomes equivalent to PA, where an individual’s ability to attract new nodes is only dependent on the number of neighbours it has. PA as we know, generates scale-free networks, but where $b$ values are low this results in the presence of a minority of defectors which in turn reduces the resultant heterogeneity. This is because cooperators’ fitness scores are decreased by any connections to defectors, which hence results in a reduced ability to preferentially attract edges from new nodes. EPA thus becomes less powerful than PA in driving the generation of scale-free networks.

We continue this explanation by now considering how increasing the proportion of defectors in the population affects fitness scores. In a hypothetical population featuring only cooperators, the range of fitness scores is between $k_{\text{min}}$ and $k_{\text{max}}$. As we have noted, the presence of a minority of defectors (low $b$ values) constrains the effect of the preferential mechanisms, thus reducing heterogeneity. However, as $b$ increases and more defectors are present in the population, there is a greater likelihood that defectors will end up as hub nodes and the range of possible scores thus increases, becoming 0 to $k_{\text{max}} \times b$. The greater disparity that exists between the highest and lowest scoring nodes,
for intermediate $b$ values where many defectors are present will therefore strengthen the preferential function of EPA, which explains our observation of scale-free topology in Fig. 4.3a for $b = 2.2$. Finally, for the highest values of $b$ (see Fig. 4.3a for $b =$
where the network contains mostly zero scoring defectors, we see that the EPA mechanism seems to have shifted to more of a *winner-take-all* mechanism. Here we have a runaway effect where one node is recruiting the majority of new edges, resulting in a star-like structure (this effect discussed previously in Section 3.5).

**Chronological Random Attachment**

We now consider the CRA model which is based on *random* addition of nodes over time. In Fig. 4.4a we show behaviour profiles for the CRA model when applied to networks initialised with an approximately equal number of cooperators and defectors. The solid lines represent simulations implemented on static networks and dashed lines represent the CRA+fluctuation model. In Fig. 4.3b we show final degree distributions obtained from CRA+fluctuation simulations run using low, medium and high temptation to defect values.

Results for static models are as observed previously for EPA: we see that greater heterogeneity corresponds with increased levels of cooperation. When fluctuation is applied (dashed lines, Fig. 4.4a), cooperation increases in the case of regular and random networks but decreases for scale-free networks. These results are generally as expected since, as we can see from Fig. 4.3b, the CRA+fluctuation model generally tends to a *compressed exponential* final degree distribution for all $b$ values. The *compressed* form of this degree distribution arises as a result of the node deletion mechanism apparently targeting higher degree nodes, thus reducing the range of degree values that would normally arise from randomly adding nodes over time (an exponential distribution). This compressed exponential distribution corresponds to a network heterogeneity greater than regular and random networks but less than scale-free networks. The direction of the shifts in behaviour profiles observed when fluctuation is introduced (comparing solid to dashed lines for each of the three network topologies) corresponds to this change in heterogeneity and hence explains the reduction in cooperation for initially scale-free networks (compare solid to dashed green lines) and the increase for initially regular and random networks (brown and pink lines).

In Fig. 4.4b we show behaviour profiles for the CRA model when applied to networks initialised only with defectors. Here we see very high consistency in outcomes, with profiles being coincident regardless of starting network topology. If we compare the position of these coincident dashed lines in Fig. 4.4b with the solid pink and green lines in Fig. 4.4a, we see that they sit between the two profiles for static random and
We now consider three questions raised by our findings, considering in particular the dependency of behaviour profiles on initial network topology (in Question i), and the dependency of final degree distribution on $b$ values (in Question iii). Whilst outcomes of cooperation are impacted by topology, and hence the fluctuation processes which change the network form a key part of answering these question, it is important to bear in mind that network heterogeneity alone cannot adequately explain findings in all cases (an example of this is illustrated in Question ii). Whilst we know that heterogeneity does indeed generally promote cooperation, it is worth remembering that, as discussed in Section 4.1.1, the first observations of reciprocal cooperation due to spatial relationships occurred in non-heterogeneous structures and are explained solely in terms of assortativity.

i) Given starting populations which contain cooperators and defectors, why do the CRA+fluctuation behaviour profiles appear to be affected by initial network topology whilst EPA+fluctuation profiles are not? (Compare dashed lines between

Figure 4.4: The effect of initial network topology on the emergence of cooperation in pre-existing networks using the CRA+fluctuation model. (a) shows results for networks initially populated with approximately equal numbers of cooperators and defectors. (b) shows results for networks initially populated entirely with defectors (in this case the profiles for static networks lie on the x-axis). Final fraction of cooperators is determined from the average of 25 replicate simulations. Simulations featured 1,000 nodes and were run for 20,000 generations. Fluctuation implementations are represented with dashed lines.
Figs. 4.4a and 4.2a.) With regards to networks initialised with a mixture of cooperators and defectors, in the CRA+fluctuation model we see greater variability in behaviour profiles for simulations based on the three different initial network topologies than for the EPA+fluctuation model. In the case of EPA+fluctuation, as existing nodes are deleted, new ones will be added by the preferential process. Thus the EPA+fluctuation model will drive networks to highly heterogeneous topologies regardless of initial topology. However, in the case of CRA+fluctuation, as existing nodes are deleted, they are replaced by a process which at most can only generate an exponential degree distribution, thus the different processes (growth and attrition) of the fluctuation model will vary in the importance of their relative contribution to outcomes, in a manner that is dependent on the initial network topology. For example, in the case of scale-free networks, changes in topology are more dependent on the microscopic details of how the fitness-based node-deletion process reduces the heterogeneity of the network, whereas in the case of regular networks, the more important factor is random node addition, which will drive an increase in heterogeneity to achieve the same final exponential degree distribution. Thus the processes of the CRA+fluctuation mechanism will react with the population differently depending on the topology present at the time. The final topologies which emerge will enhance cooperation or not according to their heterogeneity. It is also worth noting (discussed further in Question ii), that whilst we expect CRA+fluctuation final degree distributions to be generally consistent, there may be some residual structures or distributions of strategies from the initial starting conditions, which cannot readily be changed by the processes of least-fitness deletion and random node addition.

ii) Why are behaviour profiles in CRA+fluctuation simulations that are initially all defectors consistent, when those starting from an equal mix of strategies appear dependent on initial network topology? (Compare dashed lines in Fig. 4.4b with 4.4a.) In particular, it seems from Fig. 4.4a that having cooperators present at the simulation start allows for greater levels of cooperation in networks that originally have more heterogeneous topologies. This is a surprising result given that the CRA+fluctuation model will drive the networks to the same final degree distribution. (We have confirmed by inspection that similar degree distributions are achieved regardless of the strategy composition of the initial population.)

We suggest that long-term outcomes, in the case of higher $b$ values where the
dilemma is stronger, depend on whether a cooperator or a defector occupies the highest degree node (hub) in the network. In the case of initially all defector networks, the highest degree node will initially be held by a defector. As cooperators are added to a network such a defector would be in an advantageous position with potentially high fitness scores arising from interactions with its cooperator neighbours. It will be difficult for fitness-based strategy-updating to displace such a defector or fitness-based node deletion to remove the node from the network. In such a position, a defector could block a cooperator from obtaining the hub and suppress the emergence of cooperation in the long term. Alternatively, when simulations are started from a mix of strategies, then either a cooperator or defector could occupy the most influential node, in which case, we might see two states arising amongst replicates within such simulations. In Fig. 4.5, we present results which appear to support this argument, showing two different outcomes for replicates in simulations starting from a mixture of strategies. Clearly the average values for cooperation which are determined from replicates that can exist in two states will be greater than that from simulations where all replicates are dominated by defection. In cases where cooperators occupy the hub(s), it is also possible that this creates the opportunity for some residual effects relating to the early distribution of strategies (strong clusters of cooperators) to persist, despite the network’s initial topology having been modified (to compressed exponential distribution). Such a possibility would allow for our observation of higher levels of cooperation in networks which had originally higher heterogeneity. We highlight the important point that the observed levels of cooperation discussed here cannot be explained simply with respect to network heterogeneity alone.

In support of our above point regarding residual effects, Fig. 4.5a illustrates an interesting finding that is only observed for the case of initially scale-free networks, when started from a mixture of strategies, and for a limited range of $b$ values. The CRA+fluctuation model typically results in a compressed exponential distribution; although for the specific situation of initially scale-free topologies and mixed strategy types, and given $2.2 \leq b \leq 2.8$, we see that in some replicates, node deletion appears to miss high degree nodes, and is thus presumably deleting intermediate degree nodes instead. Clearly these high degree nodes must be generating high fitness values in order to avoid deletion. It is possible that they are competing nodes occupied by defectors (given that we only see them as temptation to defect increases). From these observations we see that whilst CRA+fluctuation tends to drive most networks to a compressed exponential distribution, in a few cases it is unable to fully achieve this conversion. These
residual topology effects may contribute to the increased cooperation that is observed for increased heterogeneity at higher $b$ values (in networks originally populated with cooperators and defectors).

Figure 4.5: In CRA+fluctuation, based on initial networks of higher heterogeneity (e.g. random and scale-free), populations initialsed with cooperators and defectors lead to levels of cooperation that are, on average, higher than initially all defector populations. However, the averaged data conceals an interesting effect which only becomes apparent on inspecting time plots for the replicates. Here we show time plots and corresponding final degree distributions for simulation replicates (25 of) based on initially scale-free networks, using $b = 2.5$. (a) Population initially consists of approximately equal numbers of cooperators and defectors. Two states emerge, one where the population is dominated by defectors (4 out of 25 replicates) and a second where the population appears to be about 20% cooperators (21 out of 25 replicates). (b) Population initially consists only of defectors and remains dominated by defection (all replicates). We also note here the atypical observation that for some replicates, final network degree heterogeneity in the case of (a) features some residual higher degree nodes. All simulations featured 1,000 nodes and were run for 20,000 generations.
iii) Given a starting population containing equal numbers of cooperators and defectors, why does CRA+fluctuation achieve generally consistent degree distributions regardless of b value whilst in EPA+fluctuation degree distributions appear dependent on b values? (See Fig. 4.3.) We can see that for CRA+fluctuation, as nodes are deleted, newcomers are added by random attachment. Given this mechanism of growth, an exponential distribution will result. This distribution will be compressed by the deletion mechanism, which deletes higher degree nodes if they are unable to maintain high scores. The growth mechanism is random so its function is independent of network topology. The deletion process is fitness-based. Theoretically it is possible that it may be indirectly affected by, for example, high fitness values making hub nodes immune to deletion, but the results suggest that this is generally not the case. Hence it seems reasonable that outcomes of CRA+fluctuation are largely independent of starting network topology. This is not the case for EPA (as has been mentioned in the discussion of EPA results above). We observe that EPA generally drives the formation of high network heterogeneity, but that the precise form of the resulting topology appears to be affected by the value of b. From inspection of Equation 4.2, we can see that the EPA node attachment process takes as its input fitness values which arise from the prisoner’s dilemma payoff values. Fitness values are therefore directly impacted by changes to the simulation’s b value, so there is a causative relationship between the temptation to defect value and the EPA process which drives network growth.

In summary, we see that our model of CRA+fluctuation, based on fitness-based node deletion and random node attachment, supports cooperation. We have demonstrated this for a range of initial topologies, on pre-existing networks that feature cooperators and defectors initially, and also for the more challenging case of pre-existing networks populated entirely by defectors. In comparing EPA+fluctuation to CRA+fluctuation, we see higher levels of cooperation in the EPA model, as we would expect based on a growth mechanism that generates high network degree heterogeneity, yet the questions that we have highlighted above illustrate that degree distribution or network heterogeneity alone are far from sufficient to explain the full complexity of outcomes we see in these simulations.

With regards to the functioning of EPA+fluctuation versus CRA+fluctuation we highlight the following dependencies:

- In EPA+fluctuation, final degree distributions are dependent on temptation to defect (b) values.
In CRA+fluctuation, behaviour profiles tend to be dependent on initial network heterogeneity.

### 4.4.2 Performance of Models when Applied to Cooperator-founded Networks

In Fig. 4.6 we show behaviour profiles of final levels of cooperation versus temptation to defect, $b$, for populations grown from complete founder networks of 3 cooperators. We see the emergence of cooperation in all cases. The preferential attachment models (see purple lines) result in higher levels of cooperation than random attachment (see corresponding orange lines). This result is as expected given i) our assumption that preferential attachment will result in scale-free networks and ii) our understanding that such networks, having high heterogeneity, are likely to be associated with greater cooperation.

![Figure 4.6: The effect of network growth model on the relationship between temptation to defect and cooperation in networks founded by cooperators.](image)

In Fig. 4.7, we provide final degree distributions by which we may check our assumptions regarding heterogeneity of the resulting network structures. It is important to recognise that fitness affects the different models, and therefore the resulting network structures, in different ways. The relevant fitness-based mechanisms are identified to the right of the distribution plots. (The fitness-based strategy updating process...
is present in all models. Whilst it does not directly affect node addition or deletion processes, it does have an indirect effect since it changes the fitness of individuals.) We present final degree distributions for each model at low and high values of $b$, which illustrate the topologies arising when individuals have generally high and generally low fitnesses respectively. (When populations are predominated by cooperators, at $b = 1.3$, most individuals will have fitnesses that correspond to the number of connections ($k$) they have; when populations are predominantly defectors, at $b = 3.1$, most individuals will have fitnesses of zero.)

**Final Degree Distributions for EPA and EPA+fluctuation**

The degree distribution for EPA when $b = 1.3$ looks approximately linear suggesting a power-law distribution and indicating scale-free network structure as expected for a preferential attachment mechanism. However, when $b = 3.1$ the degree heterogeneity has increased further. A very large proportion of individuals in the simulations have a degree of 2 and the maximum observed degree is high at 375 with a maximum frequency value for nodes of degree $z = 2$ at 931. This illustrates that the network has moved to a star-like structure.

**Why should increasing the temptation to defect generate extreme (star-like) heterogeneity?** Increased $b$ values allow defectors to achieve higher payoffs when playing cooperators (see Table 2.1). This will result in greater disparity of scores between defectors and cooperators. Since the probability of displacement during strategy updating is dependent on fitness differences (see Equation 3.2), this will increase the likelihood of cooperators being converted to defectors. Ultimately this will lead to the population being taken over by defectors, which results in a landscape where most individuals have zero fitness ($\text{defect: defect}$ payoffs are $0:0$). This similarity of fitnesses for most individuals does not, however, result in a random network. This is because, given the fitness-based attachment process, any existing node that has even the slightest fitness score amidst a mass of zero-fitness individuals will attract the lion’s share of the newcomer nodes. Half of these newcomers will be cooperators. On subsequent rounds of prisoner’s dilemma, these will create a positive fitness score for any defector to which they have attached, before being eventually converted to defectors during strategy updating. Thus we have a process which we can trace back to the network founders: whichever founder gets slightly more of the initial cooperators can emerge as a highly connected hub within a sea of defectors and thus be the only individual
with a fitness score that enables it to attract newcomers. We see that in this case, we end up with a runaway effect: fitness-based preferential attachment has resulted in an extreme winner-take-all scenario rather than the rich-get-richer or Matthew effect [Merton, 1968, Perc, 2014] that we would typically associate with degree-based preferential attachment. Once newcomers stop arriving, all members of the population (being defectors surrounded by defectors) will have fitness values reduce to zero. The extreme heterogeneity, nevertheless, will remain, in the absence of any mechanism to
When we add fluctuation (fitness-based growth and attrition of nodes) to the EPA model, we see a marked reduction in heterogeneity for \( b = 1.3 \) values (comparing EPA+fluctuation with EPA in Fig. 4.7). This does not, however, correspond to a marked reduction in cooperation (see purple lines in Fig. 4.6), an interesting result which supports the argument we outlined in Section 4.1.1, namely that degree heterogeneity is only a partial explanation for network reciprocity and that assortativity also needs to be considered. We emphasise this point by noting that at the temptation to defect value shown in the figure, \( b = 1.3 \), cooperation is widespread throughout a population, and that the majority of cooperators will be achieving their fitness values as a result of the number of connections they have to other cooperators. This state of self-similar connectivity has emerged from assortativity.

**How does the fluctuation mechanism, when applied to EPA models, specifically bring about the observed reduction in heterogeneity?** The EPA model achieves a network structure which becomes static after 100 generations. We see from Fig. 4.7 (EPA, \( b = 1.3 \)) that EPA achieves a scale-free distribution within this period. The EPA and EPA+fluctuation models are identical up to generation 100, so highly connected hub nodes (high \( k \) values) will have similarly been present in both models at generation 100, yet in the case of EPA+fluctuation they are gone by generation 20,000. We know that fitness-based node deletion removes low scoring nodes, so the logical conclusion here is that the removed hubs had low fitness, relative to less well connected individuals. How can this happen? In an attempt to explain how highly connected hubs may end up with low fitnesses and thus be deleted under EPA+fluctuation, we consider four possible scenarios, taking into account strategy updating, preferential attachment, deletion by tournament selection and likely evolutionary stability (see Table 2.1 for a list of payoff scores for strategy pairings):

1. A *cooperator hub surrounded by cooperators*: Such a hub would achieve a fitness score approximately equal to its degree \( (k) \), which as a hub in a scale-free network would be very high. Strategy updating does not occur given alike strategies. New nodes, cooperators and defectors, would be preferentially added to such a node, with defectors being converted to cooperators during strategy updating. If selected randomly by tournament selection, such a hub will not be the lowest fitness (in a group of tournament size 10), so will not be deleted. This scenario appears evolutionarily stable.
2. A cooperator hub surrounded by defectors: Such a hub would have zero fitness. The strategy updating processes occurring for each of the hub’s many higher scoring defector neighbours would rapidly convert such a hub to a defector. This scenario would be highly evolutionarily unstable: the node would either have its strategy displaced by a defector, thus becoming scenario 4, or it would be deleted. (Note that this scenario is likely to be restricted more to those simulations having higher values of $b$, where the majority of the population are defectors.)

3. A defector hub surrounded by cooperators: Such a defector will be high scoring (score $\approx k \times b$) relative to its cooperator neighbours (each scoring $< k$). It therefore cannot be displaced by strategy updating, given that the connected cooperator neighbours will all have lower scores. If the hub happens to be randomly selected in a tournament during the attrition step, it will not be lowest fitness in a group of 10 (hubs are rare), so will not be deleted. It is however, potentially evolutionarily unstable since on account of its fitness, strategy updating will soon convert its neighbours to defectors. If this happens, it becomes a defector hub surrounded by defectors. See scenario 4.

4. A defector hub surrounded by defectors: Such a defector will score zero. If this scenario arises, subsequent newcomers to the network will be preferentially attached to other nodes which have higher fitnesses. An important point to highlight is that in EPA, where the network structure becomes fixed, the scale-free structure will remain even if a hub has zero fitness. We note that Poncela et al. have reported the presence of defector hubs in static networks that have been formed by EPA (typically for simulations with higher $b$ values where defection is more likely) [Poncela et al., 2009a]. In EPA+fluctuation, in contrast, such a hub is likely to be deleted.

Scenario 4 seems to offer a plausible likely mechanism for our observation that EPA+fluctuation results in the loss of high degree nodes whilst in the case of EPA, these hubs remain. However, we are still left seeking an answer to our original question regarding the loss of hubs in EPA+fluctuation models when $b = 1.3$, namely, in EPA+fluctuation cases where the temptation to defect is low, and the population is predominately cooperators it is still not clear how we actually arrive at either of the two scenarios (3 and 4) where defectors may end up occupying hubs. We can see that
scenarios 2 and 3 are unstable intermediate states leading to scenario 4. Our suspicion, given that we are discussing a network grown from cooperator founders, is that hubs are likely to be initially occupied by cooperators, hence scenario 2 is the most likely ‘stepping stone’ to reach scenario 4. Such an intermediate state—cooperator surrounded by defectors—may emerge as a result of the fluctuation mechanism driving the steady influx of new nodes, half being defectors, to preferentially attach to the hub(s). It is perhaps possible that whilst defector newcomers may not be able to directly displace a cooperator hub, they might eventually be able to starve it of the cooperator neighbours it needs to maintain its score, by extending their second edges to the hub node’s primary neighbours (their first edges having joined to the hub node). This could pave the way for conversion of the hub’s primary neighbours to defectors.

Finally, in the EPA+fluctuation plot (in Fig. 4.7), looking at final degree distributions for simulations using $b = 3.1$, we see more extreme heterogeneity than that observed for the non-fluctuating EPA model. In this case, it appears that the fluctuation mechanism has eliminated the majority of nodes (presumably added early in the network’s growth) that are not degree 1, 2 or maximum. Nodes subsequently added will have extended their first edge to the winner-take-all node leaving their second edge only able to connect to a zero (or very low) scoring defector. The elimination of nodes of degree value $2 < k < k_{\text{max}}$ for EPA+fluctuation may also be furthered by the opportunity for the fluctuation mechanism to create some nodes of degree $k = 1$. (As described previously, this is an artefact of our implementation of node deletion.)

Final Degree Distributions for CRA and CRA+fluctuation

Looking at results for CRA in Fig. 4.7, we see degree distributions that, as expected, appear to correspond to the exponential form expected from random addition of nodes to a network over time [Dorogovtsev and Mendes, 2002]. The same distribution is observed regardless of $b$ value since the process is not dependent on fitness. In Fig. 4.6, we see unsurprisingly that the lower heterogeneity resulting from this growth mechanism corresponds to lower levels of cooperation than seen for EPA. On incorporating fluctuation into the CRA model, whilst we observe in Fig. 4.7 the expected reduction in degree heterogeneity (the exponential distribution is compressed by the node deletion mechanism), contrarily, in Fig. 4.6, we see an increase in levels of cooperation. This result appears to contradict the consensus view that heterogeneity is positively correlated with cooperation.
How do we explain this apparently contradictory increase in cooperation? These results can be explained by the argument we proposed earlier in Section 4.1.1. Whilst less heterogeneity may be present, which will thus disadvantage cooperation, the CRA+fluctuation mechanism offers greater opportunity for self-assortativity, and thus the possibility to escape local optima. Such local optima may be suboptimal for any given network instance. In fact even if they do reflect the highest levels of cooperation that can be achieved for an instance of a particular network, it is unlikely that they represent the highest levels of cooperation achievable for that type of network generally. In further support of this argument, we highlight that the continued perturbation of networks in our fluctuation model brings about a marked consistency in the levels of cooperation achieved when compared to results obtained from non-fluctuating networks (discussed previously in Section 3.4.1, see in particular Fig. 3.4).

4.4.3 Performance of Models when Applied to Defector-founded Networks

In Fig. 4.8, we show behaviour profiles of final levels of cooperation versus temptation to defect, \( b \), for networks grown from complete founder networks of 3 defectors. Again we see cooperation emerge in all cases, although results are less clear-cut than those for cooperator-founded networks.

In the case of non-fluctuating networks, we see that EPA results in lower levels of cooperation than CRA. This result appears initially surprising since we would assume that preferential attachment would result in higher heterogeneity than random attachment and that EPA would therefore demonstrate higher levels of cooperation than CRA. We return to discuss this result later in this section. In the case of fluctuating networks, as expected, we observe higher levels of cooperation for EPA+fluctuation when compared to CRA+fluctuation.

In Fig. 4.9, we again show final degree distributions to aid explanation of the above results. We first highlight that the two fluctuation mechanisms, EPA+fluctuation and CRA+fluctuation, produce very similar distributions (and behaviour profiles) to those seen for cooperator-founded networks (compare corresponding plots from Fig. 4.9 with those in Fig. 4.7). It seems that fluctuation in both cases enables sufficient readjustment of the network to allow assortativity to generate approximately optimal levels of cooperation. In other words, the fluctuation model supports cooperation to similar levels, independent of founder strategies. This can be verified by comparing correspondingly
The effect of different network growth models on the relationship between temptation to defect and cooperation in networks founded by defectors. Final fraction of cooperators is determined from the average of 25 replicate simulations. Simulations featured 1,000 nodes and were run for 20,000 generations. Non-fluctuation models achieved fixed network structure after 100 generations, beyond which strategy updating continued alone. Fluctuation implementations are represented with dashed lines.

Non-fluctuating CRA shows similar degree distributions in defector-founded networks to those seen for cooperator-founded networks. The reason is that this growth mechanism is independent of agent behaviour. Inspection of behaviour profiles shows slightly lower levels of cooperation in defector-founded simulations when compared to cooperator-founded (compare solid orange lines in Figs. 4.8 and 4.6). The reason for this difference becomes apparent in Fig. 4.10 where we compare time plots of the simulations for $b = 1.6$, at which value the difference appears most noticeable. From the simulations, we see the interesting observation that in defector-founded networks, 11 out of 25 simulations appear to be unable to transition (within 20,000 generations) to cooperation (thus reducing the final average result across all replicates). It is also interesting to observe that the simulations which do transition appear to achieve the same levels of cooperation as present in cooperator-founded networks. We propose that the effect in defector-founded networks is the result of unfavourable distributions of strategies arising from chance events during the network’s infancy. Such early random events may have the potential to lock in long-term defection for the population which cannot readily be overcome by strategy updating alone (for example, as discussed in Section 4.4.1, the very early capture of a high degree node by a defector...
which consequently receives high game payoffs and so cannot be deleted, may prevent the emergence of cooperation in the long term.) The introduction of the fluctuation mechanism to CRA allows the population to restructure so as to escape such initially sub-optimal demographies. From our results we observe that fluctuation catalyses the majority of simulations to transition to cooperation (although as discussed at the end of Section 3.4.1, this is not entirely guaranteed).

Finally we return to our most interesting result: that in the non-fluctuating case,
CHAPTER 4. A MINIMAL MODEL FOR PAIR-WISE COOPERATION

Figure 4.10: Comparison of time plots for non-fluctuating CRA in cooperator- vs. defector-founded networks at $b = 1.6$. Each plot shows 25 replicate simulations, each featuring 1,000 nodes. In (a), cooperator-founded networks, cooperation is observed for all replicates. In (b), defector-founded networks, 14 replicates transition to cooperation whilst 11 do not. Replicates that successfully transition appear to reach similar levels of cooperation in either case.

CRA achieves higher levels of cooperation than EPA in defector-founded networks (compare solid orange with solid purple line in Fig. 4.8). Even more striking is the reduction in the ability of EPA to support cooperation when applied to defector-founded networks in comparison to cooperator-founded networks (compare solid purple lines in Figs. 4.8 and 4.6). Clearly EPA is a poor model for the evolution of cooperation in the case of defector-founded populations. From Fig. 4.9 we can see some difference in degree distributions between EPA and CRA; heterogeneity appears extreme for EPA in defector-founded networks. As described earlier, this heterogeneity is star-like and suggests more of a winner-take-all than rich-get-richer effect. This observation, whilst interesting, does not explain our findings here. We offer a fuller explanation below.

Why does preferential attachment result in such a marked reduction in cooperation in defector-founded networks, compared to cooperator-founded networks?

We have touched on the answer to this question earlier in Section 4.4.2, whilst discussing the relationship between high values for $b$ and heterogeneity, for EPA simulations in cooperator-founded networks. Here we illustrate the answer in more detail using Fig. 4.11, focusing in particular on early node attachment to both cooperator- and defector-founded populations. In Fig. 4.11a, the three cooperator founders have
their scores boosted by their interconnections (shown with thicker lines). Added nodes (thinner lines), if cooperators, will gain scores of 2, or if defectors, scores of $2b$. Thus nodes initially added to a cooperator-founded network will tend to have scores not vastly dissimilar to founder nodes, which will receive scores of $n_C$ (number of cooperator neighbours).

![Cooperator-founded network](image)

![Defector-founded network](image)

Figure 4.11: Initial interactions between founder networks and subsequently added nodes for (a) cooperator- and (b) defector-founded networks. Blue circles represent cooperators. Red triangles represent defectors. Interaction payoffs are shown along edges. Cumulative scores are shown within nodes. Founder network connections are represented with thicker lines.

In contrast, for defector-founded networks, there is a stark disparity between the scores achieved by the founders compared with those achieved by newcomers. Defector founders gain nothing by interconnections with other founders; they only achieve scores when newcomers attach which are cooperators. As for the nodes joining, if these are defectors they will score zero; if they are cooperators, they will also score zero and will soon be converted to defectors by strategy updating.

From inspection of Equation 4.2 we can see that there exists a marked difference in the way fitness-based preferential attachment will react to the distribution of scores in the two scenarios described. For cooperator-founded networks, nodes initially added to the founding network will have scores roughly similar to the founders. Nodes added subsequently will preferentially be added to the fitter founders, but some will also
attach to the slightly less fit founders’ neighbours. Contrast this with the defector-founded scenario. Here, nodes added to the founding network will have scores of zero, so preferential attachment will ensure that subsequent nodes will continue to be added only to the founders. This creates the opportunity for a runaway effect with one founder node taking all newcomers’ connections in a winner-take-all manner. As long as some of the newcomers are cooperators, the defector founder that these newcomer cooperators connect to will continue to achieve the only positive fitness score in a sea of defector nodes all scoring zero.

Defector-founded networks thus present a severe disparity in fitness distributions, which strongly biases the population against cooperation. Nevertheless, long-term defection is not a foregone conclusion, even given such an uninspiring starting point. First, interactions within these networks are complex and subject to random events as simulations progress. One element of randomness is the \( \epsilon \) parameter in EPA (see Equation 4.2) which we have set to 0.99 to weight the mechanism heavily towards EPA. Secondly, cooperators added to unfavourable defector-founded populations are not necessarily immediately converted to defectors by strategy updating. They may persist for a limited number of generations. Their problem is that, as lone cooperators, they have no way of achieving positive fitness values. However, whilst strict EPA (\( \epsilon = 1 \)) would not allow a newcomer to attach to an existing node of zero fitness, the 0.01 element of randomness that remains by setting \( \epsilon = 0.99 \) is sufficient to allow for the possibility that a new cooperator will eventually attach to an existing cooperator. This pair of cooperators will then each achieve positive scores which creates the opportunity for cooperation to emerge. (We have tested setting \( \epsilon = 1 \) and confirm that cooperation is not observed for EPA whereas at \( \epsilon = 0.99 \) it becomes possible.)

In summary, we see that fitness-based preferential attachment, by definition, drives new nodes to connect to high fitness founder members. Under certain conditions it will exacerbate disparities in scores, and reduce the possibilities of new nodes attaching anywhere other than to the highest scoring node(s), which in a network grown from defectors is likely to be a founder node. In other words, in the case of defector-founded populations, EPA is a poor model for the emergence of cooperation. The obstacles to cooperation that EPA presents in such circumstances are avoided by random attachment which disregards fitness and thus allows newcomers to connect to fitter and zero-fitness nodes alike. One final detail to highlight here is that in the case of random attachment, the greater the number of nodes in the network, the smaller the influence of the founders. This is clearly very different to EPA, which creates the possibility
for founders to become the most influential members of a population, regardless of population size.

\section*{4.5 Conclusion}

In this chapter we have presented a model, featuring network growth by a random process and attrition based on fitness, which supports network-reciprocal cooperation. The model demonstrates the emergence of cooperation in simulated populations on networks having moderate levels of degree heterogeneity. The key to cooperation in our model is continuous assortativity, which allows agents within the simulation to capitalise on the exponential degree distribution generated by the model. In this way, self-assorting cooperators can form clusters to optimise the rewards available to them. These clusters, which return high fitness values to their members, are evolutionarily beneficial.

Our model supports cooperation in networks grown from founders and also in pre-existing networks. Cooperation is promoted beyond levels seen for well-mixed populations, in all model implementations tested, regardless of founding or initial strategies present, and for all initial topologies. The model supports cooperation without the requirement for agents to have memory, higher cognitive abilities or any form of global knowledge regarding either the network or other members of the population. Given random attachment of new nodes, there is no requirement to explain mechanisms for preferential attachment.

This minimal model points to a possible general explanation that may be applicable to the emergence of cooperation in networks of primitive organisms. The key requirements are that new nodes are connected randomly over time to an existing network and that the network is continually perturbed. We assume that a mechanism such as natural selection exists which will result in the increased frequency over time of behaviours which increase fitness.

We have found in comparing models of network growth that network-reciprocal cooperation can exist without the level of degree heterogeneity associated with scale-free structure. Such findings at first glance appear somewhat at odds with the prevailing consensus that increasing heterogeneity promotes cooperation; however, by explicitly considering the benefits to cooperation offered by the combined effects of heterogeneity \textit{and} assortativity, we can offer a different perspective that may aid in understanding the evolution of cooperation in networks. Whilst our model clearly introduces only a
relatively limited form of heterogeneity in terms of the network structure, our findings allow for the possibility that, with regards to cooperation, it is more important that co-operators are able to capitalise on opportunities for self-assortativity, than the network structure itself be highly heterogeneous.

Finally, we highlight that preferential attachment can in certain cases impede the evolution of cooperation. For fitness-based preferential attachment simulations in populations founded by defectors, the rich-get-richer effect can transform to one of winner-take-all, a change which seems likely to be detrimental to the interests of co-operators.
Chapter 5

The Role of Fluctuation as a More General Contributory Factor in the Evolution of Cooperation

In the previous chapter we described a model for cooperation, in networks grown from founder populations, by random addition of new nodes. Testing of this model demonstrated that it was able to support the emergence of cooperation without the requirement for extreme heterogeneity. Further, the model was able to support cooperation independently of the behaviour of the founder population. Thus far, we have focused on the prisoner’s dilemma game in networks having average degree, \( z = 4 \). In this chapter we extend application of the proposed model with regards to the game and also the average network connectivity. We apply the model to an alternative representation of cooperation in pair-wise interactions—the snowdrift game—and we subsequently assess the model’s performance, for both snowdrift and prisoner’s dilemma games, as we increase the connection density of the population.

5.1 Introduction

The aim of this chapter is to explore the model developed thus far to assess its robustness as an explanation for cooperation under alternative scenarios. We investigate the performance of the model when applied to the snowdrift game to test whether it achieves similar results to those previously seen for the prisoner’s dilemma. We then explore the model’s performance using both games, for networks of increasing average
connectivity (degree), in order to test how the density of connections in a population affects its ability to support cooperation. In each of the investigations we consider effects in pre-existing networks and also in networks growing from small founder populations.

5.1.1 Spatial Structure and the Snowdrift game

The prisoners’s dilemma has received the lion’s share of scientific research seeking to understand the evolution of cooperation. It has alternatively been argued that, since the prisoner’s dilemma fails to predict the ubiquity of cooperation seen in nature, the snowdrift game (described in detail in Section 2.5.2) might form a more suitable representation of cooperative dilemmas [Hauert and Doebeli, 2004, Doebeli and Hauert, 2005]. In the prisoner’s dilemma, the Nash equilibrium is to defect, and in the case of evolutionary game theory, defection also represents the evolutionarily stable strategy (ESS) for well-mixed populations. The snowdrift game, however, supports intermediate levels of cooperation—i.e. coexistence of cooperators and defectors—hence the reason why it is argued to be a more realistic representation of cooperation. The Nash solution for the snowdrift game is to play the opposite strategy to that of your opponent. Thus in the case where both players defect, either could have increased their score by choosing cooperate, whilst similarly, where both cooperate either player could have increased their score by choosing defect. In the snowdrift game, there is consequently no longer the same drive to defect that exists for the prisoner’s dilemma. Whilst defection no longer has the power of attraction that it does in the prisoner’s dilemma, the snowdrift game is still a cooperative dilemma; any individual choosing to play cooperate against an opponent’s cooperate strategy could have achieved a higher payoff by playing defect.

Moving beyond classical game theory and into evolutionary game theoretic considerations, unlike the prisoner’s dilemma, the Nash solution in the case of the snowdrift game does not translate to an ESS. In the snowdrift game, featuring well-mixed populations, there is no evolutionarily stable solution based on a pure strategy. An ESS can only be achieved for this game by the use of mixed strategies. Thus, unlike the well-mixed scenario for prisoner’s dilemma where the equilibrium is represented by all members defecting, in the snowdrift game the equilibrium is represented by a mixture of cooperators and defectors. Specifically, the equilibrium is given by $1 - r$ where $r$ represents the cost-benefit relationship (see Fig. 2.4) for mutual cooperation thus:

\[ r = \frac{c}{2b} - c \]  
(5.1)
CHAPTER 5. A GENERAL FACTOR IN COOPERATION

Our interest here is not, however, with regards to well-mixed populations; as with our previous work, we are interested in how different types of relationships between individuals might change behaviour. In this respect, the snowdrift game demonstrates rather intriguing results. The important finding of Nowak and May with regards to the prisoner’s dilemma [Nowak and May, 1992] is that the introduction of spatial structure promotes cooperation. In the snowdrift game played on lattices, a different finding is observed [Hauert and Doebeli, 2004]: the introduction of regular spatial structure of this kind is observed to reduce cooperation.

The explanation for this phenomenon is based on the dynamics which arise from the different relative payoffs for behaviour in the two games (prisoner’s dilemma: \( T > R > P > S \); snowdrift game: \( T > R > S > P \)). Where costs are low (low \( r \) values), self-assortative clustering brings the same benefits in the snowdrift game as it does in the prisoner’s dilemma: cooperators can achieve higher scores when clustered together. As costs increase, it becomes harder for cooperators to displace defectors to the same extent and rather than selection (strategy updating) driving the generation of self-similar clusters, it is only able to generate filament structures (see Fig. 5.1).

Thus there are two processes arising in the snowdrift simulations which influence assortativity differently:

i. Self-assortment, driven by selection (strategy updating), results in cooperator to cooperator connections.

ii. Other-assortment, driven by fitness-maximising agents attempting to play the opposite strategy to their opponent (Nash equilibrium), results in cooperator to defector connections.

The first of these processes dominates whilst costs are low, thus supporting cluster formation. The second process becomes increasingly influential as costs increase and cooperators struggle for survival against increasing exploitation by defectors. This combination of both processes supports filament formation.

In Fig. 5.1 we provide a detailed illustration of a filament structure which emerges as costs increase (\( r = 0.6 \)), showing how the pressures of the payoffs maintain the one dimensional form of these filaments. On a regular network of average degree, \( z = 4 \), within these filament structures, a cooperator has two neighbours which are cooperators, giving payoffs of \( R \) each, and two neighbours which are defectors, giving payoffs of \( S \) each (thus the cooperator’s score is \( 2R + 2S \)). We highlight two comparisons
with the spatial prisoner’s dilemma, which are advantageous and disadvantageous for cooperators respectively:

i. Advantage: the positive valued payoff of $S$ when a cooperator connects to a defector results in a better outcome for the cooperator than in the corresponding prisoner’s dilemma scenario where this interaction results in a zero payoff,

ii. Disadvantage: cooperators existing in filaments in this way in the snowdrift game are less well protected than those observed in clusters in the prisoner’s dilemma and they are therefore vulnerable to exploitation by defectors.

Subsequent work by Santos and Pacheco [Santos and Pacheco, 2005] observed that the reduction in cooperation seen for the snowdrift game in regular (homogeneous) networks was reversed when the game was implemented on scale-free networks. Here, as for prisoner’s dilemma, levels of cooperation were promoted beyond that which would be observed for well-mixed populations. Homogeneous networks, having a uniform degree value, $z$, impose a strict limit on a cooperator’s upper score (equal to $z$).
Heterogeneous networks, on the other hand, offer the possibility for some cooperators to have degree values of $k > z$, and hence higher scores ($>z$), thus allowing self-assortment by cooperators to generate higher fitnesses than those achievable in regular networks. Given that it is difficult for highly connected cooperators to be displaced due to the high fitness arising from larger numbers of connections to self-similar strategies and the reinforcement that is provided by age-related interconnection of older nodes, such individuals can form a stronghold or secure position from which cooperation can radiate.

It is with regards to these findings that we investigate the effect of fluctuation on the emergence of cooperation in the snowdrift game. It has previously been reported for this game that (regular) spatial structure, in the form of a lattice, reduces cooperation when compared to the well-mixed scenario [Hauert and Doebeli, 2004], whereas it has been reported elsewhere that the heterogeneity afforded by scale-free networks promotes cooperation [Santos and Pacheco, 2005]. In the following work we test a hypothesis that the fluctuation model generates sufficient network degree heterogeneity to promote cooperation.

### 5.1.2 Effect of Connection Density

The second topic we wish to address within this chapter concerns the density of connections between individuals, i.e. the average degree within a network. There are a large number of scientific publications reporting evolutionary game theoretic investigations into cooperation in networks. Many of these have tended to focus on networks of average degree $z = 4$. In the real world however, this may be thought (depending on the circumstances) to be a relatively sparsely connected network. Arguably, more realistic models should provide some level of robustness as degree is increased. We know [Ohtsuki et al., 2006] that cooperation should arise on a regular graph when the benefit-to-cost ratio for cooperation exceeds the average degree of the nodes in the network ($b/c > z$). This relationship does not provide any specific guidance with regards to heterogeneous networks; it does though, generally suggest that increasing $z$ will reduce cooperation assuming the benefit-to-cost relationship remains constant.

Here we extend our application of the fluctuation model, and look at simulations involving a range of average connectivities. We follow this approach for both the prisoner’s dilemma and the snowdrift game to observe if our findings holds for networks that are less sparse than those originally investigated. We consider networks that are initially regular, random and scale-free in structure. As previously, in the interests of
developing a robust and general model, we also consider networks grown from a small population of cooperator or defector founders.

5.2 Methods

The models implemented here follow the same approach described previously in Chapter 4. We provide a general outline of the existing method followed by more detailed information regarding matters specific to work in this chapter.

The models describe networks (i.e. graphs) with agents situated at the nodes. Edges between nodes represent interactions which correspond to behaviours of agents playing a prescribed game. Behaviours are encoded by a strategy variable which takes one of two values: cooperate or defect. The game is played in a round robin fashion, with each agent in turn playing its strategy against each of its connected neighbours. Each agent accumulates a fitness score which is the sum of all its individual game payoffs. Strategy updating between neighbours, as an analogue of natural selection, results in the displacement of less fit strategies by fitter ones.

5.2.1 Outline of the Evolutionary Model

Unless stated otherwise, the general outline of the evolutionary process we use (for one generation) is as follows:

i. **Play game**: Each agent plays one-shot prisoner’s dilemma or snowdrift game with all neighbours and achieves a fitness score that is the sum of all the payoffs.

ii. **Update strategies**: Those agents that achieve low scores may have their strategies replaced on a probabilistic basis with the strategies of randomly selected (fitter) neighbours.

iii. **Grow network**: New nodes are added to the network, connecting to distinct existing nodes via $m$ edges, by random attachment.

iv. **Remove nodes (only in the case of fluctuation models)**: If the network has reached maximum size, it is pruned by a tournament selection process that removes less fit agents.

The evolutionary simulations here consider populations in the form of pre-existing networks and also those grown from founder populations consisting of $N_0$ completely
connected nodes. Pre-existing networks are initialised with cooperators or defectors with equal probability. Founder populations will be either all cooperators or all defectors.

5.2.2 Growth of Networks

Nodes are added to networks, as per the chronological random attachment (CRA) growth mechanism described in Chapter 4 (see in particular Equation 4.3), using a rate of 10 nodes per generation. Each newcomer node extends \( m \) edges to randomly chosen existing (different) nodes, where \( m = z/2 \), with \( z \) being the desired average degree for the network. We assess networks with average degree values of \( z = 4, 8, 16 \) and 32. For networks grown from founders, in order to meet the requirement that each of the edges from a newcomer goes to a different node, we require differently sized starting populations for each degree value. We use founding population sizes, \( N_0 = m \), to provide for this. Other aspects of growth relating to the two different cases of pre-existing networks and networks grown from founders are as described previously in Section 4.3.2.

5.2.3 Snowdrift Game Implementation

We implemented the snowdrift game using the approach described by Hauert and Doebeli [Hauert and Doebeli, 2004], rescaling the relative payoffs such that the game can be defined (and models can be characterised) by means of a single parameter \( r \). This value represents the cost-to-benefit ratio for mutual cooperation as described in Equation 5.1. Setting \( c = 1 \), whilst leaving benefit variable, gives:

\[
r = 1/2\beta - 1.
\]  

(5.2)

Rewriting as \( \beta = 1/2r + 1/2 \), we are then able to set snowdrift payoffs derived from \( r \) values thus: \( T = \beta > 1, R = \beta - 1/2, S = \beta - 1 \) and \( P = 0 \), with \( 0 < r \leq 1 \), hence maintaining the snowdrift game relationship: \( T > R > S > P \). The payoff matrix for this game was presented previously in Figs. 2.4 and 2.5. The corresponding table of snowdrift payoffs for strategy pairing is shown in Table 5.1.
Strategy pairing | Scores
--- | ---
C : C | $\beta - 1/2 : \beta - 1/2$
C : D | $\beta - 1 : \beta$
D : D | 0 : 0

Table 5.1: Table illustrating payoffs for strategy pairings in single parameter snowdrift game. C and D represent cooperate and defect respectively. See Section 5.2.3 for explanation of the $\beta$ parameter.

5.2.4 General Simulation Conditions

Nominal maximum size of networks was set at $N = 1,000$ nodes with an overall average degree of approximately $z = 2m$. Simulations were run until 20,000 generations. The final fraction of cooperators values we use are means, averaged over the last 1,000 generations of each simulation\(^1\), in order to compensate for variability that might occur if just using final generation values. Each simulation consisted of 25 replicates. We used a shrinkage value of $X = 2.5\%$ of the population size to delete nodes from the network for those simulations featuring fluctuation.

5.3 Results and Discussion

We present results below initially focusing on how the fluctuation model affects the emergence of cooperation for evolutionary populations playing the snowdrift game. Here we focus solely on networks of average degree $z = 4$. We subsequently report on the extension of both prisoner’s dilemma and snowdrift in evolutionary scenarios featuring networks of increasing average degree values.

5.3.1 The Impact of Fluctuation on the Evolution of Cooperation in the Snowdrift Game

As with previous investigations, we consider the simplified scenario of pre-existing networks and the arguably more realistic scenario looking at networks as they grow from founder populations.

\(^1\)For simulations in previous chapters, we averaged over the last 20 generations. Preliminary work for this chapter showed higher variability in time plots, so we averaged over the last 1000 generations.
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Figure 5.2 shows behaviour profiles illustrating the effect of fluctuation on the snowdrift game simulations in the case of fully-formed networks having initially regular, random and scale-free topology. Here we consider, as with the work on prisoner’s dilemma in preceding chapters, networks having average degree of $z = 4$.

![Figure 5.2: Behaviour profiles illustrating the effect of fluctuation on the emergence of cooperation for populations playing the snowdrift game, on pre-existing networks of average degree, $z = 4$. Fluctuation simulations are based on random growth and least-fitness-based deletion. Dashed grey lines represent equilibrium fraction $(1 - r)$ of cooperators in well-mixed populations.](image)

The level of cooperation that would be observed in a well-mixed population is given by $1 - r$. This represents an equilibrium solution for the snowdrift game with regards to the cost-benefit parameter $r$ (where $0 < r \leq 1$), much as the baseline (defection, i.e. zero cooperation) provides the equilibrium solution for the prisoner’s dilemma with regards to the temptation to defect variable, $b$. We can use the $1 - r$ equilibrium (see dashed grey line in figures) as a benchmark to assess whether the models promote cooperation at levels beyond those which would be observed in well-mixed scenarios.

We first comment on the findings regarding networks which remain topologically static during simulations (see solid lines). Without growth or attrition, changes in behaviour arise solely from the strategy updating process (selection). We observe results for regular networks (solid brown line) that correspond with those previously reported [Hauert and Doebeli, 2004], namely that unlike results for the prisoner’s dilemma, regular (homogeneous) connectivity is detrimental to cooperation in the snowdrift game except where costs of cooperation are very low. We observe results...
for scale-free networks (solid green line) that again correspond with reported findings [Santos and Pacheco, 2005], namely that in scale-free networks we recover the same general finding as that established for the prisoner’s dilemma—scale-free networks promote cooperation in the snowdrift game. Finally we see that the effect of spatial structure is to promote cooperation in the case of random networks, albeit to a lesser extent than levels seen in scale-free networks.

Returning to regular networks, we note that for $z = 4$, extinction of cooperators occurs at approximately $r = 0.7$, whereas in well-mixed populations at the same $r$, we would expect cooperation levels at $1 - r = 0.3$. By considering the filament type structures found in such snowdrift simulations, as illustrated in Fig. 5.3, we can estimate the expected value of $r$ corresponding to this extinction point. For the purposes of this explanation, we consider the cooperator filament to be present in a sea of defectors ($\text{defect: defect}$ interactions achieve zero payoff). We can see that whilst such a structure may offer protection to cooperators with two cooperator neighbours, terminal cooperator nodes of the filament are more vulnerable. Such cooperators will start to be predated once neighbouring defectors (achieving scores of $T$) exceed the terminal cooperator’s score of $S(k - 1) + R$. This score represents 1 connection to a neighbouring cooperator within the filament whilst all other connections are to defectors. The extinction value is the $r$ value that corresponds to the payoff equality:

$$T = S(k - 1) + R. \tag{5.3}$$

We can determine the corresponding $r$ value based on how the payoff parameters derive from the cost-benefit relationships (see snowdrift game payoff matrix in Fig. 2.4):

$$T = \beta$$
$$R = \beta - c/2$$
$$S = \beta - c$$
$$P = 0$$

Setting $c = 1$ as described in Section 5.2.3 and substituting the above payoff expressions throughout Equation 5.3, we get:

$$\beta = \beta - 3(\beta - 1) + \beta - 1/2.$$
Figure 5.3: Snowdrift game cooperator filament structures become vulnerable at terminal nodes as costs ($r$ values) increase. Terminal cooperator nodes in filaments become vulnerable when $T = S(k+1) + R$. In this situation given degree of $k = 4$, the equality is satisfied by $T = 7/6$, $R = 4/6$, $S = 1/6$, $P = 0$. The diagram uses these payoffs on interactions (edges) and shows accumulated scores in nodes. The vulnerability can be seen on comparing cooperator vs. defector node scores in shaded region. These payoffs correspond to extinction value of $r = 0.75$. In a well-mixed population, this $r$ value would result in a higher final fraction of cooperators at $1 - r = 0.25$.

$$\beta = \beta - 3\beta + 3 + \beta - 1/2.$$  

Hence, our extinction value occurs when $\beta = 7/6$.

Substituting this $\beta$ into Equation 5.2, we see that this gives $r_{\text{extinction}} = 3/4$, which corresponds well to our observed value in Fig. 5.2 (solid brown line meets the x-axis at $r = 0.7$).

The introduction of fluctuation to the simulations described above (see dashed lines in Fig. 5.2) leads to approximately similar final levels of cooperation, regardless of the three different initial topologies. This outcome represents a marked rise in cooperation for initially regular and random networks (in comparison to static simulations), and a reduction in cooperation for initially scale-free networks. The consistency of the results is expected, based on our understanding that: i) the final level of cooperation is influenced by the network heterogeneity, and ii) the fluctuation model (in those cases where cooperation emerges) drives network topologies to a consistent degree distribution which corresponds to a heterogeneity lying between that of random and scale-free networks. This final heterogeneity for fluctuation models, explains the reduction in
cooperation observed when the model is applied to initially scale-free networks.

**Observations Based on Networks Grown from Founders**

Figure 5.4 shows snowdrift game behaviour profiles for networks grown from founder populations using random attachment. Here we see that in both fluctuating and non-fluctuating simulations, the initial strategy types appear to have little or no impact. Non-fluctuating simulations (solid lines) demonstrate levels of cooperation markedly above those observed in well-mixed populations (see dashed grey line). The introduction of fluctuation supports increased levels of cooperation at more challenging cost ($r$) values. At these higher cost values, the added opportunity for network restructuring that is offered by the fluctuating mechanism creates further opportunities for assortativity amongst cooperators. The profiles seen for the fluctuating models here are very similar to those for pre-existing networks as shown in Fig. 5.2 (compare dashed lines between the two figures). It appears that given 20,000 generations, the fluctuation model can sufficiently modify pre-existing networks of initially different topologies and starting scenarios, in order to similarly maximise levels of cooperation. Inspection of final degree data confirms that final distributions in all cases are highly similar, regardless of initial topologies.

![Figure 5.4: Behaviour profiles illustrating the effect of fluctuation on the emergence of cooperation for populations playing the snowdrift game in networks grown from founder populations. Average network degree is $\bar{z} \approx 4$. Populations are grown from complete networks of $N_0 = 2$ nodes, either both cooperators or both defectors. Fluctuation simulations are based on random growth and least-fitness-based deletion. Dashed grey line represents equilibrium fraction $(1 - r)$ of cooperators in a well-mixed population.](image-url)
In summary, the introduction of fluctuation changes outcomes for the snowdrift game in evolutionary simulations in a way that corresponds to results seen previously for the prisoner’s dilemma: i) levels of cooperation achieved are largely independent of starting criteria, ii) levels of cooperation are increased for initially random networks, and increased to a greater extent for initially regular networks, iii) levels of cooperation are reduced for scale-free networks. In all cases, the fluctuation model supports cooperation beyond that predicted for well-mixed populations.

5.3.2 The Effect of Increasing Average Network Connectivity on Cooperation in the Prisoner’s Dilemma

In this section we report on the effect of increasing average network connectivity for prisoner’s dilemma played in evolving populations and we consider how these effects are influenced by the introduction of fluctuation. We compare the evolution of cooperation in networks with and without fluctuation, considering first the simpler case of pre-existing networks and subsequently networks grown from founders.

Observations Based on Pre-existing Networks

In Fig. 5.5 we present results of prisoner’s dilemma simulations in fully-formed networks based on average degree values of $z = 4, 8, 16$ and $32$, initially populated with cooperators and defectors in approximately equal amounts. In static networks (solid lines) we see generally that increasing connection density has the expected outcome of reducing cooperation. For $z = 32$, cooperation is extinguished at all values of $b$. The explanation here is that the more members of the population each individual is connected to, the closer the network gets to complete connectivity—a situation which approximates the well-mixed scenario where an individual will connect to any member of the population with equal probability. For the prisoner’s dilemma, in well-mixed scenarios, cooperation is extinguished: defection is the Nash equilibrium. We also observe from the results that increased degree heterogeneity offers some reprieve from the limits imposed by increased connectivity (compare Figs. 5.5a, c and e, in order of increasing heterogeneity). Again this is an unsurprising result given our understanding that heterogeneity generally promotes cooperation.

When we consider the impact of fluctuation (dashed lines), we see marked increases in cooperation in simulations based on initially regular and random networks (compare Figs. 5.5b to a and 5.5d to c). In the case of scale-free networks (compare
Figure 5.5: Behaviour profiles illustrating the effect of fluctuation on the emergence of cooperation for populations playing the prisoner’s dilemma in pre-existing regular, random, and scale-free networks for a range of average degree ($z$) values. Fluctuation simulations, shown on the right (dashed lines), are based on random growth and least-fitness-based deletion.

Figs. 5.5f to e), we expect to see fluctuation resulting in reduced levels of cooperation, since the fluctuation process reduces final degree heterogeneity of the network. We do indeed see lower levels of cooperation, as expected, for $z = 4$ and $z = 8$, although rather surprisingly, fluctuation appears to drive an increase in cooperation for scale-free networks of higher connectivity (compare dashed green and purple lines in Fig. 5.5f with correspondingly coloured solid lines in 5.5e). We believe that this effect is more a result of artefactually reduced levels of cooperation in the static networks rather than due to the fluctuation process. The explanation for reduced cooperation
in the $z = 16$ and $z = 32$ static scale-free networks is rooted in our implementation of the Barabási-Albert (BA) method [Barabási and Albert, 1999] for constructing the networks. The BA model requires parameters: $m$, for the number of edges to attach from a new node to an existing one, and $N$, the required network size. In the case of networks having, for example, an average degree of $z = 32$, we need to specify that newcomers attach with $m = 16$ edges, but this makes the minimum degree value of the network, $k_{\text{min}} = 16$ (compared with e.g. $k_{\text{min}} = 2$ in the case of networks with average degree $z = 4$). This increase in minimum degree value can not, be matched by the necessary increase in maximum possible degree since this is a function of, and therefore limited by, the size of the network $N$, which we have left unchanged (at $N = 1,000$) for purposes of comparing results for different connectivities. Thus rather than having a true scale-free network, the degree distribution is now compressed; it has reduced heterogeneity and hence reduced ability to support cooperation. Having checked our data, for static networks of $z = 4$ we see a range of degree values from 2 to 120 (a 60-fold difference) with maximum frequency $f(k = 2) \approx 500$, whereas for $z = 32$, we see a range of degree values from 16 to 235 (only a 14-fold increase) with a reduced maximum frequency $f(k = 16) \approx 110$.

A second interesting result arises for the fluctuation model in the case of regular networks, where at higher levels of temptation the expected effect from lower connectivity is reversed (see Fig. 5.5b). Here for $b > 1.7$, fluctuation becomes less able to support cooperation in $z = 4$ networks (dashed blue lines) than for networks of greater connectivity (dashed red, green and purple lines). We do not have a full explanation for this observation but we note that it occurs for higher $b$ values, in populations where defectors form the majority. We suspect that cooperation in such networks may be hampered by the constraint that a node of degree $k = 4$ has only 5 possible neighbour arrangements (4, 3, 2, 1 and 0 cooperator neighbours). Cooperators must maintain connectivity with other cooperators to survive. One out of these 5 possible neighbour arrangements results in the cooperator being surrounded by (4) defectors and thus unable to score. A cooperator in this situation is likely to be converted to a defector during strategy updating. In a network of $z = 8$, however, more arrangements are available where a cooperator is not guaranteed to be displaced.

We can illustrate this by considering a population where 3/4 of the individuals are defectors. Assuming $z = 4$, and other considerations aside, a given cooperator node may have 1 out of 4 neighbours that is also a cooperator. The connection to another cooperator neighbour allows this node the potential to maintain a positive fitness score
and thus avoid being displaced by a higher scoring defector neighbour. Any increase in proportion of defectors within the population is likely to see the number of this node’s cooperative neighbours reduced to zero, and it is then likely to be converted to a defector. Now consider, as an alternative, a regular network of $k = 8$. Here, given a population that has the same proportion of defectors as previously (3/4), a cooperator is likely to have have 2 out of 8 neighbours that are cooperators. An increase in defectors within the wider population may reduce the number of this node’s cooperative neighbours, but it would (initially) be to 1, rather than zero, thus this node is likely to persist in a population for longer on the basis of increased average degree. We suspect that whilst values of $z$ are small this effect is noticeable, but that it rapidly becomes trivial (in comparison to other effects) as $z$ increases.

**Observations Based on Networks Grown from Founders**

In Fig. 5.6 we illustrate the effect of fluctuation on prisoner’s dilemma simulations in networks grown by random attachment from founders, for a range of average degree values. We see that in the case of static networks (solid lines), lower levels of cooperation are observed when networks are grown from defector founders than when grown from cooperators (compare Figs. 5.6c and a). Assortativity can still promote cooperation in static networks, although as described in Section 3.5, defector-founded networks (in the non-fluctuating case) may bias such a network against cooperation.

We see that in all cases fluctuation leads to an increase in cooperation (compare Fig. 5.6b with a, and Fig. 5.6d with c). Generally, the fluctuation model results seen for populations grown from cooperators are very similar to those grown from defectors, suggesting the model can support cooperation largely independent of the behaviour present in the founding networks.

### 5.3.3 The Effect of Increasing Average Network Connectivity on Cooperation in the Snowdrift Game

In this section we repeat investigations reported above, however we now model cooperation using the snowdrift game, which more readily supports cooperation, with well-mixed populations able to support the coexistence of cooperators and defectors.
Observations Based on Pre-existing Networks

In Fig. 5.7 we present results of snowdrift game simulations in fully-formed networks, based on average degree values of $z = 4, 8, 16$ and $32$, initially populated with cooperators and defectors in approximately equal amounts. In static networks we observe the expected result [Hauert and Doebeli, 2004] that regular networks generally reduce cooperation below that seen for well-mixed populations (see Fig. 5.7a). We note that for larger values of $z$ we increasingly approximate the well-mixed limit for the game (compare coloured lines, for increasing $z$ values, with dashed grey line in Fig. 5.7a). In random and scale-free networks (see Figs. 5.7c and e), we see cooperation promoted beyond the well-mixed limit (dashed grey line), with highly heterogeneous scale-free networks demonstrating higher levels of cooperation than seen for random networks (as we would expect based on [Santos and Pacheco, 2005]). Much as with homogeneous (regular) networks, we observe that increasing $z$ in heterogeneous networks
again drives the behaviour of a population towards that of the well-mixed limit (compare e.g. blue vs. purple lines with respect to the grey dashed line in Figs. 5.7c and e).

![Figure 5.7](image-url)

Figure 5.7: Behaviour profiles illustrating the effect of fluctuation on the emergence of cooperation for populations playing the snowdrift game in pre-existing regular, random, and scale-free networks, for a range of average degree ($z$) values. Fluctuation simulations, shown on the right (dashed lines), are based on random growth and least-fitness-based deletion. Dashed grey lines represent equilibrium fraction ($1 - r$) of cooperators in well-mixed populations.

The introduction of fluctuation to these models generally results in increased levels of cooperation, with increases more noticeable for smaller values of $z$ (see dashed blue lines), those being furthest away from the well-mixed limit. Exceptions to this are scale-free networks, which appear to represent a reduction in cooperation for lower
values of \( z \) (compare red and blue dashed lines in Fig. 5.7f with corresponding solid lines in Fig. 5.7e) and no change for \( z = 32 \). As described above, we believe this latter result is not due to the effect of fluctuation failing to reduce heterogeneity; rather, it is the result of our implementation of the Barabási-Albert algorithm which, in the case of higher \( z \) values, has compressed the degree heterogeneity for the intended scale-free network and has hence limited cooperation.

**Observations Based on Networks Grown from Founders**

In Fig. 5.8 we illustrate the effect of fluctuation on snowdrift game simulations in networks grown by random attachment from founders, for a range of average degree values. We see that in the case of static networks (Figs. 5.8a and c), results for cooperator- and defector-founded networks are similar. As previously observed in heterogeneous networks, levels of cooperation reduce as \( z \) values tend to the well-mixed limit (compare blue with purple lines).

The introduction of fluctuation promotes cooperation in all cases, with greater increases observed for lower connectivity (\( z \) values away from the well-mixed limit). As with the prisoner’s dilemma results, similar profiles are observed regardless of founder population behaviour.

### 5.4 Conclusion

Within this chapter, we have shown how applying the fluctuation model to the snowdrift game promotes cooperation beyond levels observed for well-mixed populations. These findings, combined with those of Chapter 4, show that fluctuation has a demonstrably positive effect in the two main game theoretic representations of cooperation: the prisoner’s dilemma and the snowdrift game. It has been reported for the snowdrift game that spatial reciprocity may be detrimental to the emergence of cooperation when network heterogeneity is absent. This finding exists in contrast to that observed for the prisoner’s dilemma where cooperation was promoted even in the case of regular networks. The fluctuation model tested here results in no such contradictions, since final networks are all of similar moderate heterogeneity. Cooperation is thus promoted, beyond the well-mixed scenario, regardless of initial network topology.

Continuing with our aim of assessing the extent to which fluctuation offers a robust and general explanation for the evolution of cooperation, we applied our model to run evolutionary simulations on networks of increasing degree values. We considered both
Figure 5.8: Behaviour profiles illustrating the effect of fluctuation on the emergence of cooperation for populations playing the snowdrift game in networks grown from founder populations. Populations are grown from complete networks of $N_0 = z/2$ individuals; all cooperators or all defectors. Fluctuation simulations, shown on the right (dashed lines), are based on random growth and least-fitness-based deletion. Dashed grey lines represent equilibrium fraction $(1 - r)$ of cooperators in well-mixed populations.

In summary, the findings described here provide strong support for our argument that a fluctuation model, based on growth by random attachment and fitness-based
deletion, is capable of generalising to support the evolution of cooperation in networks for a variety of evolutionary scenarios.
Chapter 6

A Minimal Model for the Emergence of Group-wise Cooperation in Networks

We have described in the preceding chapters how a model based on population fluctuation may support the emergence of cooperation. We have shown that when implemented, such a model demonstrates cooperation independently of initial network structure and strategy type. The model requires no assumptions of higher cognitive abilities for agents. We have tested this model with respect to different representations of cooperation, different population densities and assorted starting conditions, all of which have demonstrated the robustness of the model and supported our argument that fluctuation is potentially a general promoter of cooperation in networks.

Thus far, our work has focused on pair-wise behaviour which has been the common approach for studying cooperation in networks. In this chapter, we shift our attention to group-based interactions, which are arguably a more accurate and realistic representation of behaviour in social networks. Here we consider the application of a model based on fluctuation to public goods games (PGGs). Whilst the research described in this chapter was initially designed to further develop ideas based on our existing research, at the time this work was done no model existed within the scientific literature to describe the evolution of group-wise cooperation in networks grown from their origins.

In this chapter we describe a coevolutionary model of public goods games in networks, growing by chronological random attachment (CRA) from small founding populations of simple agents. The model demonstrates the emergence of cooperation in
moderately heterogeneous networks, regardless of original founders’ behaviour, and in the absence of higher cognitive abilities such as recognition or memory. It may thus illustrate a more general mechanism for the evolution of cooperation, from early origins, in minimally cognitive organisms. It is the first published account of a model demonstrating cooperation in public goods games on dynamic and growing networks.\footnote{Much of the material presented in this chapter has been presented in [Miller and Knowles, 2016a].}

### 6.1 Introduction

The prisoner’s dilemma has become a standard metaphor to represent cooperation in evolutionary game theory, however it only describes interactions between pairs of individuals. In nature, interactions are not necessarily constrained in this way and a broader representation of cooperation is useful, particularly in the case of social, economic and biological networks [Perc et al., 2013]. For such scenarios, the public goods game (PGG) offers a suitable alternative for groups of more than two members. Referred to variously as the N-player prisoner’s dilemma, the freerider problem, or the tragedy of the commons [Hardin, 1968], the PGG represents a group-based dilemma where there exists a tension between benefits to an individual following one (selfish) course of action versus benefits to the entire community if the individual chooses an alternative action.

The extension from pair-wise to group-wise interactions creates an additional challenge to the emergence of cooperation. In the prisoner’s dilemma, an individual is able to retaliate or reciprocate in direct response to their partner’s behaviour. Cooperation can be rewarded by returning the favour, defection can be similarly punished. In the PGG however, participants are not able to effectively target retaliation directly against the defectors in the group, since such retaliation (i.e. not contributing to the public good) will harm cooperator and defector group members alike. This difficulty is the reason behind the classical result for the PGG: that cooperation becomes less likely as group size increases. This effect can be appreciated intuitively, for networked populations, by considering that the more neighbours that individuals have (i.e. the closer the network gets to having all members of the population participating in one group—or in other words, a fully connected network), the more the game approximates the mean field scenario, or the well-mixed population limit. In this case, as we know, defection is the Nash equilibrium [Nash, 1951].
The formulation of the PGG is as follows: Each member of a group has the opportunity to contribute a cost to a central pool. They can choose to contribute, or not. The amount invested in the pool is then increased by a multiplier. The increased amount is distributed amongst all members of the group, regardless of whether they contributed or not. Those contributing to the pool can be considered cooperators whilst those withholding, defectors (freeriders). As with the prisoner’s dilemma, the choice which maximises an individual’s payoff is to not contribute (to defect)—this is the Nash equilibrium. Thus in the rational analysis, all individuals will choose to act selfishly. None will contribute and this will result in the worst case scenario for all: the minimisation of the public good. In nature however, the rational choice appears less appealing and communities are observed to cooperate, so as to preserve or maintain public goods, for example, in the sharing of prey by pack animals [Packer et al., 1990], cooperative breeding in birds [Rabenold, 1984], the establishment of communal shelters by termites [Wilson, 1971], dispersal structures in slime moulds [Gadagkar and Bonner, 1994], and the development of open source software by humans [Raymond, 1999].

Attempts to explain this apparent contradiction between theory and observed behaviour, with regards to public goods, have considered the importance of factors such as volunteering, reputation, punishment or reward [Hauert et al., 2002, Brandt et al., 2003, Szolnoki and Perc, 2010]. Whilst it is easy to appreciate that such factors may affect the choices of, for example, humans, other higher primates or perhaps birds, it is harder to extend such approaches to explaining cooperation in more primitive forms of life [Axelrod and Hamilton, 1981] such as microorganisms cooperating to establish protective shelters or forage for nutrients [Crespi, 2001].

We described in Chapter 2 how research based on pair-wise behaviour, modelled using the prisoner’s dilemma, has contributed to an understanding of how network reciprocity may support the evolution of cooperation. An approach to modelling group-wise interactions in evolving artificial social networks using the PGG, was described more recently by Santos et al. [Santos et al., 2008]. Here, the mean field formulation of the PGG was spatially extended by mapping agents playing PGG to nodes of a network. The results of this work demonstrated the emergence of cooperation on scale-free networks, thus reinforcing previous findings regarding pair-wise (prisoner’s dilemma) cooperation [Santos and Pacheco, 2006].

Existing research has established a generally consistent view of the positive role heterogeneous networks play in promoting cooperation, although the overwhelming
majority of this work has focused on the pair-wise prisoner’s dilemma and has primarily considered static networks. (A useful review of work focusing specifically on the PGG in networks may be found in [Perc et al., 2013]). Of the limited research that exists for cooperation in dynamic networks, most has focused on networks at some form of equilibrium, using approaches which involve modification of pre-existing (fully formed) networks (see reviews in [Szabo and Fath, 2007, Perc and Szolnoki, 2010]). A very limited number of publications consider network growth [Ren et al., 2006, Poncela et al., 2008, Miller and Knowles, 2015b, Miller and Knowles, 2015a]; all of the latter focusing on two-player games.

In this chapter we offer an initial attempt to fill this gap. We consider the growth of a population from its earliest origins and ask how the social network affects and is affected by the group behaviour of the individuals within it. Our motivation is to establish a model based on group-wise cooperation which demonstrates the growth of networked populations of cooperative agents from original founder members. For such a model to be of value, it cannot be initially assumed that founder members are cooperators. Further, for the model to be broadly applicable, the sort of cognitive abilities (memory, recognition, reasoning) that are required for direct reciprocity or retaliation cannot be assumed. Finally for the model to be general, we make the simplest possible assumptions about the mechanism that new nodes use to attach to the existing network.

6.2 Development of Proposed Model

Here we refer to the two existing models on which we have based the work in this chapter and we explain the rationale for the adaptations made in incorporating these into our model. We provide this explanation in terms of the dynamic aspects of our model necessary to represent fluctuation: growth and attrition.

6.2.1 An Existing Network Representation of the Public Goods Game

In the work of Santos et al. [Santos et al., 2008], the PGG was implemented within evolving social networks using an approach where each member of the network, in turn, initiates a PGG within a group consisting of the individuals it is directly connected to—its ‘neighbourhood’. Any given individual in the network will be a neighbour of several other nodes, hence in addition to the PGG that a particular node initiates itself,
it will also be a participant in PGGs initiated by others. It is this participation of an individual in games with multiple opponents, i.e. group-wise interaction, which differentiates the PGG from its cousin in game theory—the prisoner’s dilemma.

With PGGs represented this way within a network, each node takes part in $g = k + 1$ games where $k$ represents the degree of the node occupied by the agent and $g$ represents the size of a neighbourhood. An agent $x$ with direct connections to neighbours $a$ and $b$ therefore has a degree of 2 and takes part in $g = 3$ PGGs: the one initiated by itself and the ones initiated by its neighbours $a$ and $b$. The total number of games in a population is therefore equal to $N$, the number of agents in the population. In the above work (ibid.), two variants of the PGG model were investigated, i) where each agent had a fixed cost per game (FCPG) and therefore their overall contribution (based on all the games they contributed to) was proportional to $g$, and ii) where each agent had a fixed total cost (fixed cost per individual, FCPI) and therefore their contribution was divided between all $g$ games (thus giving a contribution of $c/g$ per game). The game-playing populations are incorporated into evolutionary simulations by means of a strategy updating process representing natural selection between adjacent neighbours. Thus the strategies (behaviours) of fitter nodes probabilistically displace those of less fit neighbours.

We aim to use the above approach as a basis from which to develop an extended dynamic model that describes growth from founding members. This naturalistic representation is intended to model the development of cooperation taking into account the early origins of a population.

### 6.2.2 An Existing Model of Cooperative Network Growth

As a basis for the coevolutionary element of our dynamic PGG model, we once again adapt the approach of Poncela et al. [Poncela et al., 2008], which connects the dynamic structure of a network to the behaviour of agents within the network. In this approach (discussed previously in Section 2.7.3), natural selection, fitness-based preferential attachment and agent behaviour are incorporated into a unified model of dynamic network-reciprocal cooperation (using the prisoner’s dilemma), referred to as evolutionary preferential attachment (EPA).
6.2.3 Proposed Fluctuation Mechanism

A fuller discussion regarding our approach to the growth and attrition components of our model has been presented in Sections 4.2 and 4.1. The key points are as follows:

**Attrition.** We continue with the approach developed in Chapters 4 and 5. Essentially, whilst we follow the ethos of the EPA approach in connecting agent behaviour to network topology, as far as fitness-based network effects go, we apply these to node deletion rather than attachment. The attrition mechanism is implemented relative to a nominal maximum population size (carrying capacity). On reaching or exceeding this limit, the population shrinks by means of a process which culls the least fit individuals of the population. We propose that this attrition mechanism corresponds to broad-acting *extrinsic* evolutionary effects based on environmental factors, whereas strategy updating describes *intrinsic* evolutionary effects corresponding to natural selection between adjacent individuals within the population.

**Growth.** In the interests of attempting to increasing generality of our model, we avoid concerns and constraints regarding scale-free topology and preferential attachment processes [Fox Keller, 2005, Clauset et al., 2009, Stumpf and Porter, 2012] by instead implementing growth by means of random attachment. Over time, random connection of new nodes results in an exponential Poisson degree distribution thus creating a network with degree heterogeneity lying somewhere between that of scale-free and random. We have shown in the preceding chapters that as part of the fluctuation model (which further reduces the degree distribution) random attachment results in sufficient heterogeneity to support cooperation.

6.2.4 Summary: A Model of Population Fluctuation in Social Networks

The two processes described above, attrition of least fit nodes whenever a carrying capacity is reached, and growth of the network by random addition, continue until the simulation ends. We thus have a fluctuation system which i) supports the growth of a network from founder members, and ii) avoids the unrealistic situation observed in EPA simulations where a network becomes fixed structurally on reaching maximum size. Further, as intended, this implementation gives us a minimal model for the public goods game which does not require assumption of higher cognitive abilities for its
individual members and has no requirement regarding specific underlying mechanisms for the social network structure formation.

6.3 Methods

Our model follows a broadly similar approach to that described in previous chapters for the prisoner’s dilemma and snowdrift game and also includes some elements from existing published work [Santos et al., 2008, Poncela et al., 2008, Miller and Knowles, 2015a]. Since some aspects of the implementation have been covered in depth in previous chapters, we present an outline of the model and concentrate more detailed explanation only on those matters specific to the work in this chapter.

6.3.1 Outline of the Evolutionary Model

Our model describes agents located at the nodes of networks. Interactions occur via edges connecting the agents. Each node in the network has a neighbourhood, defined by the neighbours its edges connect to. A PGG occurs for each neighbourhood and hence a network of $N$ nodes will result in $N$ PGGs. Agents can contribute to a PGG (cooperate) or not (defect). Each agent in the network has an interaction behaviour encoded by a strategy variable representing either cooperate or defect. In a round robin fashion, each agent in turn initiates a PGG which involves their primary connected neighbours (their neighbourhood). Each agent in the population accumulates a fitness score which is the sum of its rewards from all the PGGs it participates in.

Within an evolutionary simulation, this process is repeated over generations. Agents are assessed at each generation on the basis of their fitness score. Fitter agents’ strategies remain unchanged; less fit agents are more likely to have strategies displaced by those of fitter neighbours. Fluctuation of the population occurs by repeated attrition and regrowth of the network with shrinkage triggered whenever the population reaches the specified carrying capacity for the system.

The outline of the evolutionary process, for one generation, is as follows:

i. **Play public goods games**: Each agent initiates a PGG involving its neighbours. Each agent will accumulate a fitness score that is the sum of payoffs from all the individual PGGs that it participates in.

ii. **Update strategies**: Selection occurs. Agents with low scores will have their
strategies replaced, on a probabilistic basis, by comparison with the fitness scores of randomly selected neighbours.

iii. Grow network: A specified number of new nodes are added to the network, each connecting to \( m \) randomly selected distinct existing nodes via \( m \) edges.

iv. Remove nodes (only in the case of fluctuation models): If the network has reached the nominal maximum size, it is pruned by a tournament selection process that removes less fit agents.

Detailed descriptions regarding the implementation of steps iii and iv (random growth and fitness-based attrition) are covered in Section 4.3.2.

**Update Strategies**

This step is implemented in the same manner as for models in previous chapters (see Section 3.3.2) with the exception that, since there is no mathematical approach to determine the largest fitness difference between two nodes, we estimate this using simulations for all 4 combinations (of the 2 strategy types at the 2 nodes) to approximate maximum possible difference. The denominator of the equation is modified to reflect that the maximum difference is a function dependent on the degree of the two nodes.

At generation \( t \), if \( f_i(t) < f_j(t) \) then \( i \)'s strategy is replaced with that of the neighbour \( j \) with the following probability:

\[
\Pi_{S_i \rightarrow S_j}(t) = \frac{f_j(t) - f_i(t)}{f d_{max}(k_i(t), k_j(t))},
\]

where \( k_i \) and \( k_j \) are degrees of node \( i \) and its neighbour \( j \) respectively.

### 6.3.2 Public Goods Game Implementation

Each node of the network, in turn, initiates a PGG. Within a single PGG, all cooperator members of a neighbourhood contribute a cost \( c \) to the pool. The resulting collective investment \( I \) is multiplied by \( r \), and \( rI \) is then divided equally amongst all members of the neighbourhood, regardless of individual strategies.

In the FCPG variant of the PGG, each agent has a fixed cost per game and therefore their overall contribution, in one generation, is \( c(k + 1) \) with contribution \( c \) to each game, and where \( k \) is the number of neighbours (degree). The single game individual
payoffs of an agent $x$ are given by the following equations, for scenarios where $x$ is a defector ($P_D$) and a cooperator ($P_C$) respectively:

$$P_D = crn_c/(k_x + 1) ,$$  \hspace{1cm} (6.2)

$$P_C = P_D - c ,$$  \hspace{1cm} (6.3)

where $c$ is the cost contributed by each cooperator, $r$ is the reward multiplier, $n_c$ is the number of cooperators in the neighbourhood based around $x$, and $k_x$ is the degree of $x$.

In the FCPI variant, each individual has a fixed cost $c$, i.e. their overall contribution is $c$ and hence their contribution to each game is $c/(k + 1)$. The single game individual payoff for a node $y$ having strategy $s_y$ ($= 1$ if cooperator, $= 0$ if defector) present in the neighbourhood of $x$ is given by:

$$P_{y,x} = \frac{r}{k_x + 1} \sum_{i=0}^{k_x} \frac{c}{k_i + 1} s_i - \frac{c}{k_y + 1} s_y ,$$  \hspace{1cm} (6.4)

where $i$ is used to index each neighbour of $x$, and $s_i$ is the strategy of neighbour $i$ of $x$ having degree $k_i$.

### 6.3.3 General Simulation Conditions

Growth of founder networks and creation of pre-existing networks were as previously described in Section 4.3.2. In all cases, networks had an overall average degree of approximately $z = 4$, giving an average neighbourhood size of approximately $g = 5$. Simulations were run until 20,000 generations. The final fraction of cooperators values we use are means, averaged over the last 20 generations of each simulation, in order to compensate for variability that might occur from just using final generation values. Each simulation consisted of 25 replicates. We used shrinkage value of $X = 2.5\%$ of the population size for all fluctuation simulations. Simulation data is recorded after step 2 (Update strategies).

### 6.4 Results and Discussion

We now present the results of research investigating our model’s ability to support cooperation in a range of PGG simulations. Initially we consider its implementation in the type of scenarios that have dominated research into cooperation in dynamic
networks, namely fully formed or pre-existing networks. We then apply the model, as per our original motivation, to networks grown from a small number of founding members. In both types of investigation we have considered the two variants of PGG: \textit{FCPG} and \textit{FCPI} [Santos et al., 2008].

6.4.1 Simulations using Pre-existing Networks

We first consider the impact of our model in pre-existing networks. We initially consider the effect of the PGG variant (FCPG vs. FCPI) and subsequently we discuss specifically how the fluctuation mechanism achieves different outcomes to those seen for static networks.

Effect of PGG Variant in Simulations using Pre-existing Networks

It is established for the prisoner’s dilemma (equivalent to two-player PGG) that cooperation in pair-wise interactions on networks is promoted by the opportunity for cooperators to self-assort and hence form clusters [Nowak and May, 1992]. The larger the cooperator clusters which form, the greater the levels of cooperation which occur [Santos and Pacheco, 2006]. This effect is enhanced by increased network degree heterogeneity, since greater heterogeneity allows for some cooperators to have their scores increased due to having very many cooperator neighbours. Such findings for the prisoner’s dilemma generalise to the PGG, but in the PGG there is also an opposing ‘force’ that limits cooperation, which we now explain. In the conventional FCPG representation of the PGG, a cooperating individual pays a cost for every single game they participate in. Since each individual in a population can initiate a PGG among their local neighbourhood, higher connectivity (more neighbours) means that an individual will participate in more games and, if a cooperator, will thus pay a larger penalty for their increased connectivity [Boyd and Richerson, 1988b]. The classical result for the PGG in this case is that the larger the neighbourhoods become, the less likely cooperation is. This finding makes intuitive sense, since the larger a PGG neighbourhood is relative to the entire population, the closer it gets to representing a well-mixed (mean field) population, where defection is the Nash equilibrium.

We initially present results in the form of behaviour profiles as previously. These illustrate the final \textit{fraction of cooperators} in a population, relative to a parameter that represents costs versus benefits of cooperation. In the prisoner’s dilemma, we represented this in the form of \( b \), the \textit{temptation to defect}. For the PGG, we take the
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A **reward multiplier, r**, then we normalise this term by the average neighbourhood size \((z + 1 = g)\) within the population to achieve \(\eta\). Given that this term represents benefit (whereas the prisoner’s dilemma \(b\) parameter represents cost) the behaviour profiles are positive (increasing) sigmoids, and therefore models that increase cooperation will result in behaviour profiles shifted towards the y-axis.

Figure 6.1 illustrates results for FCPG PGG in pre-existing networks. In Fig. 6.1a (FCPG in static networks) we see that higher levels of cooperation are observed in static scale-free networks (green line) than in static networks of low or no heterogeneity, random and regular respectively. These results are consistent with the view that heterogeneity promotes cooperation. In the case of FCPI PGG (see Fig. 6.1b), the lack of any penalty on larger neighbourhood size weakens the dilemma i.e. it reduces the **temptation to defect** and therefore increases levels of cooperation. By comparing correspondingly coloured lines for FCPG and FCPI in Figs. 6.1a and b, we can see how FCPI causes different horizontal shifts in behaviour profiles for networks of differing heterogeneity. As network degree heterogeneity is increased, FCPG increasingly penalises cooperators when compared to FCPI (greater heterogeneity corresponds to bigger shifts in FCPI but not in FCPG). We thus see in our results, that the impact of FCPI appears non-existent for regular networks (no visible shift, see brown lines) but becomes more relevant as increasing heterogeneity allows for increasing neighbourhood size (marked shift for scale-free networks, see green lines).

Figures 6.1c and d illustrate how the two PGG variants affect fluctuating networks. Here we expect to see two general effects: i) Given that the fluctuation mechanism drives all networks to the same final degree distribution, we would expect similar behaviour profiles, within each variant of the PGG, regardless of starting network topology; ii) We would expect the final network degree distributions, based on approximately exponentially distributed final networks, to lie somewhere between the two extremes of heterogeneity represented by regular (non-heterogeneous) and scale-free (highly heterogeneous) networks, as observed in the static results corresponding to each variant (solid brown and green lines respectively, in Figs. 6.1a and b).

We find that the fluctuation profiles do indeed lie within the expected region of the graph, however we see an anomaly for the fluctuating scale-free FCPI profile (Fig. 6.1d) which achieves higher levels of cooperation than regular and random networks. This result is unexpected because given an assumption that cooperation is only dependent on the final degree distribution, we would expect to see the same behaviour profiles for all network types. We have compared final degree distributions for all
Figure 6.1: Behaviour profiles comparing the effect of network type for simulations (25 replicates) on pre-existing networks of increasing heterogeneity (regular, random and scale-free respectively). Final fraction of cooperators in population is plotted against $\eta$, the PGG reward multiplier $r$, normalised with respect to average neighbourhood size ($g = 5$). Variability is indicated by error bars showing 95% confidence intervals. Simulation details are as described in Methods section. The dashed vertical line at $\eta = 0.6$ is a reference for the eye.

network types and find no discernible difference.

We propose that the explanation of the anomaly seen for initially scale-free networks lies in the differing challenges presented by the topology of the initial networks, specifically, the diameter of the network (rather than the degree distribution). We have measured the average shortest path length in our initial networks and find these to be approximately: 125 for regular networks, infinite (network disconnected) for random networks, and 4 for scale-free networks. All final networks have lengths of 6 in the case of FCPG and 7 in the case of FCPI. In order for cooperation to percolate through the network, sufficient reward ($\eta$) has to be present to support self-assortativity and the network needs to be fully connected (consisting of a single component). Percolation (and hence self-assortativity) will be blocked in those cases where the network is fragmented, or impeded where a network lacks the small path lengths that are a defining characteristic of small-world networks. In these cases, cooperation cannot readily percolate until the fluctuation mechanism has brought about sufficient changes to reduce
the average path length and/or the number of network components. Whilst cooperation in scale-free networks is still dependent upon the value of $\eta$, such networks do not have to overcome the path length issues faced by random and regular networks. Thus, while all network topologies end up with the same final degree distributions, scale-free networks potentially start with a small-world advantage which may support the emergence of cooperation at lower values of $\eta$.

This proposed explanation raises a further question of why a difference exists between scale-free network results for fluctuating FCPG and FCPI (see Figs. 6.1c and d), or more particularly, why the scale-free fluctuating FCPG profile does not see the same increase as observed for fluctuating FCPI. In response to this, our above explanation does indeed apply to fluctuating scale-free networks for both variants of the PGG, although in the case of FCPG, cooperation is limited by the additional penalty imposed by neighbourhood size.

**Effect of Fluctuation in Simulations using Pre-existing Networks**

As we have shown in Chapters 3, 4 and 5, models based on fluctuating population size can promote pair-wise cooperation in networks. This outcome arises from the greater opportunity for strategies to self-assort, given repeated perturbation of network structure, based on deletions of low fitness nodes.

From comparing Figs. 6.1a and c, we see how the incorporation of population fluctuation affects results for FCPG PGG. Behaviour profiles for all network types become superimposed. We observe similar findings in the case of FCPI (compare Figs. 6.1b and d) except for in the case of scale-free networks—an anomaly which, as explained earlier, is believed to be due to the beneficial impact of short average path lengths found in initially scale-free networks. The general consistency of behaviour profiles is because the CRA+fluctuation mechanism drives all networks to the same final degree distribution regardless of initial topology. Figure 6.2 illustrates this change, showing initial and final degree distributions in simulations starting from a scale-free network. We note that whilst the final degree distribution due to CRA alone would be exponential, the additional effect of node deletion in CRA+fluctuation compresses the exponential curve, giving a degree heterogeneity lying between that of a Poisson and an exponential distribution.

We highlight an important point here. The fluctuation model (in those scenarios where it supports the emergence of cooperation) converts all networks, regardless of
initial type, to this compressed exponential distribution, which has moderate heterogeneity. In the case of scale-free networks, fluctuation therefore brings about a decrease in heterogeneity. It follows that, for initially scale-free networks, we should expect to see reduced cooperation in the fluctuation model compared to the static one. This is indeed true for FCPI results (compare green lines in Fig. 6.1d with b) but not the case for FCPG (compare Fig. 6.1c with a). Fluctuation does not cause the expected reduction in FCPG PGG (which would be represented by a shift of the profile to the right) because in the static FCPG implementation scale-free networks are already constrained in their ability to cooperate (the static profile is already right-shifted) i.e. they cannot achieve their full potential in supporting cooperation due to the penalties FCPG imposes on large neighbourhoods.²

Figure 6.3 presents our results so as to separately illustrate the impact of fluctuation on each of the network types studied. Here we generally see (comparing dashed to solid lines for all plots) that incorporating fluctuation results in increased or similar

²Earlier comments referred to how the PGG variant (FCPG and FCPI) impacts scale-free networks. Here we are referring to the effect of static vs. fluctuating models. Whilst the two comparisons are both impacted by the neighbourhood size penalty associated with FCPG, it is important to explain separately the impact of the effect of game variant (as discussed previously) as distinct from the effect of incorporating fluctuation (as discussed here).
levels of cooperation to those seen for static networks. We observe this effect in all cases except FCPI initially scale-free networks (Fig. 6.3f).

Figure 6.3: Behaviour profiles comparing results from pre-existing networks with static population size to those where fluctuation is implemented. Three types of pre-existing networks were investigated: regular, random and scale-free. Final fraction of cooperators in population is plotted against $\eta$, the PGG reward multiplier $r$, normalised with respect to average neighbourhood size ($g = 5$). Variability (25 replicates) is indicated by error bars showing 95% confidence intervals. Simulation details are as described in Methods section. The dashed line at $\eta = 0.6$ is a reference for the eye.

Our general observation here, that cooperation is increased or unchanged by fluctuation, is primarily a result of the fluctuation mechanism driving all networks to the same compressed exponential degree distribution, regardless of starting topology. Whilst the fluctuation model is in this way able to shift behaviour profiles to the left (increasing cooperation), such a change can only be achieved for networks having initially lower heterogeneity (random and regular networks). Hence, in the case of scale-free (highly heterogeneous) networks, observed levels of cooperation should be
lower in the fluctuating network than in the static network. However as described earlier our results for scale-free networks with regards to FCPG are not as clear cut as this simple explanation would suggest. Our observations from FCPG simulations based on initially scale-free networks are summarised below:

- **Comparing PGG variant in static networks:** In static networks, FCI sees higher levels of cooperation. In FCPG simulations, cooperation is less due to neighbourhood size penalty of FCPG.

- **Comparing PGG variant in fluctuating networks:** In fluctuating networks, FCI experiences lower levels of cooperation as a result of fluctuation causing decreased heterogeneity. We would expect FCPG to experience the same reduction in heterogeneity and hence the same levels of cooperation, but cooperation is lower than for FCI, which we attribute to the neighbourhood size penalty limiting cooperative clustering for FCPG.

- **Comparing static versus fluctuating networks:** For FCPG, we do not see the usual reduction in levels of cooperation when the fluctuation model is applied to scale-free networks, because cooperation is already reduced in the static network by the FCPG's neighbourhood size penalty. This penalty constrains cooperation in the case of static networks.

In summary we make the general observation that fluctuation is more beneficial to cooperation in the case of the FCPG variant. FCI on the other hand, enables higher levels of cooperation to be achieved without the need for any such 'further assistance'. We make the important point that the advantages offered by FCI increase with heterogeneity; it is most effective at promoting cooperation in scale-free networks and its effect is (as expected) unnoticeable in regular networks where neighbourhood size is constant.

### 6.4.2 Simulations in Networks Grown from Founder Populations

We now report on results of simulations grown from founder populations of either 3 cooperators, or 3 defectors. We compare two implementations of this model. In the first (non-fluctuating), the population grows by a process of CRA until it reaches a maximum size, after which the network structure remains constant. In the second implementation (fluctuating), the network grows by means of CRA until it reaches a
nominal maximum size, whereupon it is pruned and then allowed to regrow. This fluctuation cycle repeats thereafter, until the simulation ends. Strategy updating continues throughout the entirety of both implementations. As previously, we present results for both FCPG and FCPI variants of the PGG.

**Effect of PGG Variant in Networks Grown from Founder Populations**

In the case of cooperator-founded populations, by comparing corresponding curves (blue lines) between Figs. 6.4a and b, it appears that FCPI may result in a marginal increase in levels of cooperation compared to FCPG. Small increases would be consistent with our understanding that FCPI can relax the penalty paid by cooperator clusters in heterogeneous networks. As described earlier, networks formed by CRA and subject to fluctuation are only moderately heterogeneous, thus any increase afforded by FCPI over FCPG would be expected to be minor.

![Figure 6.4](image)

Figure 6.4: Behaviour profiles for networks grown from founder populations, comparing results from fluctuating and non-fluctuating simulations (25 replicates). We compare networks grown from 3 cooperators to those grown from 3 defectors. Final fraction of cooperators is plotted against $\eta$, the PGG reward multiplier $r$, normalised with respect to average neighbourhood size ($g = 5$). Populations were specified to have a nominal maximum size of 1,000 individuals, at which point fluctuation is triggered. Variability is indicated by error bars showing 95% confidence intervals. Further details on simulations are as described in Methods section. The vertical dashed line at $\eta = 0.6$ is a reference for the eye.

In the case of defector-founded populations (red lines in Figs. 6.4a and b), we see what may be a minor difference between FCPG and FCPI in fluctuating networks (dashed lines) and a more marked difference for non-fluctuating networks (solid lines).
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Curiously, FCPG in the case of defector founders appears to promote rather than restrict cooperation in non-fluctuating networks. This is surprising since we would expect to see lower levels of cooperation in the case of FCPG due to clustering of cooperators being penalised. A closer look at Fig. 6.4a offers a pointer towards understanding these unexpected FCPG results. We see from the error bars that high variability exists for values of $\eta > 0.8$. Inspection of the replicate time plots for the simulations providing these data points reveal that individual replicate simulations proceeded to one of two states: either a high level of cooperation or one of almost complete defection. We have been unable to establish a definitive explanation for this effect but strongly suspect that it is a result of FCPG favouring smaller neighbourhoods. In defector-founded populations, simulations where many cooperators connect to the large core neighbourhood of defectors will only result in further growth of this defector core, since added cooperators are inevitably converted by the highly-connected defector core (see detailed explanation of a somewhat similar effect arising from EPA in Section 4.4.3). By contrast, in simulations where larger numbers of cooperators randomly attach elsewhere, it may become possible for initially small groups of cooperators to get a ‘toehold’ in the population away from the main defector core. Growth of this type, where cooperation arises in smaller clusters away from the core, may be promoted by FCPG, which by penalising cooperators in larger neighbourhoods, offers a relative fitness advantage to those in smaller ones.

Effect of Fluctuation in Networks Grown from Founder Populations

For cooperator-founded populations (blue lines in Figs. 6.4a and b), levels of cooperation are not markedly changed by incorporation of fluctuation once the network has reached its maximum size. We propose that the strategy assortativity that has taken place whilst the network was growing has maximised the amount of cooperation that can occur (for a given value of $\eta$). Cooperation levels thus do not rise beyond this limit when fluctuation is added.

For the more challenging, defector-founded scenario (red lines in Figs. 6.4a and b), fluctuation brings about a marked increase in cooperation (compare dashed with solid red lines). To explain this effect we first consider the non-fluctuating system. Here, an initial defector population is likely to convert the majority of newcomer nodes connecting to it into defectors. It will therefore significantly bias the growing population
against cooperation. The founder defectors develop increased connectivity over subsequent generations and form the basis of a well-connected core of defectors, capable of converting any new cooperators that may attach. In the non-fluctuating model, the starting point of defector founders thus potentially locks in long-term defector behaviour — to the extent that even where the dilemma collapses at $\eta = 1$, populations can still grow to be predominantly populated by defectors. In this scenario, rather like the growth of a coral reef, the core of defectors is ‘dead’. ‘Life’ (positive fitness values) only occurs where new cooperators attach and hence allow random defectors to occasionally gain positive fitness values. If the newcomer nodes are defectors, they simply become part of the defector core; cooperators will do the same as soon as they have played PGG and (due to scoring poorly) been converted to defectors. Thus the defector core continues to grow. Whilst the core will primarily have zero fitness, it is still however, impenetrable to invasion by cooperators, because as mentioned these will be quickly converted as soon as they connect to the defectors.

We now consider how the fluctuation model changes the above scenario to bring about such a marked increase in cooperation. Both fluctuating and non-fluctuating models operate identically until the maximum network size is reached. After this point, in the fluctuating model, the least fit individuals and the nodes they occupy are deleted from the population. New nodes are then added which link to randomly selected existing nodes and have randomly allocated strategies. The defector core which is invulnerable in the non-fluctuating mode, contains many nodes which are highly vulnerable in the fluctuating model, due to their zero fitness. Our evolutionary model of fluctuating populations thus creates an escape from the domination of the defector core.

6.5 Conclusion

In this chapter we have presented a model of fluctuation in networks, based on growth by random attachment and fitness-based deletion, which supports the coevolution of cooperative behaviour alongside the growth of a simulated population. The cooperative behaviour under investigation was based on group-wise interactions, represented using the public goods game. In particular we observed the emergence of group-based cooperation in networks grown from non-cooperative founder members. Our results highlight that the absence of any structural perturbation of the system may potentially
lock in defector behaviour in the long term. This is a finding that appears to merit further investigation, especially given the observation that, in non-fluctuating networks, FCPI struggles to offer an escape from long-term defection—a particularly surprising result since FCPI is the PGG variant which, in heterogeneous networks, would typically result in increased cooperation. We note that our model offers an escape from such cases of widespread defection.

In addition to investigating growing networks, we have applied our model to pre-existing networks, populated with initially random strategies. Regardless of initial topology, such networks tend to the form of a compressed exponential degree distribution and the emergence of cooperation is observed. In keeping with the work of previous chapters, the model does not require underlying explanations in support of preferential attachment to create network structure. Levels of network heterogeneity that are sufficient for cooperation to emerge, arise simply as a result of random connections formed over time, combined with periodic attrition of least fit members of the population. Finally, we highlight that the model supports cooperation in cases of costly interaction (FCPG) and also where costs are trivialised (FCPI), real world scenarios being likely to lie somewhere along a spectrum between these two extrema. As mentioned earlier, the work described in this chapter represents the first published example of a model which demonstrates the emergence of group-based cooperation in growing and dynamic networks. As such we propose that it forms an important step in understanding the origins of cooperation in networks.
Chapter 7

Cooperation Catalysed by a Prosocial Migrant Clique

In the previous chapter we developed a model to describe the evolution of cooperation based on group interactions within a population. Within this chapter we attempt to apply this model to consider the question of how cooperation may spread between routinely separate subsets of a larger population.

Research into the evolution of cooperation in social networks typically implements a population as a single connected network. Here we posit a more realistic premise that populations consist of multiple networks whose members migrate from one to another. We isolate the key elements of such a scenario, whereby a minority of members from a cooperative network migrate to a network populated by defectors. Using the model developed in the previous chapter to represent the cooperative dilemma in public goods games we find that under certain circumstances, the concerted actions of a trivial number of such migrants will catalyse widespread behavioural change throughout a population. Our results also support a wider argument: that the general presence of some form of disruption contributes to the emergence of cooperation in social networks, and consequently that over-simplified models may encode a determinism that precludes the emergence of cooperation.1

7.1 Introduction

The question of how cooperation may emerge within a competitive environment is, by definition, predicated on cooperation being originally absent from the population.

1Much of the material presented in this chapter has been presented in [Miller and Knowles, 2016b].
On such a basis, the original appearance of cooperation occurs as a random event, more specifically, a mutant behaviour in (rare) individual(s). We then consider whether such a mutation will be extinguished, or if it will be copied to the extent that it eventually achieves fixation throughout a population. Within investigations of network-reciprocated cooperation [Nowak and May, 1992, Nowak, 2006b], models which abstract social networks to test mechanisms for the emergence of cooperation broadly follow approaches (implicitly) of this nature (see [Perc and Szolnoki, 2010] for a review of such investigations).

The overwhelming majority of research studies in this field (ibid.) have considered a population to be one single connected network. However in the real world, multiple (relatively) discrete dynamic networks exist within populations, and at times, members of one social network may migrate to another. This is an aspect of cooperation in real-world scenarios which requires understanding, yet has thus far received little attention. In the work that follows, we isolate the key elements of such a scenario: namely, we have a primary network of interest, predicated on defector behaviour, and we consider the arrival of a very small group of connected individuals that have emigrated from a cooperative network.

Our investigations in this chapter also derive from a second motivating principle. In previous chapters, we have demonstrated how population size fluctuation has a positive impact in promoting the emergence of cooperation in networks. Commenting on this, we have suggested the possibility that the observed effect may be viewed as a generalised response to perturbation of networks, and that population size fluctuation may be only one way, amongst several, of perturbing a network to thus yield similar results. This notion hints at a potential issue: that models of cooperation which lack any such disruptive elements through, for example, being overly deterministic, or lacking in any noise, may preclude the cooperative phenomena we seek to investigate. In the work that follows we consider whether our findings add further support to this thinking.

### 7.2 Background

The public goods game (PGG) was initially implemented within social networks [Santos et al., 2008], using an approach where each member of the network in turn, initiates a PGG within a group which consists of the individuals it is directly connected to—its ‘neighbourhood’. An individual in such a network will be a neighbour of several other nodes, hence in addition to the PGG that any particular node initiates, it will also
be a participant in PGGs initiated by other nodes. This participation of an individual in games with multiple opponents (i.e. group-wise interaction) differentiates the PGG from the two-player (pair-wise) game, the prisoner’s dilemma.

In Chapter 6 we described our extension of the above approach, demonstrating the emergence of cooperation amongst evolving populations of individuals playing PGG in dynamic and randomly growing networks subject to fitness-based attrition. Our approach differs from earlier work in its use of two evolutionary elements as follows: intrinsic effects corresponding to individuals competing with each other to breed, and extrinsic effects corresponding to broad acting events which disrupt the whole population.

In the following, we apply the model we have developed to investigate how a variety of network simulations, all predicated on originally non-cooperative behaviour, are affected by the arrival of a very small ($n \leq 3$) group of cooperative migrants. We describe the implementation of our model to this problem in the following section. We then provide behaviour profiles for a range of network scenarios and growth mechanisms, followed by deeper scrutiny of phenomena within the actual simulations that are of particular interest.

7.3 Methods

Here we apply the model presented previously in Chapter 6 to the scenario where we have a network, predicated on defector behaviour, which is connected to by a small complete network (a ‘clique’) of cooperative migrants. In the following we focus mainly on the additional methodology necessary to apply our model in this way (full details of the model itself having previously been given in Section 6.3).

7.3.1 Outline of the Evolutionary Model

Our model describes agents located at the nodes of networks. Each node in the network has a neighbourhood, defined by the $k$ nodes its edges connect to. A PGG occurs for each neighbourhood, so a network of $N$ nodes will result in $N$ PGGs. Each agent in the network has a behaviour encoded by a strategy variable: cooperate or defect, which determines whether it contributes to PGGs, or not, respectively.

The general outline of the evolutionary process, for one generation, is as follows:

i. Play public goods games: In a round robin fashion, each agent initiates a PGG
involving its neighbours. An agent’s fitness score is the sum of payoffs from all
the individual PGGs that it participates in. We implement the standard fixed cost
per game (FCPG) version of the PGG.

ii. **Update strategies**: Selection occurs. Agents with low scores will have their
strategies replaced, on a probabilistic basis, by comparison with the fitness scores
of randomly selected neighbours.

iii. **Grow network**: A specified number of new nodes are added to the network, each
connecting to randomly selected distinct existing nodes via \( m \) edges.

iv. **Remove nodes (only in the case of fluctuation models)**: If the network has reached
the nominal maximum size, it is pruned by a tournament selection process that
removes less fit agents.

### 7.3.2 Growth Mechanisms

We consider three mechanisms for network growth in this investigation: chronologi-
cal random attachment (CRA), degree-based preferential attachment (PA) and fitness-
based evolutionary preferential attachment (EPA). The probability \( \Pi(t) \) that an existing
node \( i \) receives one of the \( m \) new edges is given by the following equations, for CRA, PA and EPA respectively:

\[
\Pi_{\text{CRA}}(t) = \frac{1}{N(t)},
\]

where \( N(t) \) is the number of nodes available to connect to at time \( t \) in the existing
network. Given that in our model each new node extends \( m = 2 \) new edges, and multiple
edges are not allowed, \( N \) is therefore sampled without replacement.

\[
\Pi_{\text{PA}}(t) = \frac{k_i(t)}{\sum_{j=1}^{N(t)} k_j(t)},
\]

where \( k_i(t) \) is the degree of an existing node \( i \) and \( N(t) \) is the number of nodes available
to connect to at time \( t \) in the existing network.

\[
\Pi_{\text{EPA}}(t) = \frac{1 - \varepsilon + \varepsilon f_i(t)}{\sum_{j=1}^{N(t)} (1 - \varepsilon + \varepsilon f_j(t))},
\]

where \( f_i(t) \) is the fitness of an existing node \( i \) and \( N(t) \) is the number of nodes available
to connect to at time \( t \) in the existing network. The parameter \( \varepsilon \in [0, 1) \) is used to adjust
the strength of the preferential mechanism. (We used \( \varepsilon = 0.99 \) for strong EPA.)

Growth only occurs at times when the network is below a nominal maximum size (we used \( N_{\text{max}} = 1,000 \) nodes). For all added nodes, other than migrants, we set \( m = 2 \). Strategy types of added nodes (cooperate, defect) are allocated independently uniformly at random.

### 7.3.3 Migrant Clique Attachment

At generation 300, the migrant group connects to the existing primary network. Our migrant groups are small complete networks, i.e. cliques, consisting of between 1 to 3 nodes (specific details in results section), all having cooperator strategies. Initial connection to the primary network is via only one of the nodes in the clique. This node extends either 1 or 2 edges (specific details in results section) to existing network nodes chosen at random. Once connected, the migrants are treated as a part of the primary network and are exposed to all elements of the evolutionary process described above.

### 7.3.4 General Simulation Conditions

In networks grown from founder members, \( N_0 = 3 \) initial nodes were populated with defector strategies. In pre-existing networks, all nodes were populated with defectors. Strategy types of subsequently added nodes were allocated independently, uniformly at random (cooperators and defectors with equal probability). All networks had an overall average degree of approximately \( z = 4 \), hence an average neighbourhood size of \( g = 5 \) (since neighbourhood includes self). Simulations were run until 20,000 generations. Final fraction of cooperators values we use are means, averaged over the last 20 generations of each simulation. Each simulation consisted of 25 replicates. We used a shrinkage value of \( X = 2.5\% \) of the population size for all fluctuation simulations.

### 7.4 Results

We initially present behaviour profiles illustrating temptation to defect against \( \eta \), the PGG reward multiplier normalised with respect to the average neighbourhood size in the network. We will then consider the behaviour of the populations in more detail by focusing on the time plots for particular values of \( \eta \).
7.4.1 Effect of Migrants on Population Behaviour Profiles

In Fig. 7.1 we present behaviour profiles for results from the ‘simpler’ scenario of pre-existing networks. These networks have initially random graph topology [Erdős and Rényi, 1959] and are initialised entirely with defectors. Figure 7.2, illustrates the more ‘realistic’ scenario where we consider networks grown from their origins, in this case from 3 founder defector members. In both network scenarios we provide profiles for three attachment mechanisms: CRA, PA and EPA.

![Graphs showing behaviour profiles for CRA, PA, and EPA](image)

Figure 7.1: Behaviour profiles illustrating the impact of a migrant cooperator clique on the emergence of cooperation in pre-existing networks having initially random graph topology and initialised entirely with defectors. Three different attachment mechanisms are shown: (a) CRA, (b) PA and (c) EPA. Final fraction of cooperators present is plotted against $\eta$ (the PGG reward multiplier $r$ normalised with respect to average neighbourhood size, $g = 5$). Migrant cliques consist of 3 connected cooperators, one of which attaches to the existing network randomly by 2 nodes.

For the simpler scenario of pre-existing networks initialised with all defectors (see Fig. 7.1) where network topology is static (solid black lines), we naturally observe zero cooperation for all attachment mechanisms. In comparison, when migrants are introduced to static topology networks (see solid green lines), they are able to precipitate population-wide cooperation, once the reward value achieves a particular threshold ($\eta > 0.7$).

In the case of fluctuating networks, we see that cooperation exists in simulations
without migrants (black dashed lines), but that the migrants increase levels of cooperation further (see green dashed lines), except in the case of EPA, where levels of cooperation have already been elevated by the increased network heterogeneity associated with this attachment mechanism. (We discussed the role of heterogeneity in the emergence of cooperation in Section 2.7.2.) Thus, as we have seen in previous chapters of this thesis, fluctuation again aids cooperation; for fluctuating networks, we see that the threshold at which migrants can precipitate cooperation is reduced from $\eta > 0.7$ to $\eta > 0.6$ (compare solid with dashed green lines in Fig. 7.2).

When we consider the more complex scenario for networks grown from three founder defector nodes (see Fig. 7.2), we see that our earlier findings still hold. Again, in non-fluctuating networks, above a reward threshold of $\eta = 0.7$, the arrival of the migrants promotes widespread cooperation. We see this effect for networks that become static on reaching specified maximum size and also in those that fluctuate in size thereafter, in the latter case the threshold reducing to $\eta = 0.6$. We note that in the
case of fluctuating models, we see little difference in final outcomes when comparing pre-existing networks with networks grown from founders (compare correspondingly coloured dashed lines in Figs. 7.1 and 7.2).

Whilst the behaviour profiles shown above allow us to neatly characterise and compare different experimental simulations, they describe derived data which for the most part is of limited interest, whilst potentially masking more interesting phenomena. More specifically, as the value of the reward variable ($\eta$) is maximised/minimised, the dilemma becomes diminished and the dominant behaviour of populations becomes consistent and highly predictable. We suggest that in presenting abstracted representations of real-world scenarios, the extreme regions of the behaviour profiles are of limited relevance or interest.

It is the mid-range values of the reward variable that represent the social dilemma in its strongest form. We suggest that these regions are of particular importance in investigating the emergence of cooperation, since they represent the much more realistic challenge faced in nature by individuals attempting to balance cost versus reward, and in addition, where noise may likely be a confounding or contributory factor. Where we see transitions in population behaviour, where a mixture of competing behaviours exists, where the choice of cooperate or defect is not clear cut, and where noise may be present—these are the areas in which we are interested.

### 7.4.2 Effect of Migrants on Time Plots

We now explore those regions of interest where large-scale behavioural change occurs in the populations. We focus on the behaviour of individual simulations as they transition from defection to cooperation. From Figs. 7.1 and 7.2, we see the widest variety of outcomes in the region approximately around where $\eta = 0.8$. Figure 7.3 hence illustrates individual time plots of simulations (25 replicates in each case) based on this value, for the simpler case of pre-existing networks initialised entirely with defectors. The plots show simulations with the effects of fluctuation and immigration enabled, disabled, and acting in concert. We summarise from inspection of these plots that:

i. The fluctuation mechanism on its own (see Fig. 7.3c) enables a majority of replicates to transition to cooperation. Similar levels of cooperation are achieved by all of those replicates that transition. Transition times, however, remain variable with some replicates failing to transition over the time period studied.
ii. The isolated effect of migrant arrival (see Fig. 7.3b) drives higher levels of cooperation amongst replicates. In the case of this effect though (in contrast to our previous observation), the levels of cooperation achieved are variable.

iii. The combined impact of migrants together with fluctuating population size (see Fig. 7.3d) results in all replicates transitioning to cooperation with consistency in both final levels of cooperation achieved, and also in transition times (all replicates transition within 200 generations of the arrival of the migrants).

Figure 7.3: Simulation time plots (25 replicates) illustrating the effects of migrant clique arrival and fluctuation in pre-existing random networks initialised with defectors, with $\eta = 0.8$. Plots show number of cooperators over 20,000 generations. Migrant groups are complete networks of 3 cooperator nodes, 1 of which connects to 2 randomly selected existing network nodes. Network growth in these simulations is by chronological random attachment. All other details are described in Methods section. Number of replicates transitioned to cooperation is shown in circle inset.

In Fig. 7.4 we illustrate similar time plots, in this case for the more complex scenario featuring networks grown from founder populations of 3 defectors. We observe
that the findings from the simplified case of pre-existing networks, still hold here. We therefore see that: i) fluctuation alone promotes consistent levels of increased cooperation albeit with variable transition times; ii) migrants alone promote cooperation albeit to varying levels; and iii) the combination of cooperator migrants and fluctuation (see Fig. 7.4d) brings remarkable consistency to both transition times and levels of cooperation achieved.

Figure 7.4: Simulation time plots (25 replicates) illustrating the effects of migrant clique arrival and fluctuation for networks grown from 3 defector founders, with $\eta = 0.8$. Plots show number of cooperators over 20,000 generations. Migrant groups are complete networks of 3 cooperators nodes, 1 of which connects to 2 randomly selected existing network nodes. Network growth in these simulations is by chronological random attachment. All other details are described in Methods section. Number of replicates transitioned to cooperation is shown in circle inset.

These findings are robust to attachment mechanisms. For both of the network models illustrated above (pre-existing, and grown from founders), in addition to chronological random attachment (as represented in Figs. 7.3 and 7.4), the same observations also
held when tested using both degree-based attachment (PA), and fitness-based attachment (EPA).

7.5 Discussion

The ability of the migrant clique to invade defector networks arises from benefits conferred on the connecting migrant by the backup provided from its fellow migrants. The backup migrants are initially immune to both strategy updating and the impact of defectors in reducing their payoff values (being as they are initially not directly connected to the network). The backup migrants can boost the payoff (fitness) of a connecting migrant, so that during strategy updating, the connecting migrant node can thus readily convert the existing network node it connects to into a cooperator. Beyond initial possible payoff calculations, which can be determined ‘manually’, it becomes intractable to calculate the details of the further spread of cooperation in complex networks. Although it is clear that in the case of migrant-triggered cooperation, it is this backup that creates the initial possibility for a cooperative migrant to convert the first defector in the existing network that it connects to. We have confirmed that the addition of singleton migrants or migrant cliques, where the backup nodes have cooperate strategies replaced with defect, are unable to initiate the same effects as those described.

What is particularly interesting, is just how small the migrant group can be, whilst still being able to precipitate the emergence of cooperation through almost the entire population. The previous simulations were based on migrant groups of 3 connected individuals, one of which extends 2 connections to random existing members of the network. We subsequently reduced the size of the migrant group to 2 individuals, of which one connects only 1 edge to an existing network node. Tested at the same reward value of $\eta = 0.8$, on pre-existing defector-populated initially random networks, and on networks grown from defector founders (growth by CRA in both cases), our previous findings still hold. (Time plots were highly similar to those shown in Figs. 2 and 3, with the only difference that a delay in transition was observed infrequently, e.g. 1 or 2 replicates out of 25, for those simulations combining both migration and fluctuation.) On further reduction to 1 node (extending either 1 or 2 edges), our general findings no longer hold: the introduction of such migrants did not result in different outcomes to similar simulations without migrants. This outcome is entirely expected, as this situation is now no different to the standard attachment process by which all new individuals routinely connect—1 node, 2 edges, i.e. no backup.
These findings, based on minor adjustments to the nature of the migrant clique, highlight a potential source of concern regarding models of cooperation in networks, namely, that differing outcomes may arise from seemingly very small differences in simulation parameters. We offer the following illustration, based on the fluctuation model with chronological random attachment (as shown in Fig. 7.1a) to emphasise this point:

We can reduce our migrant mechanism to a point where it appears very similar (2 nodes, 1 edge) to the mechanism by which nodes routinely attach during network growth (1 node, 2 edges). Given such similarity, and noting that the migrant clique arrives only once in a simulation, whilst new nodes are added repeatedly in the fluctuation model, we might be inclined to therefore assume that results due to the migrant clique arrival would be trivial relative to those arising from fluctuation. However, we see in our results that the isolated, seemingly trivial, migrant event consistently brings about an increase in cooperation, which is not achieved in its absence (compare dashed green and black lines in Fig. 7.1a). The small difference, created by the addition of the migrant clique, between these two otherwise very similar implementations results in different behavioural dynamics. Despite their apparent similarities, the attachment mechanism used for routine network growth clearly cannot create the additional opportunity for cooperation that the migrant clique’s arrival can enable. We have considered the possible argument that pre-existing networks populated entirely by defectors are simply unstable states and thus ‘ripe’ for cooperation to percolate, but we reject this since our simulations grown from founders, in which we see the same effects, contain both cooperators and defectors.

These results, combined with findings of previous research, reinforce our belief that fluctuations in the network, or migrant cliques, or alternative mechanisms to perturb the system, bring an added dimension to models of cooperation in networks that simpler mechanisms fail to provide. It is these noisy perturbations of the network that disrupt the status quo and catalyse the spread of cooperation throughout the population. If our interpretation here is correct, then there is a risk that simpler, more deterministic models of cooperation in networks may lack the disruptive elements that promote cooperation and may thus preclude or impede its emergence.
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7.6 Conclusion

Using various models of cooperation based on the public goods game, we have investigated a scenario where individuals migrate, from a cooperative network, to join one predicated upon defection. Under certain conditions, notably around the region where the social dilemma is at its strongest, we find quite striking results. The effect of a few concerted migrants catalyses a marked behavioural change, precipitating the widespread emergence of cooperation throughout the population. Of particular interest is our finding that the migrant group size can be extremely small and needs only to form one initial connection in order to initiate a marked response. The actions of a seemingly trivial group of concerted cooperators initiate changes throughout a population that is orders of magnitude larger than the migrant group.

We have hypothesised that perturbation, in the form of population size fluctuation, and also in the form of invading migrants, can promote cooperation. We have demonstrated this to be the case for both of these effects in isolation, and to a surprisingly greater extent, in concert. Clearly other methods, or combinations of methods, for perturbing or disrupting networks exist that may yield similarly surprising outcomes.

These results reinforce findings of our previous work and support our argument that perturbations of networks, or possible alternative forms of disruption, are an important contributory feature in the emergence of cooperation. We also note that generally, such observations suggest the potential for oversimplified or strictly deterministic models of cooperation in social networks to actually limit or exclude the phenomena they seek to investigate. We highlight, in particular, that from a combination of two mechanisms studied here, there emerged a consistency in outcome that is unlikely to have been anticipated from studying simpler models of each mechanism in isolation.
Chapter 8

Conclusions

The work presented in this thesis extends a body of knowledge concerned with the evolution of cooperation in simulated populations. The extent to which such populations can support cooperation is subject to clear limits in the case of well-mixed populations. However, when interactions are constrained by spatial connectivity, the possibility of cooperative acts being reciprocated increases. Within evolutionary scenarios, this mechanism of network reciprocity allows cooperators to increase their fitness and hence spread further copies of themselves amongst offspring in the population. Over generations, this evolutionary self-assortment results in self-supportive clusters of cooperators and thus offers the opportunity for levels of cooperation beyond that predicted by the well-mixed limit.

We have described the development and application of models to investigate the evolution of cooperation by means of network reciprocity. At the core of our models is the principle that social networks be subject to some form of continual perturbation. We believe that the repeated adjustments to network topology that are thus enabled are what allow populations to escape local optima and thus achieve higher levels of cooperation than may otherwise occur. This proposition is appealing since the idea that network structure modulates repeatedly in this way fits naturally with the dynamic aspect of social networks in the real world.

The specific form of perturbation we have used is represented by fluctuation of a network’s topology, using repeated cycles of growth and attrition of network nodes. We have attempted in our implementation to mirror activities which would reasonably correlate with real populations, whilst relying on as few assumptions as possible. To this end, we model attachment of new nodes as a process which occurs entirely at random. The loss of nodes, by contrast, is cast as an evolutionary event where individuals
which have lower fitnesses are more likely to be deleted.

It has been established elsewhere that scale-free structure promotes cooperation in networks. We would argue that the explanatory power of models which assume high heterogeneity of this kind is limited by such an assumption. Social networks having scale-free topology almost certainly depend on the assumption of preferential attachment (PA) to explain their formation. Unfortunately the explanation of PA itself (in social networks) creates further dependencies based on assumptions of memory, recognition and possibly reasoning—cognitive abilities which are typically limited to higher organisms. Questions of how newcomers might attach to an existing network cannot readily be ignored whilst attempting to create a model which features network growth. Our mechanism of growth by chronological random addition of newcomers generates networks of moderate heterogeneity, without raising questions regarding how preferential attachment is implemented by organisms with limited abilities.

In real world examples, cooperation may appear early or late in a social network’s development. In developing models of cooperation, we have been conscious of the importance of making such models broadly applicable where possible, thus in addition to minimising assumptions and dependencies, their efficacy should extend beyond fully-formed networks to work equally well in support of cooperation when applied to immature networks growing from their ‘infancy’.

In summary, our work has demonstrated how fluctuation can support the evolution of cooperation in networks, regardless of the initial network behaviour or topology, and regardless of whether the network is mature or in its infancy. Our model implements the culling of individuals on the basis of fitness and is thus analogous with natural selection. Growth however, is implemented as a random process and thus eliminates those assumptions associated with more complex processes. We believe that this approach represents an important step in understanding the evolution of cooperation, particularly with respect to early evolutionary origins where minimal assumptions can be made, and that the general principle of repeated perturbation of networks has the potential to enable the development of further understanding in this area.

8.1 Summary of Work

We initially demonstrated that an existing model of network reciprocity, evolutionary preferential attachment (EPA), modified with a mechanism for network fluctuation, could support increased levels of cooperation amongst populations of individuals
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playing the prisoner’s dilemma. In particular, we observed that the fluctuation model was more effective in supporting cooperation from networks which were initialised only with defectors (Chapter 3). On the basis of these results we developed a minimal model for cooperation that eliminated dependency on scale-free networks and associated assumptions. Our model was able to support cooperation in mature networks and in those grown from founder populations, without the requirement for cooperators to be initially present (Chapter 4).

To test if our approach would generalise, we applied the model to a second dilemma, the snowdrift game, which is generally more favourable to cooperation but experiences differing outcomes depending on the network topology present. We also explored the extent to which our model was robust to increasing connectivity. For both dilemmas, in established networks, and also in those grown from founders, and for network topologies of increasing connectivity, from sparsely connected to those approximating the well-mixed limit, our model promoted cooperation beyond levels predicted for the well-mixed population. We observed no inconsistency in outcomes from the snowdrift game. When compared to non-fluctuating controls, our model generally demonstrated increased cooperation for regular and random but not necessarily scale-free networks (Chapter 5).

In later work we extended our approach to look at the public goods game (or tragedy of the commons), an arguably more realistic representation of the difficulties of cooperation in the real world, since it describes group-based dilemmas rather than those present simply between pairs of individuals. Again, we observed that the fluctuation model was able to support the emergence of cooperation for two variants of the public goods game (Chapter 6). We then applied this public goods model to a question regarding the spread of cooperation between subsets of a population, looking at whether small groups of cooperators could seed cooperation in groups they migrated to. We observed that under certain circumstances, where the dilemma was strongest, a very small group of migrant cooperators could invade and precipitate cooperation throughout a much larger population containing primarily, or all, defectors. In particular, we observed the emergent phenomenon of highly consistent behaviour arising from the combined interaction of migrants and fluctuation, an outcome which was not observed and would not have been anticipated from observations of each mechanism in isolation (Chapter 7). This finding indicates a possible risk that overly simplified or highly deterministic models may impede rather than promote the emergence of cooperation.
8.2 Initial Reception of our Work

Our work has been presented in an established scientific journal, Nature Scientific Reports (2015 Impact Factor 5.228) and in three conference publications: European Conference on Artificial Life (ECAL) 2015, EvoStar 2015, Unconventional Computation and Natural Computation (UCNC) 2016, with supporting presentations delivered at each. In addition we presented previously published work at the Learning and Intelligent Optimisation (LION) 2016 conference. All conference presentations were well received with subsequent follow up by email in some cases. Follow up after ECAL led to citation of two of our publications ([Miller and Knowles, 2015b] and [Miller and Knowles, 2015a]) in work by Roberto Ulloa and Tom Froese attempting to explain the long stability, and thereafter collapse, of Classic Mayan civilisation [Ulloa and Froese, 2016]. Their work makes extensive use of our model, and from their application of it they draw several conclusions which mirror findings presented within this thesis: that network fluctuation can improve cooperation, and that if a mechanism exists for readjustments of the network, this allows for cooperation without the requirement for highly heterogeneous network structure.

8.3 Effect of our Work

The aim of our research has been to develop a general model for cooperation by means of network reciprocity. As we have described in Section 2.8.3 the overwhelming majority of research seeking to model cooperative behaviour in networks has focused on static networks, with a continued strong focus on exploring cooperation within scale-free networks [Yang et al., 2012, Li and Duan, 2014, Li and Yong, 2015, Liu and Li, 2016, Wang and Liu, 2016] and with exceptions to this trend being much less common [Perc, 2011, Zhang et al., 2014]. Of the subset of work which does consider dynamic networks, we make two points: i) research tends to consist of models which rewire edges (relationships) between nodes [Zimmermann and Eguíluz, 2005, Santos et al., 2006a, Pacheco et al., 2006a, Traulsen et al., 2009], rather than changes involving the nodes (individuals) themselves [Perc, 2009, Szolnoki et al., 2009, Ichinose et al., 2013], and ii) such research almost invariably considers pre-existing or fully-formed networks, which are then subject to dynamic effects.

The research gap we have focused on is that of models which do not depend on high heterogeneity and which make minimal assumptions regarding the agents within
them. In particular we are interested in understanding how cooperation may emerge in dynamic networks, as they grow from their origins. This latter point, in particular, appears to us to be an important aspect of cooperation that has seen remarkably little activity. In pair-wise cooperation, using the prisoner's dilemma, network growth models are primarily confined to the works of Poncela et al. [Poncela et al., 2008, Poncela et al., 2009b, Poncela, 2012], although the earlier pre-print paper of Ren et al. [Ren et al., 2006] should also be mentioned. Within this thesis we have presented a general model, described in Chapter 4, which we believe usefully extends the limited material in this area of the research. In group-wise cooperation, using the public goods game, the model we have described in Chapter 6 appears to be the first example of an approach that considers the emergence of group-based cooperation in networks grown from founder populations.

There may be an argument that models which describe fully-formed dynamic networks are assumed to automatically apply to the case of networks grown from their origins, however, this has not been demonstrated in the literature, and the work in this thesis does not support such an assumption. For example, the outcomes we report in Sections 4.4.1 and 4.4.1, applying the same model to pre-existing versus grown networks respectively, are clearly different.

Finally, the principle of repeated network perturbation which underpins our work (in our models, perturbation is applied in the form of network fluctuation) has seen limited research, although we are aware of the interesting work of Behar et al., not yet published [Behar et al., 2016], which focuses as we have done on population perturbations that arise from the environment. Their paper, presented from a numerical statistical physics approach rather than an agent-based evolutionary game theoretic one, reports that small spatial fluctuations promote cooperation in public goods games.

8.4 Limitations and Further Work

The approach of this thesis uses agent-based models to represent phenomena from the real world in a highly simplified form. Whilst we aim for a correspondence with natural phenomena where feasible, our models are highly abstracted. There is clearly a limit to how much they reflect real world processes and given the difficulty in quantifying real world behaviours, research from a game theoretic perspective is at present limited to offering potential insights rather than to mapping proposed models to real world phenomena within fields such as ecology and behavioural biology. From the
game theoretic perspective, there are still potentially profitable and interesting angles of exploration possible in abstracted representations of real phenomena, such as those described by our model, however it will clearly benefit our understanding of cooperation in the real world if research is motivated by the ultimate aim of explaining empirical findings in nature.

In choosing avenues of research, our primary aims have been to test the principle that network fluctuation can serve as a general explanation for cooperation in simulated social networks and to assess the robustness of a model developed from this principle. Macroscopic population behaviour has been our main interest. Whilst we have explored a few avenues particularly relevant to understanding our findings, we have generally avoided undue focus on attempting to explain microscopic behaviour. We have also been conscious of the need to balance introducing novel aspects to our model, whilst maintaining sufficient parallels to the existing published work, so as to allow for comparison of results.

Limitations to our models may be considered from two perspectives. On one hand there are implementation choices such as specific parameters which may be more or less critical to our findings and need further sensitivity analysis. On the other hand, the correspondence of our models to any real, natural system may not have been sufficiently justified, and may turn out to be a weakness when trying to develop possible insights regarding natural cooperation. Within the work described here, we have found our model to be both general and robust, nevertheless, inspection of our evolutionary process reveals several areas in which the model is strictly defined by the exact implementation we have used. We have assessed the impact of varying those elements that we identified as most likely to cause changes in outcomes, for example, connectivity, strategies of founder and pre-existing nodes, attachment mechanisms, network types. There are clearly other elements we have not investigated which might i) merit further experimentation to test whether the model continues to function when they are adjusted and/or ii) be implemented differently in alternative abstractions of real phenomena. We identify some of these below:

8.4.1 Temporal Relationships

By adding a specified number of nodes per generation we have defined a relationship in timescales between new node addition (possibly *birth*) and strategy updating (*death* or simply *imitation* or *learning*). Regardless of the specific interpretation we place on these aspects of the model, newcomers are being added at a rate of 10 per generation
whereas any given node only experiences 1 chance in that same timescale to pass copies of itself to a subsequent generation (in strategy updating). Changes in this relationship will undoubtedly affect the behaviour of populations. Limited research exists investigating temporal relationships between game playing and strategy updating in static networks [Roca et al., 2006, Roca et al., 2009]. It is unclear what effect changes in temporal relationships between node addition and other evolutionary steps might have for different dynamic scenarios of the kind our models describe. Specifically it is unclear how faster and slower growing networks will affect the emergence of cooperation within them.

### 8.4.2 Noise and Randomness

We have proposed that structurally disruptive elements within network models may lead to more opportunities for networks to adapt in support of cooperation, whilst models that are highly deterministic might have the opposite effect, of impeding such adaptation. We have four steps occurring per generation. These feature deterministic and probabilistic elements as follows:

*Game playing* - Strictly specified round robin process. Game play is deterministic.

*Strategy updating* - Randomly chosen neighbour. Updating is probabilistic.

*Node addition* - Strictly specified number of new nodes and edges attached each generation. Attachment is random.

*Node deletion* - Strictly specified number of nodes deleted. Deletion has probabilistic element.

We can consider the impact of deterministic versus probabilistic mechanisms from two perspectives: the microscopic effects on cooperator individuals, and the macroscopic effects relating to transitions in population behaviour. We illustrate each of these below.

**Effects which might lead to greater persistence of cooperators:** We know that when cooperators are not immediately converted to defection and instead persist over several generations, there is greater chance of another cooperator node connecting to them, thus potentially forming the foundation for a cooperative cluster. This persistence could arise by introducing stochastic effects. It would be interesting to introduce
a probability for each agent as to whether they play games or not at each generation. A
similar approach could be adopted for strategy updating. Such effects might possibly
reduce the likelihood of low fitness cooperators scoring badly against, and hence be-
ing displaced by, defectors. The resulting increase in their longevity would increase the
chance of another cooperator node connecting to them and thus form the basis for a co-
operator cluster. It is possible that randomness or noise could also impact node addition
and deletion processes. We know that that the 0.01 element of randomness from setting
$\eta = 0.99$ in EPA node addition is essential for the emergence of cooperation and that
increasing to $\eta = 1$ markedly changes behaviour for defector-founded populations—
the emergence of cooperation becomes impossible. Any element of noise during node
addition in this latter, otherwise entirely deterministic, scenario would restore the pos-
sibility of cooperation emerging.

**Effects which might trigger the percolation of cooperation:** We have shown that
under certain circumstances a pair of cooperator nodes, joining a network in such a
way that one of them does not initially connect directly, is able to precipitate a tran-
sition to cooperation within a network. Such a relatively trivial event could arise by
chance given less deterministic mechanisms for edge creation, or possibly by processes
that contain an element of noise. Extrapolating these ideas, there may be other ways
that elements of randomness or noise could change outcomes within our model such
as approaches which represent *mutations* in edge connectivity, miscommunication or
misinterpretation of behaviour in game playing, or mutation of strategies during ei-
ther node addition or updating. Research into noise has proved particularly important
for the iterated prisoner’s dilemma [May, 1987,Fuddenberg and Maskin, 1990,Nowak
and Sigmund, 1993, Wu and Axelrod, 1995] and so, has potential to also be of value
for the kind of iterated behaviour which arises from spatial structure. It is possible
that such non-deterministic elements might perturb networks so that effects similar to
those reported in this thesis might be observed, thus supporting cooperation in the ab-
sence of a mechanism explicitly designed to represent periodic network fluctuation.
This is a topic which has seen recent interest in research from the physics community
although such work seems to require the removal or relaxation of population size as a
constraint [Huang et al., 2015,Chotibut and Nelson, 2015,Constable et al., 2016].
8.4.3 Synchronous versus Asynchronous Mechanisms

Each of the four steps of our evolutionary process is discretely synchronous; it completes before the next step. Effects similar to those which might arise from noise or randomness may also be achieved given some sort of asynchronicity in the model. Perhaps more importantly, whilst the synchronous approach we use in this thesis allows for easy implementation of a model and also ready comparison between models, it is a poor abstraction of the real world. In particular a model featuring a form of strategy updating that represents some form of overlap between generations would be a first step towards a more realistic asynchronicity. A very simple abstraction of this could be achieved by probabilistic strategy updating thus allowing some agents to continue through into next generations.

8.4.4 Founder Effects

We should be alert to the fact that models might give rise to specific effects early within a network’s growth which are very much artefacts of a particular model implementation and are therefore unlikely to offer meaningful general insights with respect to how real world networks develop (given the very large variety of ways real networks develop). There is a risk of over-interpreting potentially artefactual effects when we should be focusing on macroscopic behaviour. That said, we should be aware of early microscopic effects caused by the nature of certain models (or parameters) which may influence (bias) long-term macroscopic behaviour in simulations. Some experimentation to identify, characterise and understand the sort of early biases that models might typically generate would be worthwhile in order to ensure that these effects are subsequently isolated, minimised or disregarded. One obvious example is the relationship between the number of nodes and edges in the founder population and the number of nodes and edges added in the first tranche of nodes. The nature of this step has potential to bias outcomes towards or away from cooperation in highly deterministic models.

8.4.5 Strategy Type of Added Nodes

Finally, one area in particular that might be viewed as problematic for our model as an abstraction of real world phenomena, is the allocation of strategy type for nodes new to the networks. Newcomer nodes that are added to these networks have independently randomly chosen strategies, cooperate or defect, picked with equal probability. First,
this approach does not naturally correspond with ideas on how mutant behaviours may emerge and then propagate throughout populations. Secondly, we have talked about investigating populations predicated upon defection, yet clearly our model routinely introduces cooperators. We consider that these are both reasonable criticisms. We make the following points in respect of such criticisms:

- **Comparing our results with existing research.** It is of value to be able to demonstrate the performance of our model by comparing with results from existing research. Adopting the same mechanism for addition of new node strategies as that of existing published research [Poncela et al., 2008] allows for such comparison. There is a limit to how different we can make our model to existing work and still be able to justifiably form interpretations based on comparisons. We note that the published literature using this mechanism of new node strategy allocation is well-cited and positively regarded.

- **No simple alternative to achieve strategy allocation for new nodes.** Ultimately we need to add nodes to the network. The added nodes need to have an initial strategy, yet this step must minimise potential biasing of the existing population. Our approach will bias outcomes, although the bias that arises is the least worst option: bias will always be in the direction of maintaining a 50:50 mix of strategies, rather than biasing the population towards domination by one strategy or the other (see below).

- **Non ‘genetically-neutral’ alternative mechanisms would bias game outcomes inconsistently.** Our approach to strategy allocation for newcomers leaves the evolutionary attractiveness of cooperation versus defection entirely dictated by the game (social dilemma) that is being investigated. (In the absence of a game then the two choices would be evolutionarily equivalent in terms of selection.) Our approach may be criticised on the grounds that it is biasing the population away from extremes towards an equal number of cooperators and defectors, thus effectively acting in favour of any rare mutant arising where the population is largely dominated by the opposing strategy (cooperators have an advantage whilst defection prevails and vice versa). Clearly a bias does exist in the model, however the same bias is present in the growth mechanism of the model we are using as a comparator (EPA).

- **Non ‘genetically-neutral’ alternative mechanisms would increase complexity of model and make interpretation more difficult.** In our experimental
work we consider how cooperation emerges for various test cases for a given model (for example, comparing pre-existing networks with those grown from founders). In order to compare the results from different test scenarios, we characterise population behaviour by measuring cooperation in terms of the temptation to defect. A strategy allocation mechanism that in some way potentially favoured one or the other strategy according to the test scenario under investigation introduces another factor to the model which may cause effects conflated with those arising from the variable(s) under test. This would complicate efforts to interpret experimental results.

It is possible that further research may demonstrate that our model is unsuitable as an abstracted representation of the evolution of cooperation because of the mechanism that we use to allocate newcomer strategies. There may be other situations where it serves as a more fitting representation, such as cultural evolution [Boyd and Richerson, 2009] or gene-culture coevolution [Gintis, 2003].

It is also possible that the model may subsequently be improved by more sophisticated or realistic mechanisms for adding newcomers and their strategies. One possible approach that seems to us to increase realism and is potentially worthy of further investigation would be where newcomers are represented more explicitly as offspring of existing nodes and thus somehow inherit strategies of fitter parents rather than have them randomly allocated. Such nodes would subsequently be redistributed (connected) randomly within the networks.

8.5 Closing Comments

In evolution, the challenges that are created by changing environments drive the continual emergence of hereditary adaptations within populations of competing individuals. Inherited traits which confer benefits on their owners improve the chances of survival and hence reproduction. However competing individuals, by definition, do not live in isolation, and those that develop the ability to work together potentially stand to further their chances of survival. Unfortunately, there is a hurdle to overcome here in that cooperators can easily be taken for granted. What we do know, is that whilst cooperative behaviour is less likely in a crowd of strangers, it becomes more probable amongst individuals who have some sort of connections with one another. We also know something about the sort of connections that are important—namely, that uniformity isn’t ideal for cooperation. It is said that “variety is the spice of life”. This is
clearly true in evolution generally, where diversity of form allows for the preferential selection of fitter individuals. In the evolution of cooperation within populations of connected individuals, there is an interesting parallel: diversity of relationships promotes the emergence of cooperation. For cooperation to flourish yet further, it seems that this diversity needs to change, in space and over time.

At a personal level it has been both fascinating and challenging to carry out research into the highly multi-disciplinary topic of cooperation. It is interesting to consider that a behaviour that many of us take for granted forms a fairly pivotal question in a range of fields as diverse as economics and endosymbiosis. It has been proposed that cooperation is as much a fundamental component of evolution as mutation and selection. Whilst the latter two processes allow for optimisation, it is the addition of cooperation that allows for the development of adaptations of increasing complexity. This proposition points to the question of whether the combination of cooperation and competition could be used as a problem solving technique. Within the field of computer science, where this thesis originated, there are long-standing evolutionary approaches predicated on competition, yet to date, very few that also incorporate cooperation. It is possible that this is one very specific area where understanding cooperation may be of value. Moving from the specific to the general, the tragedy of the commons is perhaps more relevant now than when it was first proposed. The human race today faces several challenges which are global in their impact, such as climate change, terrorism, and meeting the world’s future food and energy needs. To collectively address such major challenges, it is vital that we learn how we can best cooperate on a global scale. To quote Bertrand Russell, “The only thing that will redeem mankind is cooperation”.

CHAPTER 8. CONCLUSIONS
Glossary

A brief summary of some of the more commonly used terms in our work. Meanings are provided only in the context of this thesis.

**Agent-based model**  A model which defines individuals (agents) and their interactions with respect to some form of environment.

**Assortativity**  See ‘Self-assortativity’

**Behaviour**  A general term that may be used to refer to the game decisions or hereditary traits within a population. The corresponding formal term in game theory is ‘strategy’.

**Carrying capacity**  The maximum population size, for a species, that an environment or ecosystem will support. We also use (nominal) maximum size ($N$).

**Chronological random attachment (CRA)**  The connection of new nodes to existing network nodes, at random, over time. Generates an exponential degree distribution.

**Clique**  A small complete network.

**Complete network**  A fully connected network. Each node is connected to every other node of the network. As far as our work is concerned, this is analogous to a well-mixed population.

**Connected network**  A network where there is a path (or route) from any one node in the network to another. This means that the network consists of one single component. (A disconnected network contains multiple components.)

**Connectivity**  A general term that may be used to indicate the extent to which nodes within a network are connected to other nodes. The corresponding formal term is ‘average degree’.
Cooperator  An individual that offers benefits to others at a cost to themselves.

Defector  An individual that may receive the benefits offered by a cooperator but will not offer any benefits to others. It thus pays no costs. (Also a cheat or freerider.)

Degree  The number of edges (and hence the number of neighbours) a node has. Typically denoted with the letter $k$. Average network degree is denoted with $\bar{z}$.

Edge  A link or connection between two nodes. In our models, these define where interactions may occur between individuals in the population.

Evolutionarily stable strategy (ESS)  A strategy which when present in an evolving population cannot be displaced by a rare mutant.

Evolutionary preferential attachment (EPA)  The connection of new nodes to an existing network such that newcomers’ edges will preferentially attach to those existing nodes which are occupied by agents having higher fitness values.

Exponential distribution  Used in this thesis to refer to networks whose degree distribution is exponential, as obtained by chronological random attachment. We refer to these as moderately heterogeneous networks.

Fluctuating network  Used in our work to describe a network that is subject to a mechanism which features addition and deletion (or growth and attrition) of nodes. (Compare ‘non-fluctuating’ and also ‘static’.)

Graph  Mathematical term used to refer to networks. We use both terms interchangeably within this thesis.

Heterogeneity  In describing network topology, this refers to the range of degree values present within a network.

Hub  A highly connected node. Most commonly associated with scale-free networks.

Nash equilibrium  A solution set of strategies for a given game. Where individuals are playing the Nash equilibrium strategies, any single individual cannot increase its score by changing strategy.

Neighbourhood  Used to refer to a given node and its immediate neighbours. (Size of neighbourhood is denoted by $g = k + 1$.)
Network grown from founders  Used to describe networks grown from a small founding population. We typically use founder populations which are complete networks of 3 nodes, all having the same strategy.

Node  A vertex within a network. It connects to other vertices by edges. In our agent-based models, agents (individuals) are positioned at nodes.

Non-fluctuating network  Used in our work to refer to networks that are dynamic only during their growth from founder networks and which, on reaching maximum size, become static.

Pre-existing network  This term refers to networks which are fully-formed (at the start of a simulation), i.e. they are at a maximum size and all nodes are occupied by agents with defined strategies.

Preferential attachment (PA)  A process of network growth where new nodes preferentially connect to nodes that are more well-connected. In the scientific literature this is sometimes referred to as rich-get-richer or the Matthew effect. It typically generates a scale-free network.

Prisoner’s dilemma (PD)  A pair-wise social dilemma used in models of cooperation. May infrequently be described as the two-player public goods game. See Section 2.5.2.

Public goods game (PGG)  A group-wise social dilemma used in models of cooperation. Also known as the N-player prisoner’s dilemma, the freerider problem and the tragedy of the commons. See Section 6.1.

Random graph (network)  A network where degree values have a Poisson distribution. (A low heterogeneity network.)

Regular graph (network)  A network where every node has the same degree. (A non-heterogeneous network.)

Scale-free graph (network)  A network where degree values are distributed according to a power-law distribution. Associated with preferential attachment mechanisms. (Highly heterogeneous network.)

Self-assortativity  Within this thesis, we use this term to describe an effect where agents with similar strategies will group together (over generations). The term
as we use it therefore relates to *assortativity by strategy*, rather than ‘assortative mixing by degree’ which is often used in ecology, physics and network science literature.

**Snowdrift game (SD)** A *pair-wise* social dilemma used in models of cooperation. Also known as *chicken or hawk-dove*. See Section 2.5.2.

**Social Dilemma** This term describes situations where self-interest drives individuals to actions which, whilst they may be rational, will result in them achieving sub-optimal outcomes. Such situations are often described in terms of individual self interest harming the collective good. They are covered in Section 2.5.2.

**Star graph (network)** A network of N nodes where $N - 1$ nodes each have a single edge to a hub node (and hence the hub has a degree of $N - 1$). There are thus only 2 degree values in the network. (Extremely heterogeneous network.)

**Static network** Used in our work to indicate networks whose topology does not change.

**Strategy** In game theory, these are decisions (choices) for playing a game. Within this thesis, where we are mainly working with an evolutionary game theoretic approach, strategies are hereditary behaviours and are unconditional: an agent having a strategy, $X$, will always play $X$ regardless of their opponent’s choice. For the prisoner’s dilemma, snowdrift and public goods games, the strategies are *cooperate* and *defect*.

**Strategy updating** An evolutionary game theoretic process intended to function as an abstraction of natural selection.

**Tournament Selection** An alternative approach to pruning a network which introduces a stochastic element to the selection of nodes for deletion.

**Truncation** This refers to pruning of a network by simply ranking nodes in order of fitness and deleting the least fit. It is a deterministic process.

**Well-mixed (evenly-mixed)** This term describes populations where an individual will interact with any of the other members of the population with equal probability.
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