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Conformity, upstream reciprocity and social diversity: secondary mechanisms for the evolution of cooperation

PENA SUAREZ Jorge Alejandro

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Faculté des sciences sociales et politiques
Institut de mathématiques appliquées

Conformity, upstream reciprocity and social diversity: secondary mechanisms for the evolution of cooperation

THÈSE DE DOCTORAT

présentée à la
Faculté de sciences sociales et politiques
de l'Université de Lausanne
pour l'obtention du grade de

Docteur en mathématique appliquée aux sciences humaines et sociales

par

Jorge Alejandro PEÑA SUÁREZ

Directeur de thèse
Prof. Henri Volken

LAUSANNE
2012

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Faculté des sciences
sociales et politiques

IMPRIMATUR

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« Conformity, upstream reciprocity and social diversity : secondary mechanisms for the evolution of cooperation » .

Lausanne, le 11 janvier 2012

Le Doyen de la Faculté

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Summary

Cooperation is ubiquitous in nature: genes cooperate in genomes, cells in muticellular organims, and individuals in societies. In humans, division of labor and trade are key elements of most known societies, where social life is regulated by moral systems specifying rights and duties often enforced by third party punishment. Over the last decades, several *primary* mechanisms, such as kin selection, direct and indirect reciprocity, have been advanced to explain the evolution of cooperation from a naturalistic approach. In this thesis, I focus on the study of three *secondary* mechanisms which, although insufficient to allow for the evolution of cooperation, have been hypothesized to further promote it when they are linked to proper primary mechanisms: conformity (the tendency to imitate common behaviors), upstream reciprocity (the tendency to help somebody once help has been received from somebody else) and social diversity (heterogeneous social contexts). I make use of mathematical and computational models in the formal framework of evolutionary game theory in order to investigate the theoretical conditions under which conformity, upstream reciprocity and social diversity are able to raise the levels of cooperation attained in evolving populations.

Résumé

La coopération est ubiquitaire dans la nature: les gènes coopèrent dans les génomes, les cellules dans les organismes muticellulaires, et les organismes dans les sociétés. Chez les humains, la division du travail et le commerce sont des éléments centraux de la plupart des sociétés connues, où la vie sociale est régie par des systèmes moraux établissant des droits et des devoirs, souvent renforcés par la punition. Au cours des dernières décennies, plusieurs mécanismes *primaires*, tels que la sélection de parentèle et les réciprocités directe et indirecte, ont été avancés pour expliquer l'évolution de la coopération d'un point de vue naturaliste. Dans cette thèse, nous nous concentrons sur l'étude de trois mécanismes *secondaires* qui, bien qu'insuffisants pour permettre l'évolution de la coopération, sont capables de la promouvoir davantage s'ils sont liés aux mécanismes primaires appropriés: la conformité (tendance à imiter des comportements en commun), la 'réciprocité en amont' (tendance à aider quelqu'un après avoir reçu l'aide de quelqu'un d'autre) et la diversité sociale (contextes sociaux hétérogènes). Nous faisons usage de modèles mathématiques et informatiques dans le cadre formel de la théorie des jeux évolutionnaires afin d'examiner les conditions théoriques dans lesquelles la conformité, la 'réciprocité en amont' et la diversité sociale sont capables d'élever le niveau de coopération des populations en évolution.

Resumen

La cooperación es ubicua en la naturaleza: genes cooperan en genomas, orgánulos en células eucariotas, células en organismos multicelulares, e individuos en sociedades. En los humanos, la división del trabajo y el comercio son elementos centrales en la mayor parte de las sociedades conocidas, donde la vida social es regulada por sistemas morales que especifican derechos y deberes, usualmente sancionados por terceros. Durante las últimas décadas, diversos mecanismos *primarios*, como la selección familiar y la reciprocidad directa e indirecta, han sido propuestos para explicar la evolución de la cooperación desde un punto de vista naturalista. En esta tesis trato el estudio de tres mecanismos *secundarios* que, aunque insuficientes para permitir la evolución de la cooperación, son capaces de promoverla actuando en sinergia con mecanismos primarios adecuados: el conformismo (tendencia a imitar comportamientos comunes), la 'reciprocidad hacia arriba' (tendencia a ayudar a alguien después de haber recibido la ayuda de otra persona) y la diversidad social (resultante de contextos sociales heterogéneos). Hago uso de modelos matemáticos y computacionales en el marco formal de la teoría de juegos evolutiva para investigar las condiciones teóricas bajo las cuales el conformismo, la 'reciprocidad hacia arriba' y la diversidad social son capaces de elevar los niveles de cooperación obtenidos en poblaciones en evolución.

Better call on evolution,
better way to make a revolution.

Cat Power

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Chapter 1

Introduction

1.1 The problem of cooperation

> It is true that certain living creatures, as bees and ants, live sociably with one another [...] and therefore some man may perhaps desire to know why mankind cannot do the same.
>
> ---
>
> Thomas Hobbes, *Leviathan*

The question of why and how individuals voluntarily give up their natural freedom in order to unite and live in society – in Hobbesian terms, why and how a commonwealth is instituted – has been central to the social and political sciences ever since Aristotle's *Politics*. During the last decades, this question has also been transferred to biology, where it is best identified with the problem of the major evolutionary transitions, whereby entities capable of independent reproduction before a transition can only reproduce as a part of a group after it (Maynard Smith & Szathmáry, 1995). Within this broader picture, the origin of social groups (be they composed of ants, bees or humans) is only one of the last major transitions in evolution, which also include the origin of chromosomes, the invention of sex and the shift from unicellularity to multicellularity, among others. The problem of living together does not start with humans nor with social insects: it has been there almost since the origin of life itself.

The snag of living with one another is that it almost invariably leads to a conflict between individual and collective interests, because what is best for the individual is not necessarily best for the group and vice versa. These situations, in which the common good is at odds with private interests, are usually referred to as *social dilemmas* (Kollock, 1998). They abound in both natural and human social systems: in microorganisms whose metabolism partially depend on extracellular enzymes, non-producers benefit from the enzymes secreted by producers without paying the associated cost (Crespi, 2001); in groups of vertebrates that hunt collectivelly, such as lion prides and hyena packs, the prey is distributed evenly among the group members independently of the effort invested in the hunt, making it possible for lazy individuals to benefit from the hunting efforts of others (Packer & Ruttan, 1988). Alarm calls against predators also embody a social dilemma: while everybody benefits from the alarm, individuals giving the alarm pay an energetic cost or a higher predation risk (Clutton-Brock et al., 1999). In humans, collective efforts such as warfare and hunting, and the contribution to public services in the form of taxes or the exploitation of common resources in modern societies (Hardin, 1968; Kollock, 1998) are typical examples of social dilemmas.

The most well-known and maybe the simplest game exemplifying a social dilemma is the so-called prisoner's dilemma. Imagine two players, each having to decide (in ignorance of the co-player's decision) whether to cooperate with their co-player or not. To cooperate (C) entails a cost c, in order for the co-player to receive a benefit b, with $b > c$. To defect (D) means refusing to cooperate and does not entail any cost. This yields the following payoff matrix:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array}. \tag{1.1}$$

Note that the payoff entries are such that the two players gain more if they opt for mutual cooperation than if they opt for mutual defection, since $b - c > 0$. Cooperation is however *strictly dominated* in this game. This means that, no matter what the other player does, one is better off not cooperating: if my co-player defects, it is better for me to defect than to cooperate, since $0 > -c$; if my co-player cooperates it is still better for me to defect than to cooperate, since $b > b - c$. Thus, *rational* players will choose to defect in the prisoner's dilemma and end up gaining nothing, while each could have earned $b - c$ if they both had cooperated. Hence the dilemma: although mutual cooperation is a preferrable outcome than mutual defection, no player has the incentive to cooperate. Using the language of game theory, we say that the Nash equilibrium of the game (the strategy profile where no player can do better by *unilaterally* changing her strategy) is Pareto inefficient (an alternative outcome that makes at least one player better off without reducing any other player's payoff is possible).

The prisoner's dilemma is an extreme example of a social dilemma, because (D, D) is the only Nash equilibrium. In many situations, less stringent games may be more realistic models of the underlying social dilemma. One such game is the stag hunt, named after the following passage of Rousseau's *A Discourse on Inequality*:

> “If it was a matter of hunting a deer, everyone well realized that he must remain faithfully at his post; but if a hare happened to pass within the reach of one of them, we cannot doubt that we would have gone off in pursuit of it without scruple and, having caught his own prey, he would have cared very little about having caused his companions to lose theirs”[1].

Imagine a two-person stag hunt. Each player has to decide either to ‘remain faithfully at his post’ to hunt the stag, which is to cooperate, or to go off in pursuit of the hare just passing by, which is to defect. Two hunters are needed to hunt a stag, but just one is required to hunt a hare. Additionally, half a stag provides more meat per person than a single hare. Payoffs are measured in kilograms of meat: h for the hare and s for the stag. This yields the payoff matrix

$$\begin{array}{c c} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} s/2 & 0 \\ h & h \end{pmatrix} \end{array}. \tag{1.2}$$

In this case, both (C, C) and (D, D) are Nash equilibria: once playing one of them, no player would be willing to unilaterally change his mind. The cooperative equilibrium is Pareto optimal, which means that no further Pareto improvements (changes in the strategy profile making at least one player better off without making the other player worse off) are possible. The defective equilibrium, however, is *risk-dominant*; no matter what my co-player does, if I decide to hunt hare I will get h; if I decide to hunt stag instead and my co-player abandons me, I will get nothing. In other words, stag hunters depend on each other whereas hare hunters are independent. This makes the defective equilibrium *salient* for risk-averse individuals, even if it is Pareto inferior. Pessimists will invariably prefer to play D.

In addition to the prisoner’s dilemma and the stag hunt, there is literally an entire zoo of games modeling social dilemmas. There is the snowdrift game, the volunteer’s dilemma, the public goods game, and many others. In all of these games, there is at least one Nash equilibrium which is not Pareto optimal and hence the possibility that rational individuals who care about their private interest (or personal risk) end up choosing to forgo the common good: hunting hares individually rather than stags collectively; opting out of helping others and therefore also of being helped in return. Hobbes’s question – why and how individuals stop living in a state of nature and institute a commonwealth in order to reap the benefits of living in society – can be recast in game theory terms as the question of why and how a population of players coordinate themselves

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[1] Rousseau, *A Discourse on Inequality*, Pt. II.

not in the Pareto inefficient equilibrium of defection but in the Pareto optimal equilibrium of cooperation.

Hobbes thought that explaining cooperation and social life in ants and bees was simpler than explaining it in humans, partly because “amongst these creatures, the common good differeth not from the private; and being by nature inclined to their private, they procure thereby the common benefit”[2]. In Hobbes's view, social insects succeed in cooperating with each other because they instinctively seek the common good; humans fail to do so in the absence of any coercive power because they act by rational self-interest: “the agreement of these creatures is natural; that of men, by covenant only, which is artificial”[3]. Hobbes is right in suggesting that social insects behave cooperatively by nature, whereas large-scale human cooperation heavily depends on the existence of laws, police and many other “artificial” contracts. He is wrong, however, in assuming that instinctive cooperation in non-human life forms, being natural, requires no further explanation. This is because what is true for rational humans is also true for genes regulating the behavior of insects and other life forms: if a rational individual can gain from defecting while others cooperate, then in a population of (genetically programmed) cooperators a (genetically programmed) defector arising by mutation will reap off the benefits of the cooperation of others without incurring in any cost and hence, because of its greater fitness, eventually outnumber cooperators and invade the population. Hobbes might be right in appealing to instinct as an answer for the question of cooperation, but by doing so he is just replacing a sociological problem involving rational self-interested individuals (humans) with a biological one concerning self-replicating molecules (genes).

How can a commonwealth be created and maintained? How do we escape from Pareto inefficient Nash equilibria? The solution proposed by Hobbes in *Leviathan* is central control under a sovereign:

> “[T]he only way to erect such a common power, as may be able to defend [men] from [...] the injuries of one another, and thereby to secure them [...] is, to confer all the power and strength upon one man, or upon one assembly of men, that may reduce all their wills, by plurality of voices, unto one will”[4].

In other words, Hobbes's solution to the N-person social dilemma game is to convert it into a one-player game – the sovereign's – where there is, by definition, no social dilemma: since the outcome of the game depends only on the sovereign's decision, the problem becomes a trivial optimization problem. According to Hobbes's account, individuals tired of living in the state of nature,

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[2] Hobbes, *Leviathan*, Pt. II. Ch. 17.

[3] *Ibid.*

[4] *Ibid.*

"where every man is enemy to every man"[5] agree to forego their individual rights (their right to play the game) and submit to a sovereign which will have the power of creating laws and policing his subjects's behavior.

Hobbes's solution is at the same time satisfactory and problematic. It is satisfactory because the institution of a state with laws and police *is* the solution to the problem of living sociably with one another currently in use by most of contemporary human societies. It is problematic because it is not at all clear how the transition from the state of nature to the establishment of the commonwealth was carried out. Hobbes's account seems to require rationality and language from the parties 'signing' the contract, but it is obvious that ants or bees (not to mention single cells or RNA molecules) lack both. Even in fully rational individuals capable of language, it is hard to see a fully-fledged state emerging out of Hobbes's *bellum omnium contra omnes*, as if it were a *hopeful monster* arising from a single incredible mutation. Like chromosomes, cells and insect colonies, human states are only the final outcomes of a gradual process of evolution. If we want to understand the origin and stability of the existing social contracts all around us, we have to adopt an evolutionary approach.

1.2 The evolution of cooperation

> In thus discovering and tracing the lost and forgotten paths which must have led men from the natural state to the civil state, in reconstructing together with the intermediate situations which I have just noted, those which lack of time has made me omit or which imagination has not suggested to me, no attentive reader can fail to be impressed by the immense space which separates these two states. It is in this slow succession of things that he will see the solution to an infinity of moral and political problems which philosophers cannot solve.
>
> Jean-Jacques Rousseau, *A Discourse on Inequality*

Hobbes imagined a hypothetical population of rational decision makers trying to agree on a social contract that would take them away from a state of nature where human life was "solitary, poor, nasty, brutish, and short"[6]. In *A Discourse on Inequality*, Rousseau took a different approach. He looked at the way a gradual change would have unraveled, taking a real human population from the state of nature to the state of society. For Hobbes, society is rationally planned; for

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[5] *Ibid*, Pt. I. Ch. 13.

[6] *Ibid.*

Rousseau, it is the outcome of evolution and historical contingency. In this sense, if Hobbes is "the grandfather of game theory" (Skyrms, 2004) Rousseau is that of *evolutionary* game theory.

What is evolution? Merrian Webster lists as one of the alternative definitions of the word: "a process of change in a certain direction". In our case, we are interested in the process of change of behaviors in a population. To a first approximation, behavior depends on at least two things: nature (biology) and nurture (culture). Accordingly, we can consider two kinds of evolution: biological and cultural. Biological evolution is the process of change of genotypes in a population of individuals capable of reproduction. Cultural evolution is the process of change of ideas in a population of individuals capable of social learning. Change should be more precisely understood as *Darwinian* change, or differential replication. Replication means reproduction in biological evolution and imitation in cultural evolution. *Differential* replication means that different types replicate at different rates, so that fitter or more successful individuals reproduce faster or are imitated more often than less fit or less successful individuals. Behaviors, coded for by genes or ideas, affect fitness: the ability of individuals to reproduce or to be imitated. Change can also be brought about by mutation and recombination in biological evolution and by their cultural analogues in cultural evolution. We focus, however, on differential replication or natural selection. Evolutionary game theory (Maynard Smith, 1982; Maynard Smith & Price, 1973) deals with the evolution of social behaviors making use of the formalism of game theory: social interactions are modeled as a game, genes or ideas code for strategies in the game, and fitness is equated to the resulting payoff.

In order to illustrate the problem of the evolution of cooperation, think of the prisoner's dilemma with payoff matrix given by Eq. 1.1. The Hobbesian's state of nature is here a population entirely comprised of defectors, where nobody helps and the payoff for everyone is equal to zero. Now, imagine that a cooperator arises by mutation. All the individuals she plays with are defectors, so that she earns $-c$ per interaction. Defectors earn nothing when they meet each other, and occasionally earn b when they meet the cooperator. The average payoff to defectors is thus slightly above zero. When it is time to reproduce or imitate, defectors are obviously more successful and the single cooperator is wiped out from the population of defectors. Now imagine the ideal world where everybody cooperates in the prisoner's dilemma. One defector arises by mutation. Cooperators get $b - c$ when they meet each other and $-c$ when they meet the defector, for an average payoff slightly less than $b-c$. The defector only meets cooperators and obtains an average payoff of b. Since $b > b - c$ the defector will reproduce faster than cooperators, so that the next generation there will be more defectors. Actually, it is easy to see that if individuals meet randomly, the average payoff for defectors is greater than that for cooperators no matter the respective proportions of cooperators and defectors. Defectors always reproduce faster so that, in the long run and in an environment with a finite carrying capacity, cooperation is doomed to extinction. The final evolutionary outcome is the state of nature feared by Hobbes. Both the origin and the stability of cooperation are impossible in this model.

In more technical terms, we say that defection is the only *evolutionarily stable strategy* (ESS) in the prisoner's dilemma. An ESS is a strategy that, when common, can resist invasion by another available strategy, provided that each other strategy invades alone and in small numbers. The concept was invented by Maynard Smith & Price (1973) when they were unaware of the concept of Nash equilibrium in classical game theory. The two concepts are however closely related. Note that a sufficient condition for a given strategy to be an ESS is for it to be a strict Nash equilibrium. This is the reason why Hobbes's appeal to instinct does no ultimately solve the problem of cooperation: in a sense, if you cannot get mutual cooperation by rational choice you cannot get mutual cooperation by evolved instincts.

How can cooperation evolve in the prisoner's dilemma? Biologists's favorite solution is *kin selection* (Grafen, 1985; Hamilton, 1964). The basic idea is that cooperation can evolve if a cooperator preferentially helps its relatives, since they will likely be cooperators as well. In the case of asexually reproducing individuals this is obviously true, since relatives are (except for mutations) clones, but the argument equally applies to sexually reproducing individuals with different sex-determination systems. Kin selection can be brought about by kin recognition, whereby individuals recognize relatives and direct their help towards them. It can also be brought about by limited dispersal, even in the absence of kin recognition: if relatives tend to stay closer to each other, then even random interactions in such a 'viscous population' can lead to kin selection (Hamilton, 1964). The evolution of sterility in the ant worker and of the suicidal honeybee worker's sting are paradigmatic examples of kin selection at work.

Although nepotism is obviously part of human behavior, it cannot be the only solution to the problem of cooperation, even in small-scale and stateless societies. Human cooperation is unique in the sense that it takes place in communities composed of large numbers of relatively unrelated individuals. Reciprocity has been often invoked as one of the most important mechanisms for the evolution of cooperation in humans (Alexander, 1987; Trivers, 1971). In the following, I succinctly review two forms of reciprocity: *direct reciprocity* and *indirect reciprocity.*

Direct reciprocity is brought about by repeated interactions with the same partner. It was already hinted at by Darwin in 1871, who wrote in *The Descent of Man*: "each man would soon learn that if he aided his fellow-men, he would commonly receive aid in return"[7]. The modern theory of direct reciprocity was however established a century after, with the seminal article by Trivers (1971) and the model by Axelrod & Hamilton (1981), which finally launched the theoretical study of this mechanism.

Let us consider individuals playing an *iterated* prisoner's dilemma game implementing the most famous strategy coding for direct reciprocity: tit-for-tat (TFT). TFT prescribes cooperation on the first move and whatever the co-player previously played on all subsequent moves, thus rewarding cooperation with cooperation and punishing defection with defection. In Axelrod (1984)'s words, individuals implementing TFT are 'nice', 'provokable' and 'forgiving'. They are nice because they are never the first to defect: they cooperate as long as their partners cooperate. They are however provokable, in the sense that they respond by defecting at once in response to defect. Finally, they are forgiving, as they readily return to cooperation once their partners do so.

How do TFT-based reciprocators fare against defectors? Imagine a very large population in which individuals implement one of two strategies, TFT and ALLD (which defects in every round). Each generation, a large number of pairs of individuals are randomly sampled from the population and play the iterated prisoner's dilemma with payoffs per round given by Eq. 1.1. With probability w, another round of the game is played, while with probability $1 - w$ the game ends. The average number of rounds per game is thus $1/(1 - w)$. When two TFTs play with each other both always cooperate, for a total average payoff of $(b - c)/(1 - w)$ for each player. When a TFT meets an ALLD, TFT cooperates and ALLD defects on the first round. On each subsequent interaction, TFT also defects since ALLD defected on the previous round. The payoffs for ALLD and TFT are thus respectively equal to b and $-c$. Finally, when two ALLDs meet they defect during each round, each obtaining a total average payoff of zero. The payoff matrix for TFT versus ALLD in the iterated prisoner's dilemma is thus given by

$$\begin{array}{cc} & \begin{array}{cc} TFT & ALLD \end{array} \\ \begin{array}{c} TFT \\ ALLD \end{array} & \left(\begin{array}{cc} \frac{b-c}{1-w} & -c \\ b & 0 \end{array} \right). \end{array} \tag{1.3}$$

Note that ALLD is *always* an ESS since $0 > -c$ always hold. TFT is an ESS if $(b - c)/(1 - w) > b$ or, equivalently, if $b/c > 1/w$. Cooperation based on reciprocity in repeated interactions with the same partner is stable, as long as w – 'the shadow of the future' – is high enough.

Direct reciprocity depends on repeated interactions between the same two partners. In his seminal paper on direct reciprocity (which he called "reciprocal altruism"), Trivers (1971) suggested the possibility of expanding such minimal

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[7] Darwin, *The Descent of Man*, Pt. I, Ch. 5.

circle. In what he named "generalised altruism", "[i]ndividuals [...] may respond to an altruistic act that benefits themselves by acting altruistically toward a third individual uninvolved in the initial interaction". Alexander (1987) extended this idea and coined the term *indirect reciprocity* for referring to cases where A helps B and A does not expect a return directly from B, but from someone else. One of the possibilities suggested by Alexander is that, by helping B, A acquires a good reputation that can be then rewarded by a player C when she finds herself in the position of helping A. Likewise, by refusing to help B, A acquires a bad reputation, that can be then punished by C. In the words of Alexander, "indirect reciprocity is a consequence of direct reciprocity occurring in the presence of others", a mechanism which "involves reputation and status, and results in everyone in the group continually being assessed and reassessed".

Boyd & Richerson (1989) were the first to put the insights of Alexander (1987) in mathematical form, but we owe the first successful models to Nowak & Sigmund (1998a,b). Consider the simplest of such models. In a large population, individuals meet in randomly sampled pairs and interact in a prisoner's dilemma. With probability w the population plays another round, so that on average each individual is paired with $1/(1-w)$ other players. Since the population is large, every pair is new: no individual meets the same partner again. Individuals can implement one of two strategies: Discriminator (DSC) cooperates on the first interaction and then cooperates on each subsequent interaction if the co-player cooperated on the previous round; ALLD never cooperate. It can be easily shown that DSC is an ESS in this model, and that the conditions are exactly the same as the above-mentioned model of direct reciprocity. This shows that the key concept in reciprocity is knowledge about past behavior. Both direct and indirect reciprocity implement strategies which are *conditional* on the past behavior of co-players, allowing cooperators to channel cooperation towards cooperative members of the community. Such knowledge can be direct (via personal experience) or indirect (via observation of others or gossip).

There are two snags with considering direct and indirect reciprocity as solutions for the problem of the evolution of cooperation[8]. The first snag is the so-called *second order free rider problem.* I will illustrate the phenomenon for the case of direct reciprocity, but pretty much the same happens for indirect reciprocity. In the model of direct reciprocity presented in this section, I assumed individuals implemented one of two strategies: TFT or ALLD. Consider now the effects of adding a third strategy: ALLC, which prescribes unconditional cooperation. If TFTs are common and there are rare individuals playing ALLC, they

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[8] The same two problems are to be found in another mechanism proposed to explain the evolution of large-scale human cooperation: altruistic punishment (Boyd et al., 2003; Boyd & Richerson, 1992; Fehr & Gächter, 2002). Altruistic punishers punish those who do not cooperate, at a personal cost.

will have the same payoff as TFTs because all individuals cooperate during all the rounds. Since the fitness of both TFTs and ALLCs are the same, there is no selection and evolution will operate by random drift only. Eventually, drift will cause the proportion of ALLCs to exceed a critical threshold frequency above which ALLD can invade, leading to a world of universal defection (which is stable against both ALLCs and TFTs). If ALLDs are first order free riders that do not cooperate but enjoy the cooperation of others, ALLCs are second order free riders: they cooperate but then free ride on the policing and punishing of defectors made by TFTs. There are several plausible solutions to the second order free rider problem. In the case of direct and indirect reciprocity, the reciprocator strategy can be made to be an ESS by considering the possibility of making implementation errors (i.e. defecting when intending to cooperate) in combination with more sophisticated social norms prescribing cooperation. For instance, an indirect reciprocity strategy known as 'standing' can be shown to be evolutionarily stable against both ALLDs and ALLCs (Leimar & Hammerstein, 2001; Ohtsuki & Iwasa, 2007). Standing prescribes cooperation to individuals in good standing and defection to individuals in bad standing, with an individual acquiring bad standing only if defecting against an individual in good standing.

Once the second order free rider problem is solved by considering more complex social norms, cooperation based on reciprocity or punishment can be shown to be *stable*. ALLD, however, is obviously also stable both for models of direct and indirect reciprocity. The problem is now exactly that of *equilibrium selection* in the stag hunt game, in which both the defective and the cooperative equilibrium are stable. In a sense, repetition, reputation and punishment do not *solve* the problem of the evolution of cooperation under the prisoner's dilemma: they simply *transform* the underlying game into a stag hunt (Skyrms, 2004; Taylor & Nowak, 2007). Cooperation under the stag hunt is however easier to achieve, as the problem of the stability of cooperation is now solved. The only problem now is the origin or initial viability of cooperation: given that cooperation is stable, how can it get a foothold in a population entirely comprised of defectors?

The key concept to give a satisfactory answer to this question is *population structure*. Darwin (always Darwin) already had a hint at this. In an oft-cited passage of *The Descent of Man*, he writes:

> "It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an increase in the number of well-endowed men and an advancement in the standard of morality will certainly given an immense advantage to one tribe over another. A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage,

> and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection. At all times throughout the world tribes have supplanted other tribes; and as morality is one important element in their success, the standard of morality and the number of well-endowed men will thus everywhere tend to rise and increase"[9].

Evolving populations are not monolithic blocks nor perfect gases: they always possess some kind of structure. Darwin observed that human populations are subdivided in groups (tribes) and suggested that although selection within groups disfavors altruism ('although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe [...]') selection between groups can favor it ('an increase in the number of well-endowed men and an advancement in the standard of morality will certainly given an immense advantage to one tribe over another').

Darwin's insight on the balance between within-group and between-group selection is neatly captured by the mathematical formalism due to Price (1970, 1972). According to Price's equation, the change in frequency of cooperators Δx in the whole population can be written as

$$\Delta x \propto \underbrace{V_G \beta_G}_{\text{between groups}} + \underbrace{\overline{V_W \beta_W}}_{\text{within groups}} .$$

The first term gives the change due to selection between groups and the second the change due to selection within groups. β_G and β_W are regression coefficients giving, respectively, the effect of behavior on the fitness of groups and individuals. A behavior which is beneficial to the group but costly to the individual leads to $\beta_G > 0$ and $\beta_W < 0$. Finally, V_G and V_W give, respectively, the variance in the proportion x between groups and within groups. Note that, for x to increase, it is necessary that $|V_G \beta_G| > |\overline{V_W \beta_W}|$.

Interdemic group selection as the one characterized by Price's equation is unlikely to be an important evolutionary process in the absence of multiple stable equilibria. This is because migration (the movement of individuals between groups) and selection within groups makes V_G to be very small and, unless $\beta_G \gg \beta_W$, between-group selection cannot overcome within-group selection. When there are multiple stable equilibria, however, and assuming that selection within groups is much stronger than migration, V_W will be small and V_G will be large. Boyd, Richerson and co-workers have argued that if evolution is cultural rather than biological, selection is strong enough for counterbalancing migration,

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[9] Darwin, *The Descent of Man*, Pt. I, Ch. 5.

so that *cultural group selection* could be an important mechanism for equilibrium selection among multiple stable equilibria such as those arising in the presence of reciprocity or altruistic punishment (Boyd & Richerson, 1985, 2010; Henrich, 2004).

Population structure can also have other forms. In their seminal paper, Axelrod & Hamilton (1981) thought of "clustering" as another way of introducing population structure in the population of players. They imagined a small, clustered group of TFTs in a population of ALLDs such that a proportion p of the interactions of members of the cluster are with other members of the cluster. In this case, the average payoff to TFTs is

$$p\left(\frac{b-c}{1-w}\right)+(1-p)(-c),$$

while that of ALLDs (if the cluster of TFTs is small enough) is still 0. From this, it follows that the cluster of TFTs can invade provided that

$$b/c > \frac{(1-w)(1-p)}{p}. \tag{1.4}$$

If p and w are large enough, an initial cluster of TFTs can invade a population where ALLD is common.

Later on, Axelrod (1984) proposed another kind of population structure, which he called "territoriality". He imagined sessile individuals interacting in a simple territorial structure in which each individual has four neighbors: one to the north, one to the east, one to the south and one to the west. Interaction is constrained to nearest neighbors so that the success of a given strategy depends on how well it does when interacting with neighbors. Evolutionary competition is also constrained to nearest neighbors. Evolutionary competition can be biological, by a colonization process allowing "the location of a less successful strategy [to be] taken over by the offspring of a more successful neighboring strategy" Axelrod (1984). Or it can be cultural. In the words of Axelrod: "A neighbor can provide a role model. If the neighbor is doing well, the behavior of the neighbor can be imitated. In this way successful strategies can spread throughout a population, from neighbor to neighbor" Axelrod (1984). In the former case such population structure leads to kin selection operating via limited dispersal. In any case the logical consequence of restraining imitation or dispersal to nearest neighbors would allow for clusters of individuals of the same strategy to develop, much as they were hypothesized in the original paper by Axelrod & Hamilton (1981), and to TFTs to be evolutionarily viable. In another seminal paper, Nowak & May (1992) showed that even unconditional cooperators (ALLCs) could be evolutionarily viable in a world of defectors by means of such territoriality, albeit to a lesser degree than TFTs. This possibility is already evident from Eq. 1.4 by letting $w = 0$ (in which case the iterated prisoner's dilemma becomes the one-shot prisoner's dilemma and TFT becomes equivalent to ALLC) and observing that cooperation can still invade provided that $b/c > (1 - p)/p$. Reciprocity is not required for cooperation to evolve in a spatial setting, but it obviously help.

In summary, the *first stages* of the evolution of large-scale cooperation in humans can be hypothesized as a combination of reciprocity, altruistic punishment and other mechanisms converting prisoner's dilemmas into stag hunts, and population structures conducive to a process of equilibrium selection and/or destabilizing the defective equilibrium. The resulting societites rely in a distributed form of social control via reciprocity, gossiping and moralistic punishment. Such societies represent a midpoint between the Hobessian state of nature and the commonwealths envisaged by the moral philosophers with laws, police and central control.

1.3 Secondary mechanisms: conformity, upstream reciprocity and social diversity

As it is evident from the last section, many different mechanisms have been advanced during the last decades in order to explain the evolution of cooperation. Recent review papers have proposed several classification frameworks aiming to compare models and mechanisms (Lehmann & Keller, 2006; Nowak, 2006b; Sachs et al., 2004; West et al., 2007). According to the conceptual framework proposed by Lehmann & Keller (2006), at least one of four conditions must be fulfilled for cooperation to evolve: (i) *direct* fitness benefits to the focal individual performing the cooperative act, e.g. mutualism or weak altruism, and "altruistic" punishment, (ii) *indirect* fitness benefits to the focal individual performing the cooperative act via preferential interactions between related individuals, i.e. kin or group selection, (iii) *direct* or *indirect* information about the cooperativeness of partners in repeated interactions allowing for direct or indirect reciprocity to work, and (iv) genetic correlation between genes for altruism and identifiable phenotypic traits, i.e. green beards. Condition (i) implies social interactions modeled after games different from the prisoner's dilemma. Conditions (ii), (iii) and (iv) make cooperation to be preferentially channeled towards cooperative individuals, so that helping evolves "because there is a positive association between individuals at the genotypic and/or phenotypic levels" (Lehmann & Keller, 2006). Such positive association, referred to as "assortment" in other papers, has been identified as "the most fundamental requirement for the evolution of altruism" (Fletcher & Doebeli, 2009) in interactions modeled after the prisoner's dilemma.

The classification framework proposed by Lehmann & Keller (2006) together with the concept of positive assortment between cooperative genotypes and cooperative phenotypes allows us to distinguish between *primary* and *secondary* mechanisms for the evolution of cooperation under the prisoner's dilemma. *Primary mechanisms* are to be understood in this thesis as those that either (1) change payoffs in the one-shot game so that there is a direct fitness benefit arising from the cooperative act, or (2) introduce the necessary assortment for cooperation to be preferentially directed to cooperative members of the population. *Secondary mechanisms* are those that fail to do any of these two things, but, under some conditions, are able to enhance the levels of cooperation that are achieved *in the presence of a primary mechanism.* The key idea behind the concept of a secondary mechanism for the evolution of cooperation is that although it does not allow for cooperation to evolve *per se*, it can further promote the evolution of cooperation when acting in tandem with a primary mechanism.

In this thesis, I explore three secondary mechanisms that have been proposed to be important for the evolution of cooperation, particularly in humans: conformity, upstream reciprocity and social diversity. Conformity is the tendency to imitate common behaviors argued to be a key component of our social learning psychology (Boyd & Richerson, 1985). Upstream reciprocity (Boyd & Richerson, 1989; Iwagami & Masuda, 2010; Nowak & Roch, 2007; Nowak & Sigmund, 2005), also known as generalized reciprocity (Barta et al., 2011; Hamilton & Taborsky, 2005; Pfeiffer et al., 2005; Rankin & Taborsky, 2009; van Doorn & Taborsky, 2011), is a special kind of indirect reciprocity that, instead of prescribing cooperation to those that you know have cooperated with somebody, prescribes cooperation to somebody if the focal individual has experienced cooperation. Social diversity means heterogeneity in the social contexts experienced by individuals, e.g. heterogeneity in the number of interactions per individual and/or in the number of individuals per interaction group. Standard models of the evolution of cooperation assume that individuals implementing the same strategy are the same in all respects, including for instance the number of interaction partners. In reality some individuals can have more interaction partners than others and groups facing social dilemmas can greatly vary with respect to the number of participants.

Conformity, upstream reciprocity and social diversity are not primary mechanisms for the evolution of cooperation: acting alone, they do not select *for* the evolution of cooperation. However, existing models have shown that, in some cases, and in the presence of proper population structures, the addition of one of these mechanisms can significantly promote cooperation under the prisoner's dilemma. Conformity, for instance, and if sufficiently strong, can stabilize any behavior and thus be conducive to generate multiple stable equilibria in a population subdivided in demes, favoring the evolution of cooperation by cultural group selection (Boyd et al., 2011; Boyd & Richerson, 1985, 2009, 2010). It has also been proposed as a solution for the problem of the second order free rider problem in models of altruistic punishment (Henrich & Boyd, 2001). Upstream reciprocity has been shown to be conducive to the evolution of cooperation in small and/or structured populations and under some modeling assumptions (Iwagami & Masuda, 2010; Nowak & Roch, 2007; Pfeiffer et al., 2005; van Doorn & Taborsky, 2011). Finally, when social diversity takes the form of heterogeneous population structures leading to a high variation in the number of interaction partners per individual, the evolution of cooperation has been shown to be greatly promoted in the one-shot prisoner's dilemma game (Santos & Pacheco, 2005; Santos et al., 2006, 2008).

1.4 From spherical to cylindrical cows

> In that Empire, the Art of Cartography attained such Perfection that the map of a single Province occupied the entirety of a City, and the map of the Empire, the entirety of a Province. In time, those Unconscionable Maps no longer satisfied, and the Cartographers Guilds struck a Map of the Empire whose size was that of the Empire, and which coincided point for point with it. The following Generations, who were not so fond of the Study of Cartography as their Forebears had been, saw that that vast Map was Useless, and not without some Pitilessness was it, that they delivered it up to the Inclemencies of Sun and Winters. In the Deserts of the West, still today, there are Tattered Ruins of that Map, inhabited by Animals and Beggars; in all the Land there is no other Relic of the Disciplines of Geography.
> Suárez Miranda: *Viajes de varones prudentes, libro cuarto, cap. XLV, Lérida, 1658.*
>
> Jorge Luis Borges, *On Exactitude in Science*

Borges's short story *On Exactitude in Science* (credited as a quotation from the fictional writer Suárez Miranda and originally published under the pseudonym B. Lynch Davis) further develops an idea from Lewis Carroll's *Sylvie and Bruno Concluded* about "a map of the country, on the scale of a mile to the mile". Like "the following Generations" in Borges's short story, the characters of *Sylvie and Bruno Concluded* also recognize the inconveniences of such degree of exactitude on the art of cartography: "The farmers objected: they said it would cover the whole country, and shut out the sunlight! So now we use the country itself, as its own map, and I assure you it does nearly as well".

The point of both Borges's short story and Lewis Carroll's passage is that maps are useful only when they are smaller than the city, the country or the world they represent. Ideally, a map should be small enough to fit in your pocket and contain only the information you need. A map for guiding pedestrians in a given city's old town shouldn't be obfuscated with the details of networks of gas or electricity distribution. If all you need to know about Switzerland is how to get to Lausanne from Madrid or Brussels, a very sketchy drawing of mine with one dot for Geneva (where there is the closest international airport) and one dot for Lausanne (the final destination) connected by a path representing the railway will be enough. There is no need for me to digress by accurately representing the shape of the country, its 26 cantons, its 16 (large) lakes and the whole of its railway network. Exactly the same can be said of models and scientific theories: they are most useful when they contain all the necessary details, but ignore all the rest.

The futility of complicated models and the utility of simple ones is also nicely illustrated by an old joke about a mathematician, an engineer and a physicist who are asked to calculate the volume of a cow by a farmer. The mathematician suggests to use geometry, representing the irregular shape of the cow as the union of many small regular polyhedra. "The volume of the cow", the mathematician says, "would be equal to the sum of the volumes of the regular solids, each of which can be calculated exactly". Although aesthetically pleasing, the idea is rejected by the engineer and the physicist on the grounds of it being extremely time-consuming. The engineer proposes to emulate the great Archimedes of Syracusa and submerge the cow in a pool of water. "The volume of the cow", the engineer says, "would be equal to the amount of water displaced". Although interesting, the idea is rejected by the mathematician and the physicist not only because it is impractical, but also because it could put the life of the animal in danger. Finally, when it is the physicist's turn, he unabashedly proposes to assume that the cow is a sphere with a radius r equal to half the lenght of the animal, its volume being equal to $(4/3)\pi r^3$ (the volume of a sphere, whose formula was first given by the same Archimedes of the engineer's solution).

The physicist's solution may be a gross oversimplification, but it delivers. Does the farmer *really* need to know the *exact* volume of the cow? Most likely not. He just needs a hint of what the volume would be, and that is exactly what is offered by approximating the cow by a sphere.

Spherical cows and extremely sketchy maps, though useful, obviously also open the door to oversimplification. Following the famous Einsteinian commandment, we should make models as simple as possible, but not simpler. Maybe I could add a quick drawing of the Lake Léman to the map for your travel from Geneva Airport to Lausanne, so that you know the name of the lake you will be looking at through the window. I could also add a note specifying the expected travel time: 42 minutes if you take the InterCity, 48 if you take the InterRegio.

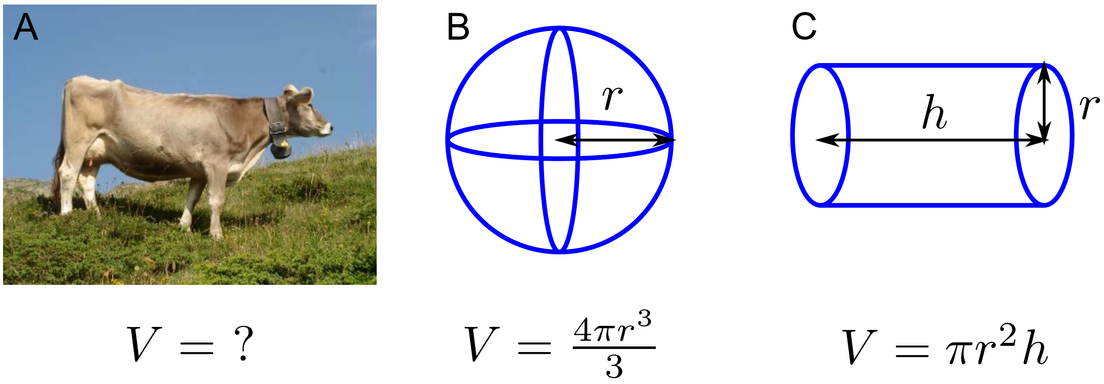

Figure 1.1: The utility of simple models. **A.** A Swiss cow. **B.** A spherical cow. **C.** A cylindrical cow.

If we wish to give an approximation for the volume of a cow, maybe we could do slightly better if instead of a sphere we think of a right regular cylinder with radius r equal to half the height of the animal and height h equal to the length of the animal. In this case, the volume of our now cylindrical cow would be equal to $\pi r^2 h$, almost certainly closer to the volume of the actual cow that the one previously approximated assuming the cow was a sphere.

This illustrates the general methodology I have used in all of the models presented in this thesis (see Fig. 1.1). Aiming to explain how cooperation evolves in a given context, I start with an existing but maybe oversimplified model (a spherical cow) and try to add a bit of more detail until I have a slightly more realistic model (a cylindrical cow). In doing so I replace some unrealistic assumptions (the cow is a sphere) by somewhat less unrealistic assumptions (the cow is a cylinder) in order to add a bit of more realism to the model, but without going all the way up to extremely complex models that become intractable or difficult to analyze (the cow is a cow). Once I have the cylindrical cow, I solve it (measure the volume of the cylinder) and compare the results with those of the original model (provided that the length of the animal is greater than its length, the volume of a cylindrical cow is always less than that of a spherical cow).

Each of the 'spherical cows' used as starting points for the models presented in the following chapters are built using one of the two following tools from the standard toolkit of evolutionary game theory: the *replicator dynamics* and the modeling framework of *games on graphs*.

The replicator dynamics, or the replicator equation, is a deterministic, nonlinear game dynamic often used in evolutionary game theory for modeling selection in the absence of mutations and in the limit of very large, well-mixed populations (Hofbauer & Sigmund, 1998; Taylor & Jonker, 1978). In its standard continuous form, the replicator dynamics is given by the system of differential equations:

$$\dot{x}_i = x_i \left[f_i(\mathbf{x}) - \phi(\mathbf{x}) \right], \tag{1.5}$$

with

$$\phi(\mathbf{x}) = \sum x_i f_i(\mathbf{x}), \tag{1.6}$$

where x_i is the proportion of players of type i, $\mathbf{x} = (x_1, \ldots, x_n)$ is a vector giving the proportion of types in the population, $f_i(\mathbf{x})$ is the average payoff to players of type i and $\phi(\mathbf{x})$ is the average *population* payoff. In the simplest case where there are only two kinds of players, equations 1.5 and 1.6 reduce to

$$\dot{x} = x(1-x)f(x), \tag{1.7}$$

where $x_1 = x$ and $f(x) = f_1(x) - f_2(x)$. This is the general form of the replicator dynamics used in chapter 3 (equation 3.1 with $\alpha = 0$), chapter 4 (equation 4.2) and chapter 6 (equation 6.1). In chapter 2, I use a *discrete* instead of a continuous form of the replicator dynamics, so that evolution unfolds in discrete time according to:

$$\Delta x = x(1-x)f(x). \tag{1.8}$$

In chapters 2, 3, 4 and 6, *modified* replicator dynamics are derived by changing the assumptions of the replicator dynamics used in standard models. I will show how the introduction of conformity (chapters 2 and 3), participation costs in games of upstream reciprocity (chapter 4) and variable group sizes in public goods games (chapter 6) automatically lead to structural changes in the resulting replicator dynamics and, thus, to different evolutionary outcomes.

One of the main implicit assumptions of the replicator dynamics as a model of social evolution is that populations are not only large but also well-mixed. This means that any individual is equally likely to interact and compete with (or socially learn from) any other individual in the population. Well-mixed populations are obviously only a first approximation to real evolving populations, that most likely possess some kind of structure so that individuals interact and/or compete with some individuals more often than with others. *Games on graphs* (Szabó & Fáth, 2007), sometimes called *evolutionary graph theory* (Lieberman et al., 2005), studies the influence of population structures represented by graphs on the evolutionary dynamics of different games. According to this approach, the individuals of a population occupy the vertices of a graph (one per vertex). The edges of the graph determine both who interacts with whom and who competes with whom. A given individual's fitness is determined by the games she plays with neighbors. Evolution by natural selection is modeled by defining an *updating rule* that prescribes how individuals change their strategies as a function of their own fitness and the fitness of their neighbors. Due to the huge number of possible configurations arising by combinatorial explosion, games on graphs are not, in general, straightforward to analyze mathematically. They are, however, well suited for computer simulations. I make use of the formal approach of games on graphs in all of the chapters of this thesis, with the exception of chapter 6, which only deals with large and well-mixed populations.

In games on graphs, different kinds of graphs (or networks) represent population structures with different structural properties. Among these, the *degree distribution*, the *characteristic path length* and the *clustering coefficient* are particularly important. The *degree distribution* is the probability distribution of the degrees of the nodes of a family of graphs, where the *degree* of a node is the number of its connections to other nodes. The *characteristic path length* is the number of edges in the shortest path between two vertices, averaged over all pairs of vertices in the graph. Finally, the *clustering coefficient* is a measure of the degree to which nodes tend to cluster together, that can be defined as the probability that any two neighbors of a given node are neighbors themselves.

In this thesis, and among all the possible network models, I make use of cycles (chapter 5), rings (chapters 3, 4, 7, and 8), square lattices (chapter 2), regular random networks (chapters 4), Erdős-Rényi random networks (chapter 8) and Barabási-Albert scale-free networks (chapters 3, 4, 7, and 8). Examples of all these different graphs are shown in Fig. 1.2.

A *cycle graph* (Fig. 1.2A) is the simplest kind of population topology. It consists of a single cycle, so that all of its vertices are connected in a closed chain and each vertex has exactly two neighbors. Due to the simplicity of this topology, some mathematical results of the evolutionary dynamics on this topology can be readily available (e.g. Ohtsuki & Nowak (2006a); van Veelen & Nowak (2012)). I make use of cycles in chapter 5 to study (mathematically) the evolutionary dynamics of upstream reciprocity in structured populations. A *ring* (of degree k) is a straightforward generalization of a cycle, in which each vertex is connected to the k nearest neighbors, with $k \geq 2$ (Fig. 1.2B). *Square lattices* are graphs whose drawings correspond to lattices, so that the vertices of the graph are the nodes of the lattice and the edges are the connections between the nodes. Two different types of square lattice are common in the literature. The *square lattice with von Neumann neighborhoods* is a square lattice with edges defined in such a way that each node has four neighbors: the nodes located at the north, east, south and west (Fig. 1.2C). In the *square lattice with Moore neighborhoods* a given node is also connected to the nodes located at the northeast, southeast, southwest and northwest positions.

Cycles, rings and square lattices are all characterized by a *regular* or *ho-*

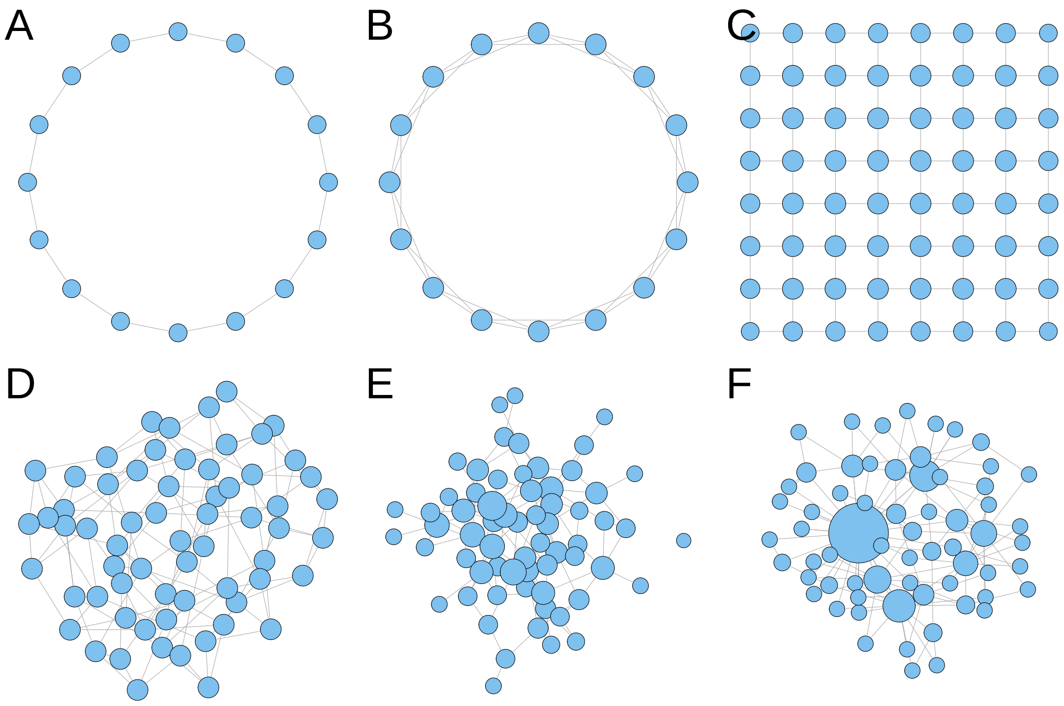

Figure 1.2: Different kinds of networks used as population structures in this thesis. **A.** Cycle. **B.** Ring. **C.** Square lattice with von Neumann neighborhoods. **D.** Regular random network. **E.** Erdős-Rényi random network. **F.** Barabási-Albert scale-free network. The size of the nodes is proportional to their degree in the networks. With the exception of the cycle all networks have an average degree of $\langle k \rangle = 4$.

mogeneous degree distribution (all vertices have the same degree), a relatively large characteristic path length and a high clustering coefficient. *Regular random networks* (Fig. 1.2D) are 'rewired' lattices characterized by a regular degree distribution but also, unlike 'ordered' lattices, by short path lengths and low clustering. *Erdős-Rényi random networks* (Fig. 1.2E) are graphs constructed by either of two related random process, first proposed by Erdős & Rényi (1959): the $G(n,p)$ model and the $G(n,m)$ model. The $G(n,p)$ model (the one used in this thesis) connects n nodes randomly so that each possible edge is included with a probability p. The degree distribution of a $G(n,p)$ is binomial, so that the probability that a given vertex v has a degree k_v equal to k is given by

$$\Pr\left(k_v = k\right) = \binom{n-1}{k} p^k (1-p)^{n-1-k},$$

where n is the number of nodes of the graph. In the limit $n \to \infty$ (with np held constant), the degree distribution is Poisson:

$$\Pr\left(k_v = k\right) = \frac{(np)^k\, e^{-np}}{k!}.$$

In addition to some heterogeneity in the degree distribution, Erdős-Rényi random networks of the $G(n,p)$ type are characterized by short path lengths and low clustering. Finally, *Barabási-Albert scale-free networks* (Fig. 1.2F), first proposed by Barabási & Albert (1999), are random networks generated by a *growing mechanism* involving *preferential attachment*, so that the more connected a node is, the more likely it will be connected to new incoming nodes during the growing procedure. The resulting networks are characterized by short path lengths, low clustering and *highly heterogeneous* degree distributions. Indeed, for networks of large size, the degree distribution follows a power law of the form

$$\Pr\left(k_v = k\right) \propto k^{-3}.$$

The use of different models of networks allows us to investigate how different structural properties of the population structure (e.g. clustering, heterogeneity in the degree distribution) affect the outcome of evolutionary games on graphs. For instance, by comparing the evolutionary dynamics on regular random networks and on square lattices with the same degree distribution, clustering has been identified as a structural property promoting the evolution of cooperation in social dilemmas modeled after the Stag Hunt game, but hindering it in the Snowdrift game (Roca et al., 2009a). Likewise, highly heterogeneous degree distributions have been shown to promote the evolution of cooperation in different social dilemmas, by comparing evolutionary games on regular random networks and on scale-free networks (Santos et al., 2006). In this thesis, and by making use of the same approach, I show that the addition of conformity to the social learning strategies of players can promote cooperation in clustered networks such as lattices and rings, but it can also significantly hinder the evolution of cooperation on scale-free networks (see chapters 2 and 3). I also show how the addition of participation costs to the payoffs of upstream reciprocity games hinder cooperation in several network topologies (see chapter 4). Chapters 7 and 8 suggest ways of extending the formal framework of games on graphs, usually defined for *symmetric two-player* games, in order to take into account *multiplayer* and *asymmetric* games as well.

The replicator dynamics and the framework of games on graphs are simple models of evolutionary processes, much as spheres are simple models of Swiss cows. The replicator dynamics, for instance, does not incorporate mutation, recombination nor genetic drift, and the population is not subdivided into demes of finite size linked by migration events, as in more elaborated models used in population genetics (Ewens, 2004). Networks used in models of games of graphs are usually static, while most real populations are dynamic, with links being deleted and created and nodes leaving and joining the population. The particular network models used in this thesis (see Fig. 1.2) are also far simpler than even static representations of real social networks, which are not single nor scale-free, but broad scale, exhibiting modularity, high clustering and important correlations (Newman, 2010). Despite these limitations (but maybe also *because* of these limitations) the replicator dynamics and the formalism of games of graphs, together with the modified versions of these models (our cylindrical cows) help us understand the complex phenomena they aim to model, sharpening our intuition about the way natural selection acts on evolving populations.

1.5 Outline of the thesis

The organization of the remainder of this thesis is as follows. In part I (comprising chapters 2 and 3) I start off by studying the effects of conformity in the evolutionary dynamics of different social dilemmas both in well-mixed and network-structured populations. I show that while conformity promotes cooperation in regular networks, it can greatly hinder it in scale-free newtorks (otherwise great amplifiers of cooperation). In part II (chapters 4 and 5) I deal with the relative merits of upstream reciprocity as a secondary mechanism for the evolution of cooperation. In chapter 4, I challenge the assumptions of a model by Nowak & Roch (2007) and show how the addition of participation costs can hinder the evolution of cooperation by upstream reciprocity. Then, in chapter 5, I construct a different model of upstream reciprocity, based on less restrictive assumptions, and show how upstream reciprocity is never stable against both unconditional cooperation and unconditional defection, even in the case of a population structured as a cycle. Part III studies social diversity in public goods games (chapters 6 and 7) and the asymmetric Donation game (chapter 8). In these chapters I show that social diversity at different levels can greatly affect the evolutionary dynamics, sometimes favoring and sometimes hindering the evolution of cooperation. Finally, chapter 9 draws some general conclusions.

Part I

Conformity

> When I am at Rome, I fast on a Saturday; when I am at Milan, I do not. Follow the custom of the church where you are.
>
> St. Ambrose

The advice given by Aurelius Ambrosius (better known as St. Ambrose) to Aurelius Augustinus Hipponensis (St. Augustine) has remained in English as the saying ‘when in Rome, do as Romans do’. Other languages use exactly the same formula[10] or have a related saying[11] meaning ‘conform to what others do’. Conformity is the idea that humans show a disproportionated tendency to imitate common behaviors, specially when they are uncertain about what is the best behavioral choice. Boyd & Richerson (1985) and co-workers (e.g. Henrich & McElreath (2003)) have argued that conformity is a particularly important component of our social learning psychology, a heuristic for efficiently acquiring locally adaptive behaviors. Conformity also plays an important role in some models of the evolution of cooperation. If sufficiently strong, conformity can stabilize any behavior and thus be conducive to generate multiple stable equilibria in a population subdivided in demes, favoring the evolution of cooperation by cultural group selection (Boyd et al., 2011; Boyd & Richerson, 1985, 2009, 2010); see, however, Lehmann et al. (2008). Conformity has also been proposed as a solution for the problem of the second order free rider problem in models of altruistic punishment (Henrich & Boyd, 2001).

One standard interpretation of models of games on graphs is that they are models of cultural evolution taking place in human network-structured populations (Ohtsuki et al., 2006; Szabó & Fáth, 2007). Despite this interpretation, and to the best of my knowledge, no model has explored the effects of adding a conformist bias in the social learning strategies of the individuals. The first part of this thesis attempts to fill this gap. Chapter 2 focuses on the evolution of cooperation under three games representing social dilemmas (the prisoner’s dilemma, the snowdrift game and the stag hunt) when the population structure is given by square lattices. The model considers individuals that imitate not only according to a payoff-based bias (the usual assumption in evolutionary models) but also according to a conformist bias, so that locally common behaviors are, *ceteris paribus*, more likely to be imitated. For comparison purposes, large populations devoid of population structure, i.e. infinite well-mixed populations, are also studied. In this case the addition of conformity is found to lead to a standard replicator dynamics with a transformed payoff matrix. Chapter 3 is an extension of the study presented in chapter 2. Other network topologies, particularly scale-free networks, are considered as population structures. An analytical

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[10] French: ‘à Rome, fais comme les Romains’; Portuguese: ‘quando en Roma, faça como os Romanos’; Hungarian: ‘ha Rómában élsz, élj úgy, mint a rómaiak’.

[11] Spanish: ‘allí donde fueres, haz lo que vieres’; Italian: ‘paese che vai, usanza che trovi’.

solution of the model given by the method of pair approximation is also presented. Overall, the obtained results indicate that conformity can promote or hinder the evolution of cooperation, depending on the type of social dilemma and network topology under consideration. Particularly, scale-free networks are not the strong amplifiers of cooperation suggested by some studies [e.g. Santos & Pacheco (2005, 2006)] when individuals imitate according to partially conformist social learning.

Chapter 2

Conformist transmission and the evolution of cooperation[†]

Abstract

We study the effects of conformist transmission on the evolutionary dynamics of the Prisoner's Dilemma, the Snowdrift and the Stag Hunt games in both well-mixed and spatially structured populations. The addition of conformism introduces a transformation of the payoff matrix that favours the stability of pure equilibria and reduces the basin of attraction of risk dominant equilibria. When both conformism and local interactions are present, the system can exhibit higher levels of cooperation than those obtained in the absence of either of the two mechanisms.

2.1 Introduction and related work

Evolutionary game theory (Gintis, 2000; Hofbauer & Sigmund, 1998) is the theory of evolutionary dynamics when selection is frequency-dependent, i.e. when the success of an individual is conditioned not only by the strategy he or she follows but also by the strategies followed by other individuals in the population. Although originally developed as an application of game theory to the study of genetic evolution (Maynard Smith, 1982), evolutionary game theory has also been used to investigate cultural evolutionary processes, that is the way ideas or beliefs spread through a population of individuals capable of imitation.

In *cultural* evolutionary game-theoretic models, ideas are transmitted via bi-

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[†] J. Peña. In S. Bullock, J. Noble, R. W. and Bedau, M. A. (eds), *Artificial Life XI: Proceedings of the Eleventh International Conference on the Simulation and Synthesis of Living Systems, MIT Press* pp. 458-465 (MIT Press, Cambridge, MA, 2008).

ased imitation. Most of these models posit that the only important psychological bias underlying imitation is *prestige* or *payoff-based bias*, defined as the predisposition to imitate successful individuals. Assuming a very large and well-mixed population, payoff-based biased transmission can be shown to generate a famous differential equation, named the *replicator dynamics* (Gintis, 2000; Taylor & Jonker, 1978). In the context of evolutionary game theory, the equilibrium points and other characteristics of the dynamics of different games are studied in order to better understand the evolutionary processes involved.

The Prisoner's Dilemma (PD), Snowdrift[1] (SD) and the Stag Hunt (SH) are among the most studied two-person, symmetric games in the literature. They are used for investigating under which circumstances altruistic traits can become fixed in a population of "selfish" individuals. In social dilemmas of cooperation, individuals' behaviours are of two types: cooperative and non-cooperative. Cooperators are willing to engage in cooperative tasks, while non-cooperators (usually called *defectors*) prefer not to. The success resulting from the interaction of cooperators and defectors is given by the payoff matrix:

$$\begin{array}{c|cc} & C & D \\ \hline C & R & S \\ D & T & P \end{array}$$

where C denotes cooperators and D denotes defectors. R is the *reward* for mutual cooperation, P is the *punishment* for mutual defection, T is the *temptation* to defect and S is the *sucker's payoff*.

In all three social dilemmas, mutual cooperation is favoured over both mutual defection ($R > P$) and an equal probability of unilateral cooperation and defection ($2R > T + S$). The three dilemmas however differ in their ordering of payoffs. In the PD, $T > R > P > S$; in SD, $T > R > S > P$, and in the SH, $R > T > P > S$.

The evolution of cooperation can be studied by looking at the stable equilibria of the replicator dynamics for each of these games. In the PD, the only stable equilibrium occurs when the population is entirely comprised of defectors. In the SD game cooperators and defectors coexist in equilibrium. In the SH there are two equilibria: when all individuals cooperate and when all individuals defect. This last equilibrium is however risk dominant, i.e. it has the largest basin of attraction.

The replicator dynamics is a rough approximation of actual cultural evolutionary dynamics as it assumes that populations are very large and well-mixed, and that payoff-based bias is the sole psychological mechanism guiding cultural transmission processes. More realistic models of cultural evolutionary processes

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[1] Also known as Hawks-Doves or Chicken.

correct at least one of these assumptions and arrive at different results from those predicted by the standard replicator dynamics.

Evolutionary graph-theoretical models (Lieberman et al., 2005; Szabó & Fáth, 2007), for instance, go beyond the assumption of large, well-mixed populations by restricting interaction and imitation to near neighbours in a graph representing spatial locality or a social network. In many cases, this graph structure has been shown to promote cooperation beyond the limits of the replicator dynamics in a well-mixed population (Nowak et al., 1994; Nowak & May, 1992; Santos & Pacheco, 2005; Skyrms, 2004).

Other researchers have augmented cultural evolution models by including different psychological biases that, together with payoff-based bias, could influence the way people imitate. In particular, *conformism* or *conformist bias* (Boyd & Richerson, 1985), which is the propensity for preferentially imitating common behaviours, has been suggested to be an important component of our social learning psychology[2] (Asch, 1951; Coultas, 2004). When conformist transmission is introduced in cultural evolution models, the result (in the case of large, well-mixed populations) is a *modified* replicator dynamics that can lead to different equilibrium points and different dynamics from those predicted by the standard replicator dynamics (Henrich, 2001; Skyrms, 2005). By making use of such equation, Henrich & Boyd (2001) have shown how even limited levels of conformism are able to stabilise cooperative behaviour in a public goods game if punishment is also included in the model. In related work, Skyrms (2005) has explored the effect of conformist bias in a number of symmetric two-by-two games. Analyses in that work were however restricted to some specific numerical cases and no general conclusions were formally drawn.

The aim of this paper is to study the effects of conformist transmission on the evolution of cooperation when considering two-person symmetric games such as the PD, SD and the SH. We propose an evolutionary graph-theoretical model in which cultural transmission is guided by both payoff-based and conformist biases, and study it both analytically and by means of simulation.

The paper is organised as follows. The next section gives the agent-based level specifications of the model. It is then shown how to recover the modified replicator dynamics in the limiting case of a large and well-mixed population, and the equation is studied by means of equilibrium analysis. This is followed by a simulation study of the particular case of a population organised into a regular 2D lattice. Finally, conclusions are drawn.

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[2] From an evolutionary psychology perspective, conformist bias could have evolved because it is adaptive in the face of costly information. Boyd & Richerson (1985) and Henrich & Boyd (1998) have theoretically shown that conformist transmission is adaptive in spatially and/or temporally varying habitats since it provides a simple heuristic rule that increases the probability of acquiring locally adaptive beliefs and behaviours.

2.2 The model

Our model considers a population of n individuals, where the i-th individual is represented by the vertex v_i of an undirected graph $G(V, E)$ with $v_i \in V \; \forall i$. The open neighbourhood of i, $N(i)$, is the set of all individuals j such that there is an edge $e_{ij} \in E$. The number of neighbours of individual i is thus the degree k_i of vertex v_i. The closed neighbourhood $N[i]$ is the set of i's neighbours plus i itself.

Each individual is characterised by its *cultural trait* or *strategy* $s_i \in \{A, B\}$. Social interaction is modelled by means of a two-person, symmetric game with a payoff matrix M given by[3]:

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

Each time step t, individuals simultaneously engage in social interactions. As a result of these interactions, individual i collects an *average payoff* given by:

$$u_i(t) = \frac{1}{k_i} \sum_{j \in N(i)} M\left(s_i(t), s_j(t)\right).$$

After interactions are completed, individual i randomly chooses one of its neighbours $j \in N(i)$ as its *model* for cultural transmission. Imitation is assumed to be conformist-biased with probability α and payoff-biased with probability $1 - \alpha$. Parameter α thus weighs the importance of conformism relative to payoff-biased transmission.

The adoption of individual j's strategy by the focal individual i depends on j's *cultural fitness* w_{ij}. Cultural fitness (the direct analogue to biological fitness in genetic evolution) is a measure of the attractiveness or the transmissibility of a model's strategy. If transmission is payoff-biased, j's cultural fitness is given by the difference of average payoffs between j and i:

$$w_{ij}(t) = u_j(t) - u_i(t).$$

If transmission is conformist, j's cultural fitness is given by

$$w_{ij}(t) = q_{ij}(t) - \frac{1}{2},$$

where q_{ij} is the proportion of agents in $N[i]$ having the same strategy as j. Notice that w_{ij} is positive whenever $u_j > u_i$ (payoff-biased transmission) or j follows the strategy followed by the majority of i's neighbours (conformist transmission).

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[3] Without loss of generality, payoffs are assumed to be non-negative values.

Agent i copies j's strategy with a probability proportional to w_{ij}. Formally:

$$\Pr\left(s_i(t+1) = s_j(t)\right) = f\left(w_{ij}\right),$$

where f is assumed to be a monotonically increasing function, in order for models with high cultural fitness to propagate their strategies more often than models with low cultural fitness. Three alternative definitions of f are considered in this paper, each one specifying a different imitation rule: (i) imitate-if-better (IIB); (ii) replicator dynamics 1 (RD1); and (iii) replicator dynamics 2 (RD2)[4].

The IIB rule is given by:

$$f_{IIB}(w_{ij}) = \begin{cases} 0 & \text{if } w_{ij} \leq 0 \\ 1 & \text{if } w_{ij} > 0 \end{cases},$$

whereas RD1 and RD2 are respectively defined by:

$$f_{RD1}(w_{ij}) = \begin{cases} 0 & \text{if } w_{ij} \leq 0 \\ \beta w_{ij} & \text{if } w_{ij} > 0 \end{cases},$$

and

$$f_{RD2}(w_{ij}) = \frac{1}{2}\left(1 + \beta w_{ij}\right).$$

Parameter β normalises w_{ij} such that $0 \leq \Pr\left(s_i(t+1) = s_j(t)\right) \leq 1$. Thus, $\beta = 2$ in the case of conformist transmission and

$$\beta = \frac{1}{\max\left\{a,b,c,d\right\} - \min\left\{a,b,c,d\right\}} \tag{2.1}$$

in the case of payoff-biased transmission. Fig. 2.1 depicts f for each imitation rule.

The three imitation rules described above have been traditionally used in the literature, either directly in evolutionary graph-theoretical models (e.g. RD1 by Hauert & Doebeli (2004) and Santos & Pacheco (2005)) or in order to derive population-level analytical models (e.g. RD2 by Henrich (2001) and Boyd & Richerson (2002)).

From the previous definitions it is possible to derive $\Pr\left(s_i(t+1) = A\right)$, which is the probability of individual i following strategy A at time step $t+1$ after having chosen a neighbour j as a model. Individual i's strategy will become or remain A whenever: i) A is the current strategy of both i and j ; ii) i's current strategy is A, j's current strategy is B, but i does not imitate j; or iii) i's current strategy is B, j's current strategy is A, and i imitates j.

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[4] We give RD1 and RD2 these names because both imitation rules can be shown to recover the replicator dynamics in the well-mixed, 100% payoff-biased transmission case (Gintis, 2000; McElreath & Boyd, 2007).

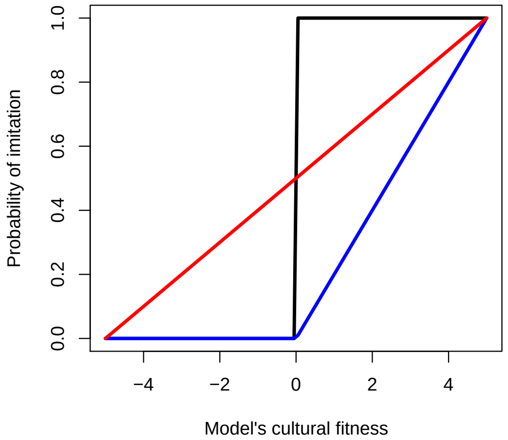

Figure 2.1: Imitation rules. IIB is shown in *black*, RD1 ($\beta = 0.2$) in *blue* and RD2 ($\beta = 0.2$) in *red*.

The formal equation is given by

$$\begin{aligned}\Pr\left(s_i(t+1)=A\right) = {} & \Pr\left(s_i(t)=A, s_j(t)=A\right) \\ & + \Pr\left(s_i(t)=A, s_j(t)=B\right)\times \\ & \left\{(1-\alpha)\left[1-f\left(u_j(t)-u_i(t)\right)\right]+\alpha\left[1-f\left(q_{ij}(t)-\frac{1}{2}\right)\right]\right\} \\ & + \Pr\left(s_i(t)=B, s_j(t)=A\right)\times \\ & \left\{(1-\alpha)\left[f\left(u_j(t)-u_i(t)\right)\right]+\alpha\left[f\left(q_{ij}(t)-\frac{1}{2}\right)\right]\right\}. \end{aligned} \tag{2.2}$$

2.3 Exact analysis for the case of large, well-mixed populations

2.3.1 General games

Here we analyse the limiting case of a complete graph with large n, which is equivalent to having the large, well-mixed population that is traditionally assumed in standard evolutionary game theory.

Let p_t denote the frequency of individuals with strategy A at time step t. For a complete graph with $n \to \infty$, $k_i = n - 1 \approx n \; \forall i$, and

$$u_i(t) = \begin{cases} u_A(t) & \text{if } s_i(t) = A \\ u_B(t) & \text{if } s_i(t) = B \end{cases}$$

$\forall i$, where $u_A(t)$ and $u_B(t)$ are the average payoffs collected by individuals with strategies A and B at time step t, respectively given by

$$u_A(t) = ap_t + b(1 - p_t), \tag{2.3}$$

and

$$u_B(t) = cp_t + d(1 - p_t). \tag{2.4}$$

Additionally, since $N[i] = V \; \forall i$:

$$q_{i,j}(t) = \begin{cases} p_t & \text{if } s_j(t) = A \\ 1 - p_t & \text{if } s_j(t) = B \end{cases} \quad \forall i, j.$$

Using these relations and RD2 as imitation rule, Eq. 2.2 can be shown to reduce to

$$\begin{aligned} \Delta p \;=\; & p_t(1 - p_t)\{(1 - \alpha)\beta \left[u_A(t) - u_B(t)\right] \\ & + \alpha(2p_t - 1)\}, \end{aligned} \tag{2.5}$$

where $\Delta p = p_{t+1} - p_t$ is the change in the proportion of individuals with behaviour A between time steps t and $t+1$. The recursion of Eq. 2.5 is a modified replicator dynamics that had been already derived in related work on cultural transmission processes including both payoff-biased and conformist imitation (Carpenter, 2004; Henrich, 2001; Henrich & Boyd, 2001; Skyrms, 2005).

Let us first analyse the particular case when cultural transmission is payoff-biased only. Making $\alpha = 0$, Eq. 2.5 reduces to:

$$\Delta p = p_t(1 - p_t)\beta \left\{u_A(t) - u_B(t)\right\},$$

which is the discrete-time equivalent of the standard replicator dynamics (Gintis, 2000; Hofbauer & Sigmund, 1998; Taylor & Jonker, 1978). Substituting Eq. 2.3 and 2.4 in the last expression and doing little algebra:

$$\Delta p = p_t(1 - p_t)\beta \left\{(a - b - c + d)p_t + b - d\right\}. \tag{2.6}$$

Equilibria of this equation can be found by looking at the values of p_t that make $\Delta p = 0$. The two *pure equilibria* are given by $p_t = 0$ and $p_t = 1$. In the following, these equilibria will be respectively called all-B and all-A. A third *internal equilibrium*, in which players with strategies A and B are present in the population, may exist. When this is the case, the proportion of individuals with strategy A in equilibrium is given by

$$p^* = \frac{d-b}{(a-c)+(d-b)}.$$

In general, the equilibrium p is stable[5] whenever

$$\left| \left. \frac{dp_{t+1}}{dp_t} \right|_{p_t=p} \right| < 1.$$

From this, it can be easily shown that

- all-B is stable when $b < d$,
- all-A is stable when $a > c$, and
- p^* is stable when both $a < c$ and $b > d$.

Depending on the ranking of the entries of the payoff matrix, four different possibilities[6] for the imitation dynamics can thus be distinguished (Nowak, 2006b):

1. $a > c \wedge b > d$: only all-A is stable (A *dominates* B).
2. $a < c \wedge b < d$: only all-B is stable (B *dominates* A).
3. $a > c \wedge b < d$: both all-A and all-B are stable (A and B are *bistable*). In this case, the internal unstable equilibrium p^* determines the sizes of the basins of attraction of the two pure equilibria. The equilibrium with the largest basin of attraction is called *risk dominant.* In particular
    (a) all-A is risk dominant if $d - b < a - c$, and
    (b) all-B is risk dominant if $d - b > a - c$.
4. $a < c \wedge b > d$: pure equilibria are unstable and the internal equilibrium is stable (A and B *coexist*).

How this picture changes when cultural transmission has also a conformist component ($\alpha > 0$)? In order to answer to this question, an equilibrium analysis

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[5] The condition is necessary and sufficient for hyperbolic equilibria only. All-B (resp. all-A) is non-hyperbolic when $b = d$ (resp. $a = c$).

[6] Actually, there is a fifth possibiity: A and B are neutral when $a = c$ and $b = d$. In this case there is no evolution since $\Delta p = 0$ $\forall p_t$.

similar to the one done in the case $\alpha = 0$ can be performed here for $\alpha \neq 0$. A second possibility is to rewrite Eq. 2.5 as

$$\begin{aligned}\Delta p &= p_t(1-p_t)\{[(1-\alpha)\beta(a-b-c+d)+2\alpha]\,p_t \\ &\quad +(1-\alpha)\beta(b-d)-\alpha\},\end{aligned}$$

and perform the following variable substitutions

$$\begin{aligned} a' &= (1-\alpha)\beta a + \alpha, \\ b' &= (1-\alpha)\beta b, \\ c' &= (1-\alpha)\beta c, \\ d' &= (1-\alpha)\beta d + \alpha, \end{aligned}$$

to obtain

$$\Delta p = p_t(1-p_t)\left\{(a'-b'-c'+d')p_t + b' - d'\right\}. \tag{2.7}$$

Notice (see Eq. 2.6) that this recursion is equivalent to the discrete replicator dynamics of a population game with the following payoff matrix M'

	A	B
A	a'	b'
B	c'	d'

Hence, in the framework of the replicator dynamics, *the addition of conformism to the cultural evolutionary process is equivalent to a transformation of the payoff matrix of the underlying game.* Observe that $\alpha = 0$ recovers the original game and $\alpha = 1$ completely transforms the original game into a pure coordination game with the following payoff matrix

	A	B
A	1	0
B	0	1

The addition of conformism to imitation dynamics can have considerable effects in the nature of equilibria of the modelled cultural evolutionary process (Boyd & Richerson, 1985; Henrich, 2001; Henrich & Boyd, 2001; Skyrms, 2005). In particular, since the entries of M are non-negative and $0 \leq \alpha \leq 1$,

$$\begin{gathered} a < c \nRightarrow a' < c' \\ b > d \nRightarrow b' > d', \end{gathered}$$

which means that i) originally unstable pure equilibria could become stable and ii) an originally stable internal equilibrium could become unstable. Furthermore, if A and B coexist, the proportion of individuals with strategy A in equilibrium is now given by

$$p'^{*} = \frac{(1-\alpha)\beta(d-b)+\alpha}{(1-\alpha)\beta\left\{(a-c)+(d-b)\right\}+2\alpha}.$$

Not everything changes in the dynamics of the game when conformism is introduced. In particular,

$$\begin{aligned} a > c &\Rightarrow a' > c', \\ b < d &\Rightarrow b' < d', \end{aligned}$$

which means that originally stable pure equilibria will continue to be stable in the transformed game. Moreover,

$$\begin{aligned} d-b < a-c &\Rightarrow d'-b' < a'-c', \\ d-b > a-c &\Rightarrow d'-b' > a'-c', \end{aligned}$$

which means that, if A and B are bistable, the risk dominant equilibrium of the transformed game will be the same as the one of the original game.

The new conditions for stability are

1. All-B is stable if
$$\alpha > \frac{\beta(b-d)}{1+\beta(b-d)} \tag{2.8}$$
2. All-A is stable if
$$\alpha > \frac{\beta(c-a)}{1+\beta(c-a)} \tag{2.9}$$
3. The internal equilibrium, when it exists, is stable if neither Eq. 2.8 nor Eq. 2.9 holds.

2.3.2 Social dilemmas

Let us now focus on the effect of conformist biases in games reflecting social dilemmas, such as the PD, SD and the SH. In order to simplify the analysis for these games, it is customary to rescale their payoff matrices so that they depend on a single parameter. For the PD, we follow Nowak & May (1992) and make $T = b$, $R = 1$, $P = \epsilon \approx 0$ and $S = 0$, where $1 < b < 2$ characterises the advantage of defectors against cooperators. For the SD game, we follow Hauert & Doebeli (2004) and make $T = \gamma > 1$, $R = \gamma - 1/2$, $S = \gamma - 1$ and $P = 0$, such that the cost-to-benefit ratio of mutual cooperation is given by $r = 1/(2\gamma - 1)$, with $0 \leq r \leq 1$. For the SH we make $T = P = 1$, $R = g$ and $S = 0$, with $1 < g < 2$.

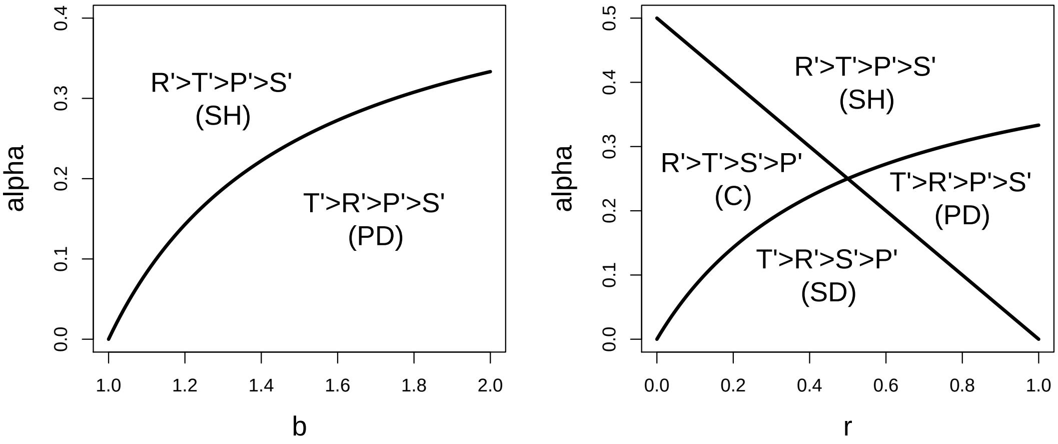

Figure 2.2: Effect of conformist bias in the PD (*left*) and the SD game (*right*).

With these settings, $\beta = 1/b$ for the PD, $\beta = 1/\gamma$ for SD and $\beta = 1/g$ for the SH in the case of payoff-based biased imitation (see Eq. 2.1).

As it has been previously analysed, the effect of conformist transmission may be interpreted as a transformation in the payoff matrix that can alter the original ordering of its entries. This in turn can drastically change the nature of the game played. In the PD with conformism, the all-C equilibrium (unstable in the original game) can become stable if $R' > T'$. This holds when

$$\alpha > \frac{b-1}{2b-1}.$$

The resulting ordering of the payoffs ($R' > T' > P' > S'$), and the fact that all-D is always the risk-dominant equilibrium, effectively converts the game into a SH (see Fig. 2.2).

In the case of the SD game, the ordering of the entries of the transformed payoff matrix M' can be different from that of the original matrix M if $R' > T'$ (all-C becomes stable), $P' > S'$ (all-D becomes stable) or both conditions hold. For the rescaled version of this game, $R' > T'$ whenever

$$\alpha > \frac{r}{1+2r},$$

and $P' > S'$ when

$$\alpha > \frac{1-r}{2}.$$

There are thus 4 different possibilities for the SD game with conformist transmission (see Fig. 2.2):

1. $T' > R' > S' > P'$ (the game is still a SD),
2. $R' > T' > S' > P'$ (C dominates D),
3. $T' > R' > P' > S'$ (the game becomes a PD), and
4. $R' > T' > P' > S'$ (the game becomes a SH). In this last case the game is a proper SH (C and D are bistable and all-D is the risk-dominant equilibrium) when $r > 0.5$. When $r < 0.5$, all-C is both payoff and risk dominant.

Finally, in the case of the SH the ordering of the payoffs is not importantly affected, but the unstable equilibrium moves towards $p = 1/2$, thus reducing the basin of attraction of all-D, i.e. the riskiness of all-C.

Broadly speaking, conformist transmission can promote cooperation in the PD by turning it into a SH, and in the SH by diminishing the basin of attraction of all-D. In the SD game, results are dependent on the cost-to-benefit ratio of mutual cooperation. For $r < 0.5$, cooperation is generally favoured: all-C can become the only stable equilibrium (when $R' > T' > S' > P'$), or the risk dominant equilibrium (when $R' > T' > P' > S'$). For $r > 0.5$ the opposite happens, with all-D possibly becoming the only stable equilibrium (when $T' > R' > P' > S'$) or the risk-dominant equilibrium (when $R' > T' > P' > S'$).

Although conformist transmission opens the possibility of a cooperative equilibrium in the PD and diminishes the riskiness of engaging in cooperative actions in the SH, populations with an initial majority of defectors are always doomed to a non-cooperative equilibrium in these two games. In the SD case, defection prevails for $r > 0.5$, and this for any amount of conformism. In this sense, conformist transmission alone is unable to sustain cooperation in both PD and SH, and it promotes cooperation for the SD game only when $r < 0.5$. For cooperation to be sustained, other mechanisms are necessary to be present along with conformism. Punishment has been suggested as one such possible mechanism (Henrich & Boyd, 2001). In the next section, we explore another mechanism: graph reciprocity.

2.4 Simulation results for the case of medium-sized, spatially structured populations

Here, the evolutionary dynamics of the three social dilemmas discussed above are studied by means of computer simulations for the case of medium-sized populations (1024 individuals) organised into a 32 × 32 square lattice with periodic boundary conditions. For the three games, the rescaled versions presented in the last section were used[7].

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[7] We effectively set $P = \epsilon = 0$ in the PD.

Square lattices were implemented using both Moore and von Neumann neighbourhoods with ranges equal to 1. Simulations were conducted using each of the three imitation rules previously defined (IIB, RD1, RD2), varying values of the game parameters (b in the PD, r in SD and g in the SH) and different amounts of conformism ($\alpha \in \{0.0, 0.125, 0.25, 0.375, 0.5\}$). Agents were updated synchronously.

For each simulated condition, 50 runs were executed. Each simulation was initialised with 50% cooperators and terminated whenever the population converged to any of the two absorbing states (all-C, all-D) or after 3000 simulation steps. In this last case, the equilibrium proportions of cooperators were calculated by averaging over the last 1000 time steps of each run, well after transients have passed.

Fig. 2.3 shows the average level of cooperation in equilibrium for the Moore neighbourhood case. Results for the von Neumann neighbourhood case are qualitatively similar and are not reproduced here for reasons of space. In the figures corresponding to the SD game, the dashed lines represent the equilibrium fraction of cooperators predicted by Eq. 2.7 (the well-mixed case).

Fig. 2.3 shows how cultural transmission including a conformist component consistently promotes higher levels of cooperation than payoff-based biased transmission alone for both the PD and the SH. Moreover, the larger the amount of conformism, the larger the proportion of cooperators at equilibrium, as it can be seen from the nice ordering of the curves for different values of α. For the SD game, the addition of conformist bias results in higher frequencies of cooperators for small r but also in lower frequencies of cooperators for large r. Thus, the general observations made for the effects of conformist transmission on the well-mixed case continue to hold for the case of spatially structured populations, i.e. that conformism promotes cooperation in the PD and the SH for the whole range of their game parameters, and that it promotes cooperation in the SD game for $r < 0.5$ while inhibiting cooperation for $r > 0.5$.

Regarding the effects of embedding the population in a lattice, our results confirm those already classic in evolutionary game theory: spatial structure promotes cooperation in the PD (Nowak et al., 1994; Nowak & May, 1992) and the SH (Skyrms, 2004), but can inhibit cooperation in the SD game (Hauert & Doebeli, 2004). In general, for the SD game, cooperators in a lattice do better than their counterparts in a well-mixed population for i) $\alpha < 0.25$ and small r, and ii) $\alpha > 0.25$ and large r.

Notice that these qualitative results do not depend on the specific imitation rule being used. However, quantitative results do depend on the specificities of these rules. For instance, the higher stochasticity of the RD2 with respect to the other two imitation rules seems to hinder the evolution of cooperation in the PD and SH games, where only moderate levels of cooperation can be sustained, and

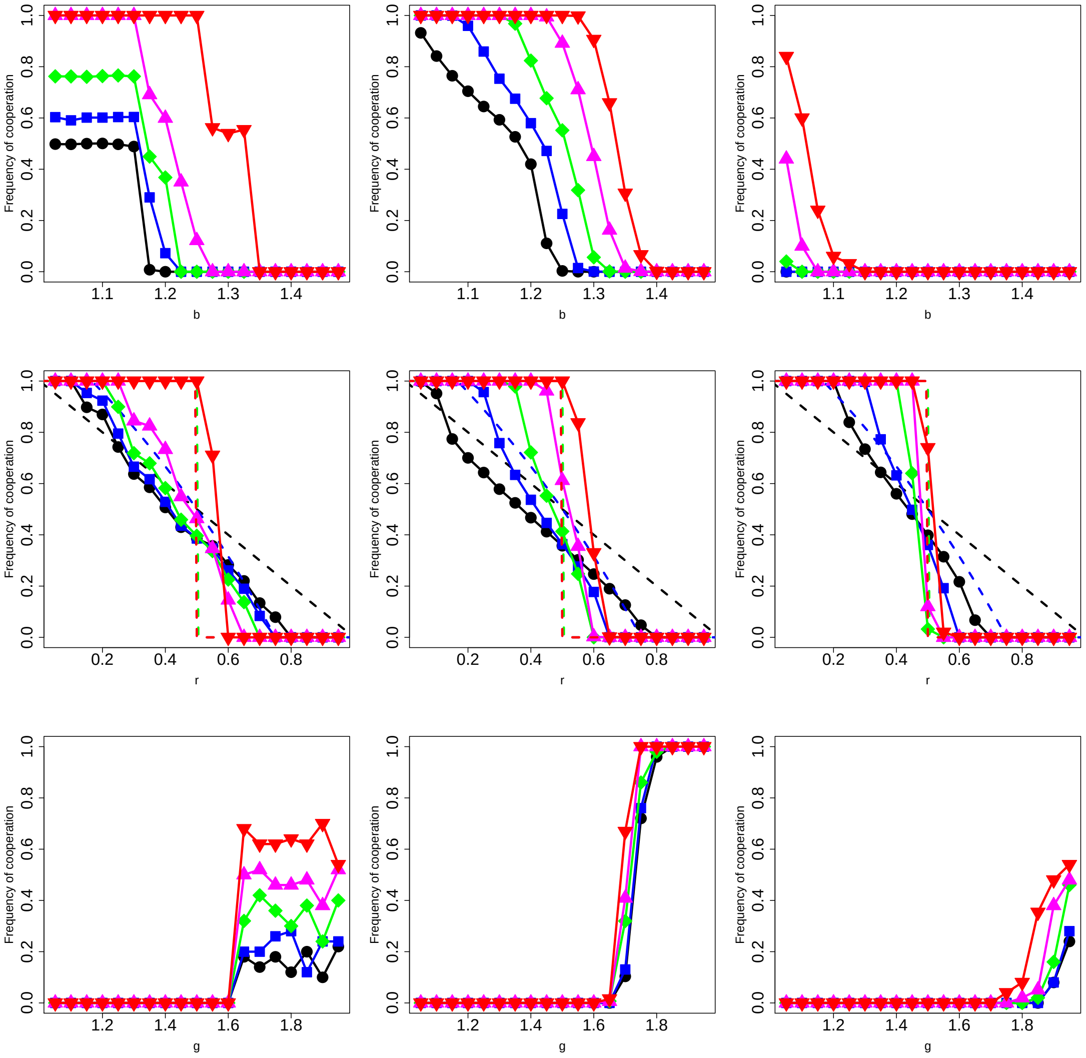

Figure 2.3: Average values of the equilibrium proportion of cooperators as a function of the game parameter for the PD (*first row*), the SD game (*second row*) and the SH (*third row*). Results are given for IIB (*first column*), RD1 (*second column*) and RD2 (*third column*) imitation rules and different amounts of conformism: $\alpha = 0.0$ (*black*), $\alpha = 0.125$ (*blue*), $\alpha = 0.25$ (*green*), $\alpha = 0.375$ (*magenta*) and $\alpha = 0.5$ (*red*). For the SD game, the corresponding proportions of cooperators in well-mixed populations for each value α are also reported (*dashed lines*).

only for very small b or very large g.

2.5 Conclusions

We have augmented traditional evolutionary graph-theoretic models with conformist transmission (the tendency to imitate common behaviours) and studied the effects of this extension on the evolutionary dynamics of social dilemmas. From a replicator dynamics perspective, the addition of conformism is equivalent to a simple transformation of the payoff matrix favouring the stability of pure equilibria. In particular, a Prisoner's Dilemma can become a Stag Hunt, and a Snowdrift can become a Stag Hunt, a Prisoner's Dilemma or a game in which cooperation dominates defection. In the Stag Hunt case, where both pure equilibria are already stable, conformist transmission moves the unstable equilibrium towards $p = 1/2$, thus reducing the basin of attraction of the non-cooperative equilibrium. Although unable to sustain cooperation by its own when cooperators are not the majority at the beginning of the evolutionary process, conformist transmission enhances cooperation when other mechanisms, such as spatial locality, are also present in the model, at least for the PD and the SH cases. For the spatial SD, conformism can also be shown to promote higher levels of cooperative behaviour, but only for small cost-to-benefit ratios.

Acknowledgements

This work is funded by the Future and Emerging Technologies programme IST-STREP of the European Community, under grant number IST-034632 (*PERPLEXUS*). The author would like to thank Isis Fuchs, Olivier Jorand, Andrés Pérez-Uribe and Henri Volken for valuable discussions, and the three anonymous reviewers for their comments on this paper.

Chapter 3

Conformity hinders the evolution of cooperation on scale-free networks[†]

Abstract

We study the effects of conformity, the tendency of humans to imitate locally common behaviors, in the evolution of cooperation when individuals occupy the vertices of a graph and engage in the one-shot Prisoner's Dilemma or the Snowdrift game with their neighbors. Two different graphs are studied: rings (one-dimensional lattices with cyclic boundary conditions) and scale-free networks of the Barabási-Albert type. The proposed evolutionary-graph model is studied both by means of Monte Carlo simulations and an extended pair-approximation technique. We find improved levels of cooperation when evolution is carried on rings and individuals imitate according to both the traditional pay-off bias and a conformist bias. More important, we show that scale-free networks are no longer powerful amplifiers of cooperation when fair amounts of conformity are introduced in the imitation rules of the players. Such weakening of the cooperation-promoting abilities of scale-free networks is the result of a less biased flow of information in scale-free topologies, making hubs more susceptible of being influenced by less-connected neighbors.

3.1 Introduction

Understanding the emergence and stability of cooperation is a central problem in many fields of both natural and social sciences. Researchers have tradition-

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[†] J. Peña, H. Volken, E. Pestelacci and M. Tomassini. *Phys. Rev. E* **80**, 016110 (2009).

ally adopted evolutionary game theory (Weibull, 1995) as common formal framework for studying the dynamics of strategy change, and games like the Prisoner's Dilemma (PD) and the Snowdrift Game (SG) as metaphors for the tension between group welfare and individual selfishness. The PD and the SG (also known as Chicken or Hawks-Doves) are two-person, symmetric games in which a given player can be, at each time step, either a Cooperator (C) or a Defector (D). Cs are willing to engage in cooperative tasks, while Ds prefer not to, thus exploiting Cs. If two individuals of the same type interact, they both get the reward for mutual cooperation R if they cooperate or the punishment for mutual defection P if they defect. If a D and a C interact, the D receives the temptation to defect T and the C receives the sucker's pay-off S. In the PD, the pay-offs are ordered such that $T > R > P > S$ with $2R > T + S$. Since $T > R$ and $P > S$, the only Nash equilibrium of the game is the pure strategy (D,D). In this case, the dilemma is caused both by "greed" (or the temptation to cheat) and "fear" that the other player cheats. In the SG, the order of P and S is reversed, yielding $T > R > S > P$. Thus, when both players defect they get the lowest possible pay-off. The pairs of pure strategies (C,D) and (D,C) are Nash equilibria of the game. There is also a third equilibrium in mixed strategies in which strategy D is played with probability p and strategy C with probability $1 - p$, where p depends on the actual pay-off values. The dilemma in this game is caused only by "greed", i.e. players have a strong incentive to threat their opponent by playing D, which is harmful for both parties if the outcome happens to be (D,D).

Conventional evolutionary game theoretical models assume an infinite population in which pairs of randomly drawn individuals interact according to a given game. Selection is strictly pay-off biased, which implies that fitter individuals reproduce more (genetic evolution) or successful individuals tend to be imitated more frequently (cultural evolution). In both genetic and cultural evolution, the evolutionary process can be analytically described by a set of equations called the replicator dynamics (Weibull, 1995). In the SG, the only stable equilibrium of such equations is an internal one, corresponding to the mixed strategy of classical game theory, while the two pure equilibria are unstable. In the PD, the only stable rest point occurs when the population is entirely composed of Ds: Cs are doomed to extinction in this game.

Given these unfavorable predictions for the evolution of cooperation, several mechanisms have been invoked in order to explain why altruism can actually emerge, such as kin selection, group selection, direct reciprocity, indirect reciprocity and network reciprocity (Nowak, 2006a). Network reciprocity (Lieberman et al., 2005; Nowak & May, 1992; Santos & Pacheco, 2005; Szabó & Fáth, 2007) arises when individuals occupy the vertices of a graph (modeling spatially subdivided populations or social networks) such that interactions are constrained to direct neighbors. When the population of players possesses such a structure, Cs can survive in clusters of related individuals for certain ranges of the game parameters, as it has been known since the pioneering work by Nowak & May (1992). Among the different conceivable population topologies, scale-free networks have received particular attention since they have been found to promote cooperation to a point that Cs dominate Ds in a significant portion of the parameters' space (Santos & Pacheco, 2005).

In addition to positing infinite well-mixed populations, the replicator dynamics relies on the assumption that selection is entirely pay-off biased. Such a premise, although natural to posit in genetic evolution, is less straightforward to postulate in cultural evolution where information is transmitted by means of imitation. Humans not only have a bias for imitating more successful people, but also to conform, or to show a disproportionate tendency to copy the behavior of the majority (Boyd & Richerson, 1985). Recent empirical research has shown that conformity is an important bias in our social learning psychology (Coultas, 2004; Efferson et al., 2008), and that it can partially account for the results obtained in laboratory experiments on social dilemmas (Bardsley & Sausgruber, 2005; Carpenter, 2004). Theoretical research has also shown that conformity can promote cooperation in the PD. In the standard case of a large, well-mixed population, the dynamics can lead either to full defection or to bi-stability, depending on the amount of conformity (Henrich, 2001; Henrich & Boyd, 2001; Peña, 2008). In Peña (2008) the case of square lattices was studied by simulation, with the result that conformity stabilizes cooperation in such population topologies, a result confirmed for rings in Mengel (2009) and, in a more detailed way, in the work presented here.

In this paper we investigate the evolution of cooperation when individuals imitate with a given amount of conformity and both interaction and imitation are constrained to nearest neighbors in a network. In order to extend previous work (Doebeli & Hauert, 2005; Hauert & Doebeli, 2004; Nowak & May, 1992; Peña, 2008; Santos & Pacheco, 2005; Tomassini et al., 2006) and to study the influence of the network topology, we use rings and Bárabasi-Albert scale-free networks as examples of, respectively, simple degree-homogeneous (i.e. regular) and highly degree-heterogeneous graphs. It will be shown that, while conformity reinforces the cooperation-promoting advantages of network reciprocity in rings, the very same mechanism may strongly hinder the evolution of cooperation when the network topology is scale-free. Indeed, when Cs are not initially in the majority and imitation is partly conformist, scale-free networks are no longer the powerful amplifiers of cooperation expected from the results of previous studies. There is thus an interesting interplay between conformity and network reciprocity so that the cooperation-promoting effects of conformity depend on the particular type of networks on which evolutionary dynamics are played.

3.2 Model

We consider a population of size N where the i-th individual is represented by the vertex v_i of an undirected, simple graph $G(V, E)$. The neighborhood of i, $\Gamma(i)$, is the set of all individuals j such that there is an edge $e_{ij} \in E$. The number of neighbors of i is thus the degree k_i of vertex v_i.

At each time step, each individual is either a C or a D. The system evolves by the successive application of interaction and imitation phases. During the interaction phase, individuals simultaneously engage in a single round of the game with their neighbors. As a result, individual i collects an accumulated payoff $\Pi_i = \sum_{l \in \Gamma(i)} \pi_{il}$, where π_{il} is the pay-off player i receives when interacting with player l (e.g. T, R, P or S). During the imitation phase, each individual randomly chooses one of its neighbors as its *cultural model.* Let us denote i's cultural model by j. We consider two update rules for the cultural evolutionary dynamics: pay-off biased imitation and conformist imitation. (i) For pay-off biased imitation, i copies j's strategy with a probability given by $f\left((\Pi_j - \Pi_i)/(\theta k_>)\right)$, where $f(x)$ is equal to x if $x > 0$ and 0 otherwise, $k_> = \max\{k_i, k_j\}$, $\theta = T - S$ in the PD and $\theta = T - P$ in the SG. This update rule is a local, finite population analogue of the replicator dynamics, commonly used in the literature (Hauert & Doebeli, 2004; Santos & Pacheco, 2005). (ii) For conformist imitation the probability that i copies j's strategy is given by $f\left((n_{j|i} - n_{i|i})/k_i\right)$ where $n_{l|i}$ is the number of i's neighbors with strategy l. This update rule is related to the majority rule and to the voter model, commonly used in interdisciplinary physics studies (Cox & Durrett, 1991). In our model individuals imitate according to a pay-off bias with probability $1 - \alpha$, and according to a conformist bias with probability α. Thus, the parameter α represents the amount of conformity in the individuals' behavior and gives the average proportion of players imitating according to the conformity rule at each time step. When $\alpha = 0$ our local dynamics reduce to the strictly pay-off biased imitation rule used in previous studies (Hauert & Doebeli, 2004; Santos & Pacheco, 2005). Figure 3.1 gives some illustrative examples of the imitation dynamics of the proposed model.

In order to allow comparison with previous studies, we focus on the commonly used rescaled version of the PD (Nowak & May, 1992; Santos & Pacheco, 2005), for which $T = b$, $1 \leq b \leq 2$, $R = 1$ and $P = S = 0$. The parameter b represents the advantage of defectors over cooperators. For the SG we make, as in Santos & Pacheco (2005), $T = \beta > 1$, $R = \beta - 1/2$, $S = \beta - 1$, and $P = 0$, such that the cost-to-benefit ratio of mutual cooperation is given by $r = 1/(2\beta - 1)$. It is worthy of note that, in degree-inhomogeneous networks, the local replicator dynamics using accumulated payoff is not invariant with respect to affine transformations of the payoff matrix (Luthi et al., 2009; Tomassini et al., 2007). Although this fact invalidate generalizations of the obtained results to the extended parameter

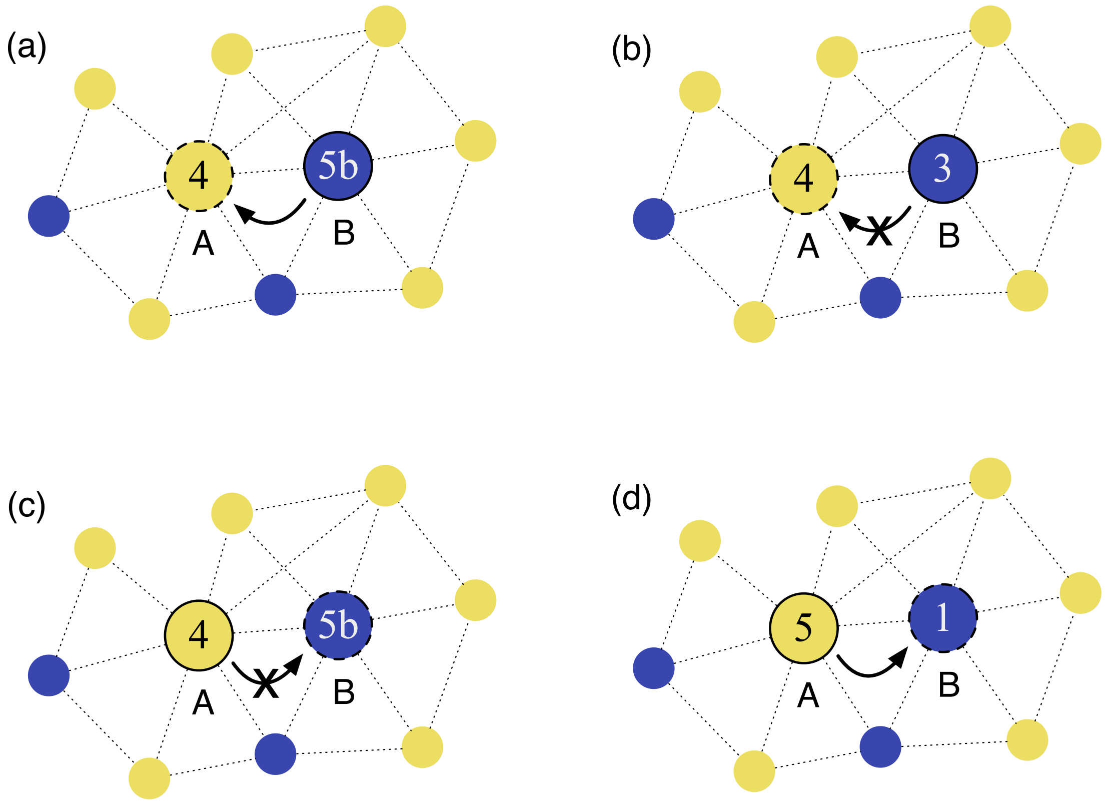

Figure 3.1: Individuals imitate following two different update rules, each reflecting a different bias of our social learning psychology: pay-off based imitation and conformist imitation. Cooperators are shown in light yellow; defectors in dark blue. Social interaction is modeled by a rescaled Prisoner's Dilemma with $T = b > 1$, $R = 1$, $P = S = 0$. (a) Successful pay-off biased transmission. When applying a pay-off biased rule of imitation, A can copy B's strategy and become a defector, since B's pay-off is greater than A's. (b) Unsuccessful conformist transmission. If A were to imitate B according to conformity, no transmission would take place, since defectors are in the minority of A's neighborhood (3 defectors vs. 4 cooperators). (c) Unsuccessful pay-off biased transmission. B will not copy A's strategy under a pay-off biased rule since A's pay-off is smaller than B's. (d) Successful conformist transmission. Conformist transmission from A to B can take place because cooperators constitute the majority in B's neighborhood (5 cooperators vs. 1 defector).

space, it allows us to compare our results with relevant previous work.

Before studying our model with actual network models (rings and scale-free networks) by means of numerical simulation, we briefly present analytical results obtained using the mean-field method and the pair approximation. Such analytical results are important in order to identify the dynamical regions of the system and to serve as starting point for comparisons with the dynamics on actual networks studied in Section 3.4.

3.3 Analytical results

3.3.1 Mean-field approach

Within the framework of the traditional mean-field approach (Szabó & Fáth, 2007) network locality is ignored and the system is assumed to have an infinite size, leading to an infinite, well-mixed population. In this case, it is easy to show that the time evolution of the fraction of Cs ρ is ruled by the following equation:

$$\dot{\rho} = \rho(1-\rho)\left\{\gamma\left[\pi_C - \pi_D\right] + \alpha(2\rho - 1)\right\}, \tag{3.1}$$

where $\pi_C = \rho R + (1-\rho)S$ and $\pi_D = \rho T + (1-\rho)P$ are the average pay-offs to Cs and Ds, and $\gamma = (1-\alpha)/\theta$. Equation 3.1 (or a similar formula) has been derived in related work on cultural transmission processes including both pay-off biased imitation and conformist imitation (Carpenter, 2004; Henrich, 2001; Henrich & Boyd, 2001; Peña, 2008; Skyrms, 2005). The dynamics has the two trivial fixed points $\rho_0^* = 0$ and $\rho_1^* = 1$, as well as (possibly) one internal non-trivial equilibrium given by

$$\rho^* = \frac{\gamma(P-S) + \alpha}{\gamma\left\{R - T + P - S\right\} + 2\alpha}.$$

For $\alpha = 0$ (pure pay-off biased transmission) Eq. 3.1 recovers the standard replicator dynamics of the original game, whereas for $\alpha = 1$ (pure conformist transmission), Eq. 3.1 is equivalent to the replicator dynamics of a pure coordination game with internal (unstable) equilibrium $\rho^* = 1/2$. For $0 < \alpha < 1$, variations in the amount of conformity and the entries of the pay-off matrix can change the evolutionary dynamics of the social dilemma. In particular, the global behavior of the system depends on the two critical values $\alpha_D = (S-P)/(\theta + S - P)$ and $\alpha_C = (T-R)/(\theta + T - R)$ so that the system is in one of the following four dynamical regions:

1. Dominant defection ($\alpha > \alpha_D \wedge \alpha < \alpha_C$): $\rho_0^* = 0$ is the only stable equilibrium. In this case, Cs are doomed to extinction regardless of their initial frequency in the population.

2. Co-existence ($\alpha < \alpha_D \wedge \alpha < \alpha_C$): only the internal equilibrium ρ^* is stable. Cs and Ds coexist in equilibrium at proportions given by ρ^* and $1 - \rho^*$, respectively.

3. Bi-stability ($\alpha > \alpha_D \wedge \alpha > \alpha_C$): both $\rho_0^* = 0$ and $\rho_1^* = 1$ are stable whereas the internal fixed point ρ^* is unstable. In this case, the evolutionary dynamics depends on the initial frequency of Cs, $\rho(0)$. For $\rho(0) > \rho^*$ cooperation prevails, whereas it vanishes for $\rho(0) < \rho^*$.

4. Dominant cooperation ($\alpha < \alpha_D \wedge \alpha > \alpha_C$): $\rho_1^* = 1$ is the only stable equilibrium; Cs get fixed regardless of their initial frequency in the population.

These regimes can be seen in Fig. 3.2, which shows the phase diagrams of the two rescaled games. In the PD with conformity, $S < P \Rightarrow \alpha_D < 0$, so that only dominant defection and bi-stability are possible. In particular, for the rescaled version of the game, conformity can make the system bi-stable if $\alpha > (b-1)/(2b-1)$. However, for all values of b in the bi-stability region, the basin of attraction of ρ_0^* is greater than the basin of attraction of ρ_1^*, i.e. Cs initially in the minority are doomed to extinction regardless of their initial proportion and the values of b and α. In the SG with conformity, the four dynamical regions above described are possible, with $\alpha_D = (1-r)/2$ and $\alpha_C = r/(1+2r)$. In the co-existence region, the equilibrium proportion of Cs is larger than what is expected in the $\alpha = 0$ case when $r < 1/2$ and smaller when $r > 1/2$. In the bi-stability region, the basin of attraction of ρ_1^* is greater than the basin of attraction of ρ_0^* for $r < 1/2$.

In sum, conformity can promote cooperation in the PD to a certain degree in the mean-field limit. If in the majority (and if conformity is strong enough) Cs now have a chance of surviving invasion from Ds, and eventually take over the whole population (Peña, 2008). In the SG, whether conformity helps or hinders the evolution of cooperation actually depends on the cost-to-benefit ratio r. Cs are favored for $r < 1/2$ and disfavored for $r > 1/2$.

3.3.2 Pair approximation

Pair approximation (Matsuda et al., 1992; van Baalen & Rand, 1998) improves over traditional mean-field approach for structured populations by considering the frequency of strategy pairs (i.e. C-C, C-D and D-D). Since the technique assumes regular graphs without loops, it only applies to Bethe lattices in a strict sense (Hauert & Szabó, 2005). However, pair approximation has been used to predict evolutionary dynamics on more general regular graphs with considerable success (Hauert & Doebeli, 2004; Hauert & Szabó, 2005). We extended the pair-dynamics model presented in the Supplementary Information of Hauert & Doebeli (2004) to investigate the cultural evolutionary dynamics of social dilemmas on

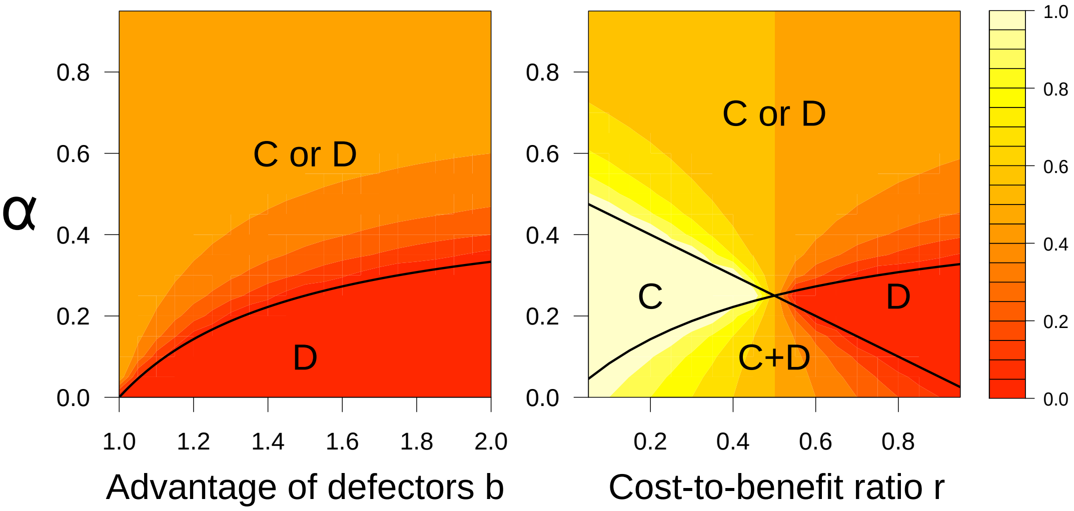

Figure 3.2: Mean-field solutions of the phase diagrams for the PD with conformity on the b-α plane (left) and for the SG with conformity on the r-α plane (right). For the PD, the system can be in the dominant defection (D) or the bi-stability (C *or* D) regions. For the SG, dominant cooperation (C) and co-existence (C+D) are also possible outcomes. Darker colors indicate more defection in the average. In the C *or* D region, colors indicate the size of the basin of attraction for the cooperative equilibrium. In the C+D region, colors indicate the equilibrium proportion of Cs.

graphs. The pair approximation of our model leads to a system of ordinary differential equations tracking changes in the proportions $p_{c,c}$, $p_{c,d}$ and $p_{d,d}$ of, respectively, the C-C, C-D and D-D links in the population graph. The resulting system, although impossible to solve analytically due to the nonlinearity of the equations, can be solved numerically after specifying suitable initial conditions.

Figure 3.3 shows the phase diagrams for the pair approximation of our model, for regular graphs with degree $k = 4$ and $k = 8$. The figures were constructed by numerically integrating the equations under different initial proportions of Cs ($\rho(0) = \{0.1, 0.2, \ldots, 0.9\}$) and averaging over all initial conditions. Pure spatial effects can be seen when $\alpha = 0$. For the PD, the dynamical regime of the game is no longer of dominant defection, but of co-existence. Locality of interactions thus favors Cs by allowing them to survive extinction. In addition to this classical result, for $k = 4$ conformity is largely favorable to Cs. Indeed, augmenting α increases the proportion of Cs in the co-existence region and, depending on the value of b, can shift the system to the region of dominant cooperation. In the SG with $k = 4$ conformity has similar effects, resulting in an analogous dynamic picture. The fact that the SG represents a less stringent dilemma makes larger the area of dominant cooperation. For $k = 8$, phase diagrams get closer to those predicted by the mean-field method (see Fig. 3.2) but important levels of cooperation are still sustained. In the PD, for instance, the basins of attraction of the cooperative equilibrium in the bi-stability region are larger than those expected in a well-mixed population (compare the top right panel of Fig. 3.3 with the left panel of Fig. 3.2).

In a nutshell, when the population of players possesses local structure, a given amount of conformity in the imitation rules of the players is able to foster cooperation, at least for low values of the mean degree k. The reason for this is the easier formation of clusters of individuals playing the same strategy induced by conformist imitation.

3.4 Simulation results

We now turn our attention to actual networks as population topologies, in particular (i) rings (regular 1D-lattices with cyclic boundary conditions) with degrees $k = 4$, $k = 8$ and $k = 16$, and (ii) Barabási–Albert scale-free networks (Albert & Barabási, 2002) with average degrees $\bar{k} = 4$, $\bar{k} = 8$, and $\bar{k} = 16$. For both types of networks we generated graphs of size $N = 10^4$. In the case of rings, graphs are constructed by arranging the nodes on a circle and connecting each node to the k most-neighboring nodes.

We study the model by Monte Carlo simulations in populations randomly initialized with 50% Cs and 50% Ds (but see Section 3.4.3 for other initial con-

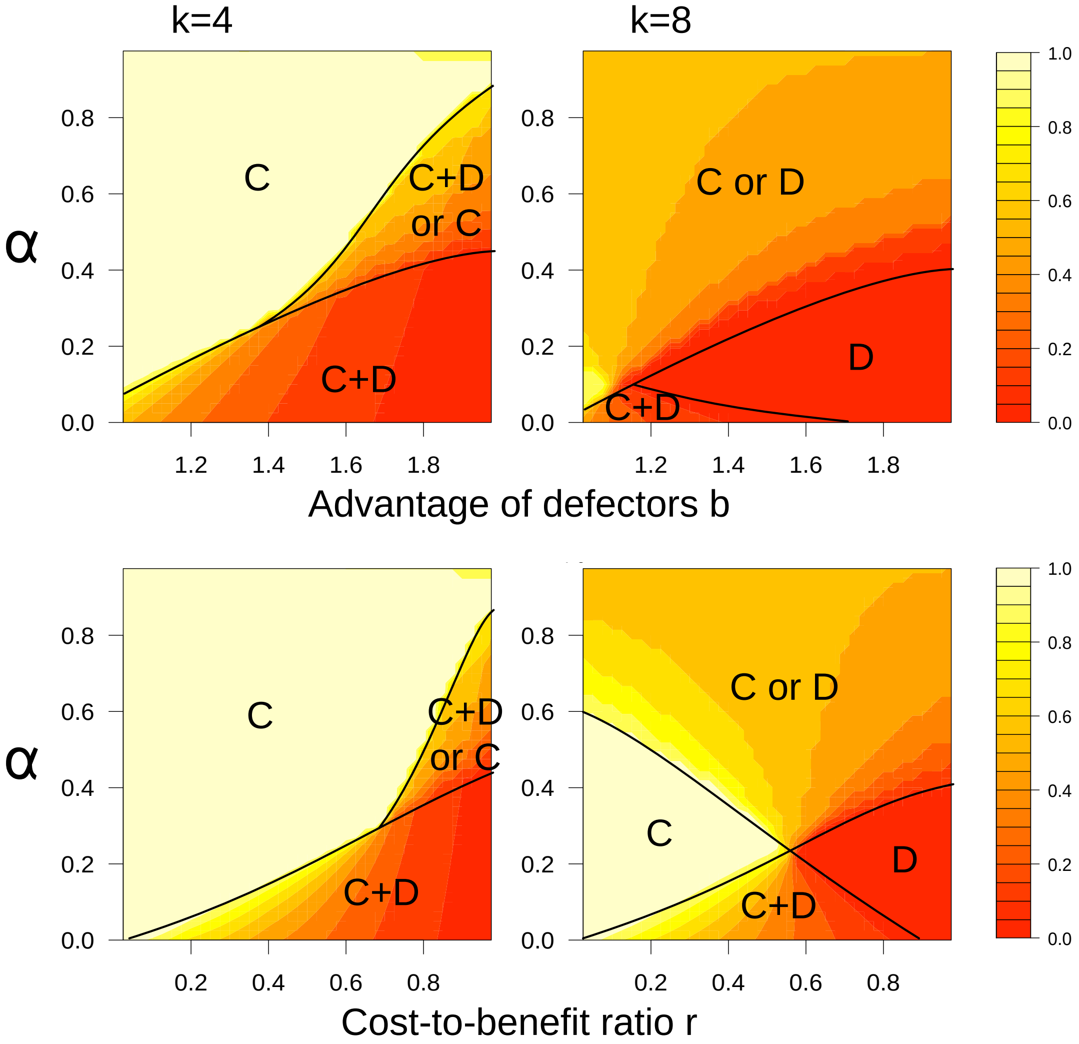

Figure 3.3: Pair approximations of the phase diagrams for the PD with conformity on the b-α plane (top row) and the SG with conformity on the r-α plane (bottom row). The first column shows the results for $k = 4$, the second column for $k = 8$. The system exhibits different dynamical regimes depending on the game: dominant cooperation (C), dominant defection (D), coexistence (C+D), and bistability (C *or* D and C+D *or* C). In the C+D *or* C region, the system can stabilize in a mixed state or in pure cooperation. Darker colors indicate more defection in the average.

ditions). The probability α of conformist transmission was set to $\alpha \in [0, 0.5]$ in steps of 0.1. We privilege values of $\alpha \leq 0.5$ so that dynamics are primarily driven by pay-off differences in the competing strategies. However, we also study the limiting case $\alpha = 1$ in Section 3.4.4 and the case $0 \leq \alpha \leq 1$ in Section 3.4.3. The advantage of defectors b (PD) and the cost-to-benefit ratio r (SG) were varied in steps of 0.05. We carried out 50 runs for each couple of values of α and the game parameter. For the scale-free networks, we used a fresh graph realization in each run. The average final frequency of Cs $\hat{\rho}$ was obtained by averaging over 10^3 time steps after a relaxation time of 10^4 time steps.

3.4.1 Results for rings

Figure 3.4 summarizes the results obtained for the PD and the SG on rings with $k = 4$. These plots confirm the results previously obtained for the standard $\alpha = 0$ case on these population topologies (Santos & Pacheco, 2005; Tomassini et al., 2006), which in turn are qualitatively similar to those obtained for square lattices (Hauert & Doebeli, 2004; Nowak & May, 1992). In the PD, Cs are able to survive for low values of b by forming clusters wherein they interact more often with their own strategy than what is expected in well-mixed populations. Cs can thus benefit from mutual cooperation and counterbalance the exploitation of Ds at the borders of the clusters (Doebeli & Hauert, 2005). In the SG, spatial structure hinders the evolution of cooperation (Hauert & Doebeli, 2004), such that only for small values of r (i.e. $r < 0.3$) the final fraction of Cs is higher than what is expected in a well-mixed population. As it is evident from our results, conformity enhances cooperation in rings, moving rightward the critical value b^* for which $\hat{\rho} = 0$ in the PD, and the value r^* for which the $\hat{\rho}$ becomes smaller than the corresponding proportion in a well-mixed population in the SG. Furthermore, the different curves are ordered in a way that the higher α, the higher $\hat{\rho}$ for all values of b and r (except for the SG, $r = 0.5$, $\alpha = 0.1$) and the larger the critical values b^* and r^*.

Figure 3.5 plots the results for rings with $k = 8$. In the PD, conformity enhances cooperation even more pronouncedly than in the $k = 4$ case. Indeed, the threshold b^* has moved rightward for every value of α. Such trend is still present in the results obtained for rings with $k = 16$ (not shown here to avoid cluttering the figures). In the SG, the increase in the degree of the graph makes conformity cooperation-enhancing up to a threshold value $\hat{r}$ (where a curve with $\alpha > 0$ crosses the curve with $\alpha = 0$) but detrimental afterwards. As b^* in the PD, also $\hat{r}$ moves rightward as α increases.

With respect to simulation results, pair approximation tends to underestimate cooperation for low values of α and b or r and to overestimate it for medium to large values of these parameters. For the PD with conformity, results for

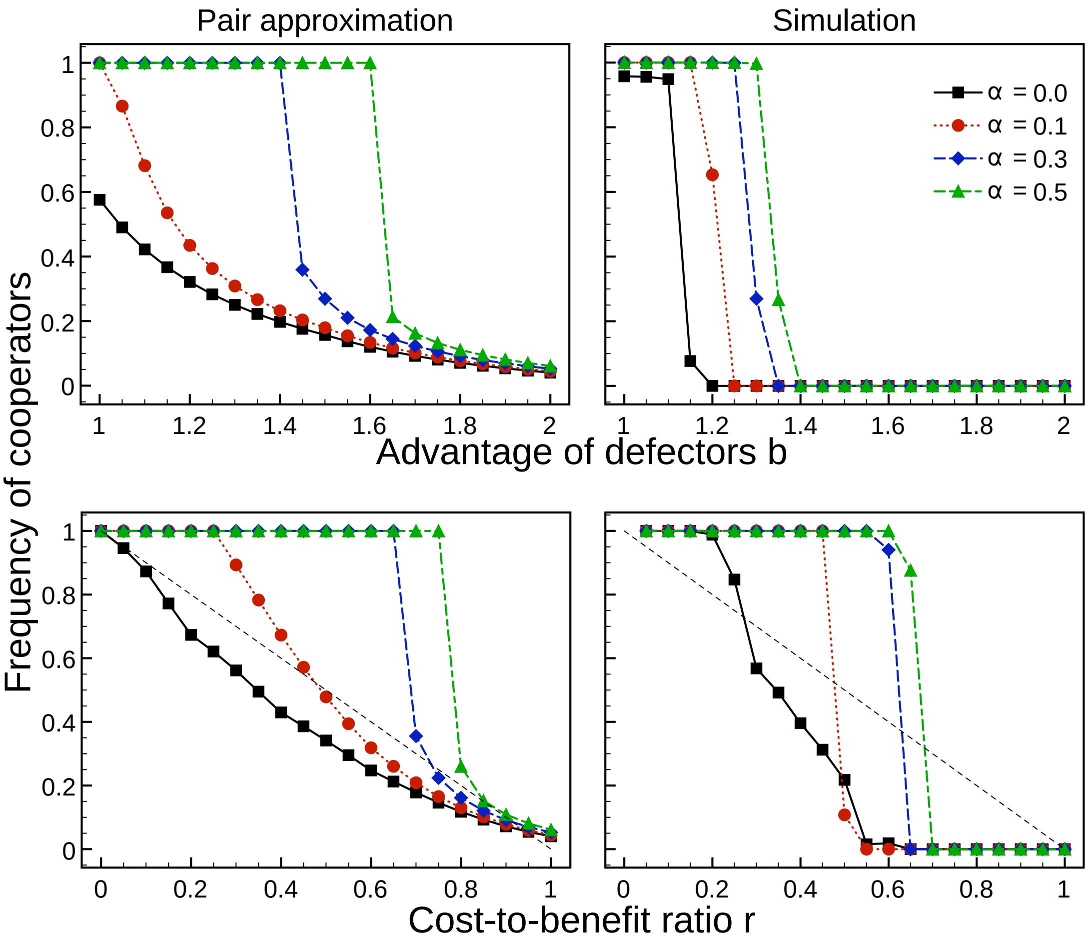

Figure 3.4: Final average frequency of Cs on rings with $k = 4$ for the PD (upper panels) and the SG (lower panels) as a function of b or r for different values of the propensity to conform α. Results by Monte Carlo simulations are shown in the right panels while predictions by pair approximation are shown in the left panels. Mean-field approximations for the SG and $\alpha = 0$ are shown with dotted lines.

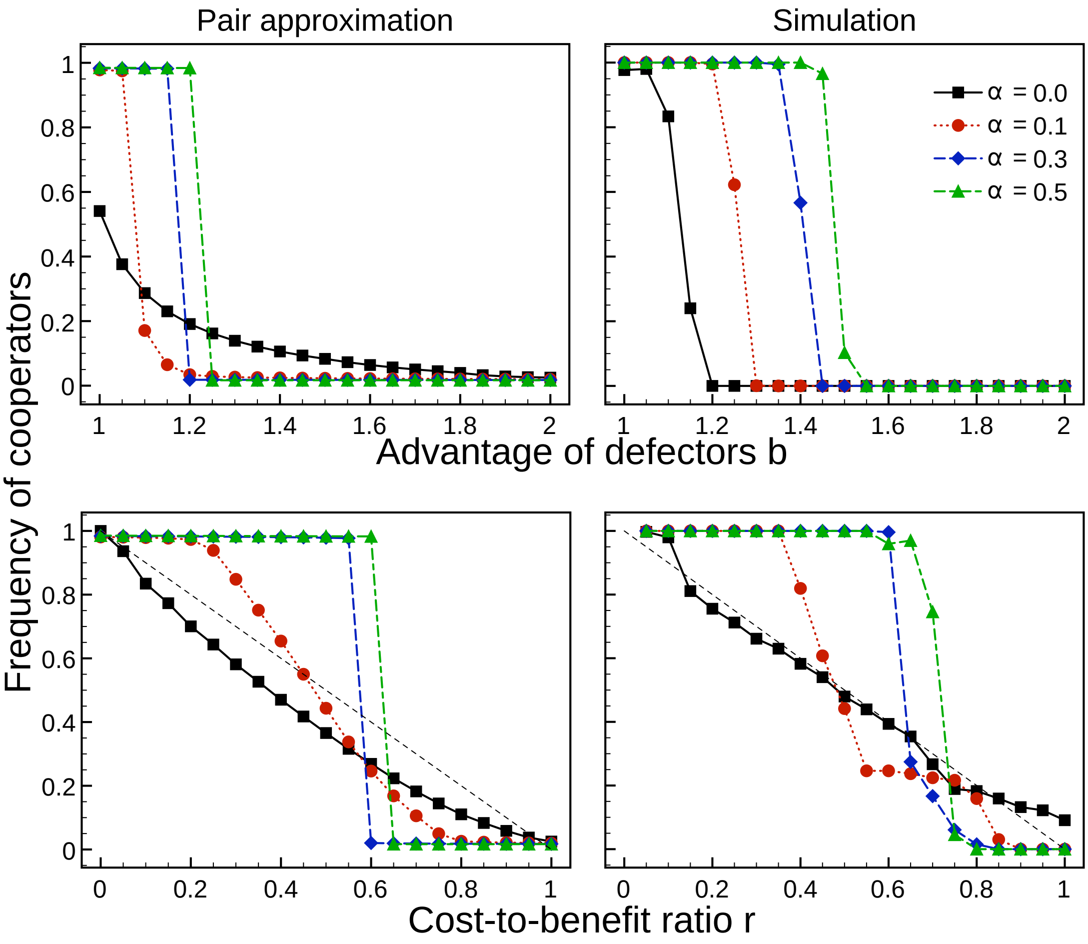

Figure 3.5: Final average frequency of Cs on rings with $k = 8$ for the PD (upper panels) and the SG (lower panels) as a function of b or r for different values of the propensity to conform α. Results by Monte Carlo simulations are shown in the right panels while predictions by pair approximation are shown in the left panels. Mean-field approximations for the SG and $\alpha = 0$ are shown with dotted lines.

$k = 8$ are rather pessimistic and are much closer to what we have obtained for random graphs (data not shown here). This is not surprising since random graphs are locally similar to Bethe lattices (Bollobás, 1995). Notice, however, that pair approximation predicts reasonably well the cooperation-enhancing effects of conformity in the PD and the ordering of the curves for different values of α. Also, for the SG, pair approximation accurately predicts the fact that the curves with conformity ($\alpha > 0$) are above the curve without conformity ($\alpha = 0$) when $k = 4$ (Fig. 3.4, lower panels), but that they cross it when $k = 8$ (Fig. 3.5, lower panels). This means that pair approximation correctly predicts the fact that, for $k = 8$, there is a point up to which conformity helps Cs but beyond which Ds are favored with respect to the standard case without conformity.

3.4.2 Results for scale-free graphs

Let us now turn our attention to the results obtained for scale-free networks (Fig. 3.6). When imitation is strictly pay-off biased ($\alpha = 0$) these degree-heterogeneous graphs importantly foster cooperation in both the PD and the SG with respect to what is obtained in rings and other degree-homogeneous graphs (Santos & Pacheco, 2005). As an aside, we note that the higher the average degree $\bar{k}$, the lower the gains in cooperation[1]. The addition of conformity has important consequences in the evolution of cooperation on scale-free graphs. In the PD, conformity improves $\hat{\rho}$ for all values of b only for a scale-free topology with $\bar{k} = 4$ and $\alpha < 0.3$. For the other cases, conformity does not hamper cooperation for small values of b but is detrimental for medium to large values of the game parameter. Furthermore, the threshold value $\hat{b}$ above which $\hat{\rho}$ is higher than in the case without conformity is a monotonically decreasing function of both α and $\bar{k}$, such that the higher the amount of conformity and the average connectivity of the graph, the smaller the value of $\hat{b}$. Particularly, for scale-free networks with $\bar{k} = 8$ and $\alpha \geq 0.2$, conformity weakens the advantage of these graphs in promoting cooperation to a point that $\hat{\rho}$ becomes comparable to the corresponding fraction obtained in rings (compare the right upper panels of Fig. 3.6 and Fig. 3.5).

Results for the SG on scale-free networks (lower panels of Fig. 3.6) are qualitatively similar to those obtained for the PD. Again, conformity is beneficial for cooperation for all values of the game parameter r only for $\bar{k} = 4$ and $\alpha < 0.3$. For the remaining cases, there is a threshold value $\hat{r}$ of the cost-to-benefit ratio above which $\hat{\rho}$ is smaller than the corresponding frequency of Cs in the $\alpha = 0$ case. We note again the fact that the higher the value of α, the lower the value

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[1] When comparing our results with those of Santos & Pacheco (2005), note that the curves are in the wrong order in Santos & Pacheco (2005) as cooperation should decrease with increasing mean degree for scale-free networks.

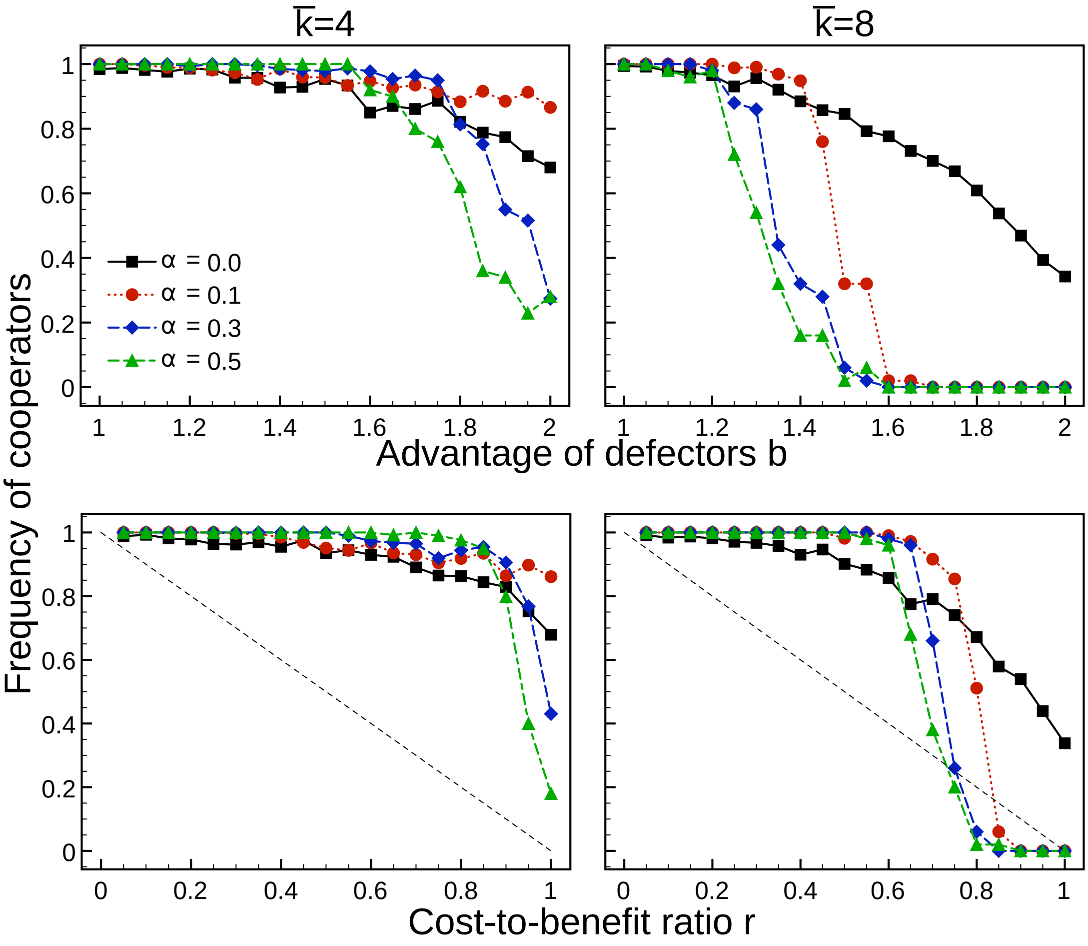

Figure 3.6: Final average frequency of Cs on scale-free networks for the PD (upper panels) and the SG (lower panels) as a function of b (PD) or r (SG) for different values of the propensity to conform α. Results are shown for $\bar{k} = 4$ (left panels) and $\bar{k} = 8$ (right panels). Mean-field approximations for the SG and $\alpha = 0$ are shown with dotted lines.

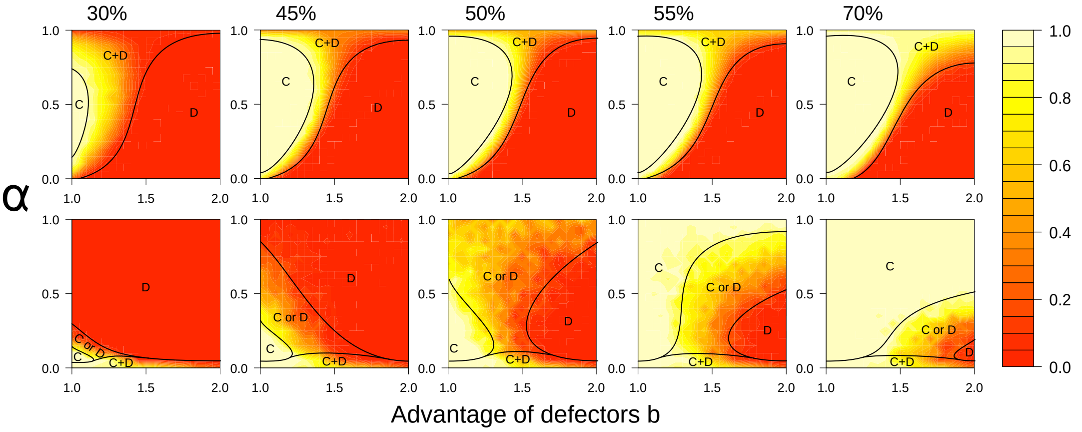

Figure 3.7: Phase diagrams for the PD game on rings with $k = 8$ (top row) and for scale-free graphs with $\bar{k} = 8$ (bottom row) as a function of b and α. The images are for increasing initial fractions of cooperation $\rho(0)$ from left to right.

of $\hat{r}$. Finally, and as in the PD, for $\bar{k} = 8$ and $\alpha \geq 0.2$ there are no important quantitative differences in $\hat{\rho}$ between rings and scale-free networks: scale-free networks have again lost the cooperation-enhancing capabilities they feature when imitation is strictly pay-off biased. For $\bar{k} = 8$ and high values of r, the addition of conformity can even make Cs go extinct, which would not happen in the non-conformist case.

3.4.3 Dependence on the initial conditions

In order to investigate the robustness of cooperation and to study the influence of the initial fraction of Cs $\rho(0)$ we have also run simulations for the PD on rings and scale-free graphs for $\bar{k} = 8$ starting from values of $\rho(0)$ other than 0.5, and on an extended range of values of α going from 0 to 1. Results are shown in Fig. 3.7 in the form of phase diagrams for each initial condition. In contrast to the notion of bi-stability in a system of ordinary differential equations (such as those resulting from the mean-field approach and the pair approximation), here we define bi-stability as the ability of the system to reach either full cooperation or full defection starting from the same *global* initial conditions, due to its stochastic dynamics and finite size.

Not unexpectedly, initial conditions influence the final outcomes of the simulations, so that the strategy initially in the majority is always favored with respect to the case when $\rho(0) = 0.5$. Notice, however, that the effects of conformity are still qualitatively different for each of the two types of networks considered in this

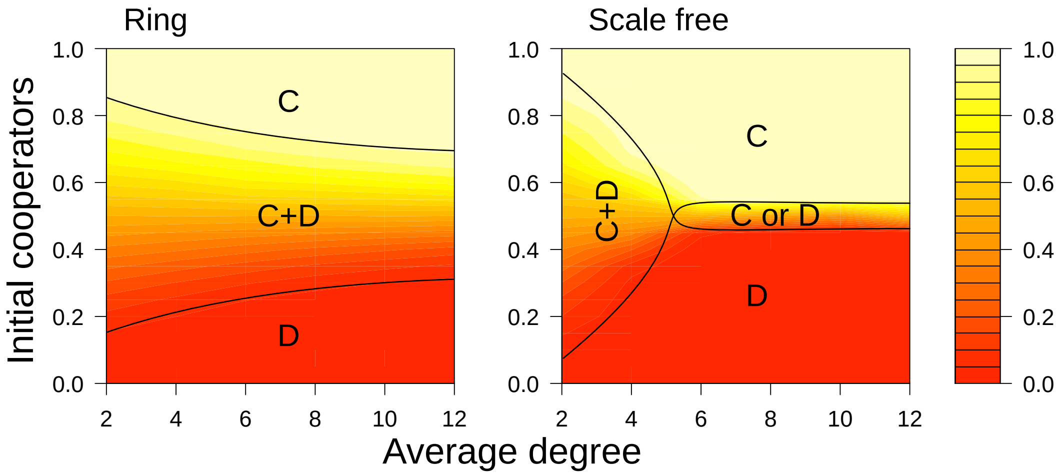

Figure 3.8: Final population composition as a function of the average degree $\bar{k}$ and the initial proportion of cooperators when imitation is purely conformist ($\alpha = 1$).

study. On these phase diagrams the transition from the region of dominant cooperation (C) to dominant defection (D) is steeper on rings, where the two zones with monomorphic populations are divided by a narrow region of co-existence (C+D). On scale-free networks a large region of bi-stability (C *or* D) tends to be formed in the middle of the parameter's space, being the largest for $\rho(0)$ close to 50%. Indeed, the cultural evolutionary dynamics are much more sensitive to the initial conditions when applied on top of scale-free networks than when they are played on top of rings. For rings, conformity favor Cs even if they are initially in the minority, such that, in general, the higher the value of α the higher the final fraction of Cs in the population. For scale-free networks, conformity can be favorable to cooperation when Cs are initially in the majority, but decidedly detrimental if they are in the minority. The remarkable observation is that in scale-free networks even a small change in the initial fraction of Cs can drastically change the final outcome (see the second and fourth images in the lower row of Fig. 3.7 for $\rho(0) = 0.45$ and $\rho(0) = 0.55$). It would be tempting to compare the numerical results for scale-free graphs with those obtained analytically in the mean-field case and with the pair approximation (Figs. 3.2 and 3.3). However, this cannot be done as both the mean-field and pair approximation approaches give poor results in highly degree-inhomogeneous networks.

3.4.4 Pure conformist dynamics

We briefly comment on the case with $\alpha = 1$ which is special as the dynamics is completely driven by the majority rule and games' payoffs play no role. Figure 3.8 shows what happens in this case as a function of the network's average degree $\bar{k}$ and the initial proportion of Cs. For $\bar{k} = 2$ there is a large co-existence region for both graphs, and the pure equilibria have relatively small basins of attraction. With increasing $\bar{k}$, the co-existence region decreases so that a greater connectivity favors fixation in a monomorphic population. Whereas in rings co-existence is still reached for $\bar{k}$ as large as 12, for scale-free networks such regime disappears for $\bar{k} > 5$. For these networks, only in the narrow central strip around $\rho(0) = 0.5$ may bi-stability arise. Note that in this case the C and D labels indicating cooperators or defectors are purely conventional as payoffs (and so, the behavioral strategies of the individuals) are completely ignored.

3.5 Discussion

Conformity and network reciprocity are able to act together and foster cooperation in degree-homogeneous graphs for social dilemmas such as the PD and the SG. The basic principle behind network reciprocity is the formation of clusters of related individuals leading to assortative interactions that favor Cs. Conformity further helps such cluster formation thus improving the efficiency of cooperative behavior in a network of interacting individuals.

More interestingly, conformity may hinder the evolution of cooperation on the otherwise cooperation-promoting scale-free networks. The different dynamical organization of cooperation in degree-heterogeneous graphs with conformity can explain the reason of such phenomenon. When individuals imitate exclusively according to a pay-off bias, Cs and Ds coexist in quasi-equilibrium, with some nodes fixed in cooperative or defective behavior and others where there is no fixation and cycles of invasion follow indefinitely (Gómez-Gardeñes et al., 2007). Thus, the gradual drop in cooperation seen in Fig. 3.6 for the case $\alpha = 0$ is mostly due to fluctuating individuals spending less and less time engaging in cooperative behavior. This dynamical picture changes when individuals imitate not only according to a pay-off bias, but also to conformity. In this case, for $\bar{k} = 8$, the population always reaches one of the two absorbing states, so that in the limit only one strategy gets fixed: Cs for low values of b, Cs or Ds (with a certain probability) for intermediate values of b, and Ds for large values of b (see also the bottom row of Fig. 3.7). In general, and contrary to what happens without conformity, intermediate levels of cooperation for $\alpha > 0$ (when averaging over several runs) are not the result of the co-existence or fluctuation of different strategies but of the fact that, for an interval of values of b, whose length

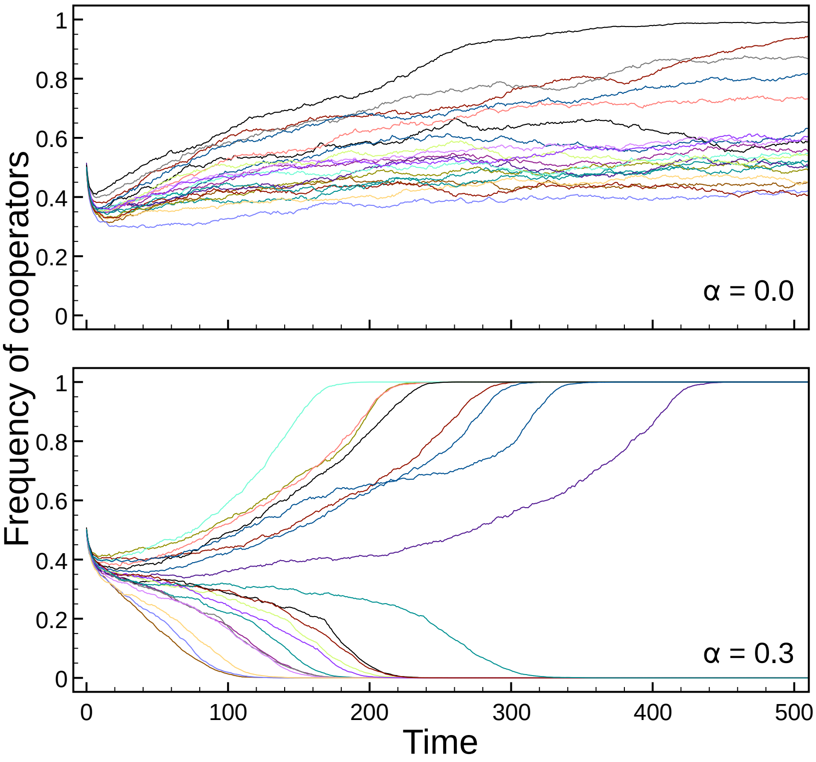

Figure 3.9: Evolution of the frequency of Cs on scale-free networks ($\bar{k} = 8$) during the first 500 time steps for the PD, without conformity (upper panel) and with conformity (lower panel). In both figures, $b = 1.35$. 20 distinct curves are shown.

increases with α, the system sometimes converges to the cooperative equilibrium and some others to the defective equilibrium (see Fig. 3.7 bottom row, central image). Additionally, evolutionary dynamics develop much faster in the presence of conformity. Figure 3.9 illustrates these observations for the case of scale-free networks with $\bar{k} = 8$ and $b = 1.35$. Without conformity (upper panel of Fig. 3.9) the fraction of Cs for each run slowly increases during the initial part of the simulation until, eventually, it stabilizes around 0.9. Conversely, with conformity (lower panel of Fig. 3.9), very early in the evolutionary process the population goes either to full cooperation or to full defection.

We can gain an insight into the interplay between network reciprocity and conformity by making use of the notion of the temperature of players (Lieberman et al., 2005; Masuda, 2007). Hot players are those who play more since they have a large number of neighbors, whereas cold players are those who have few neighbors and, consequently, play less games. By playing more often, and provided that pay-offs are positively biased (i.e. $S \geq 0$ in the PD), hot players get higher

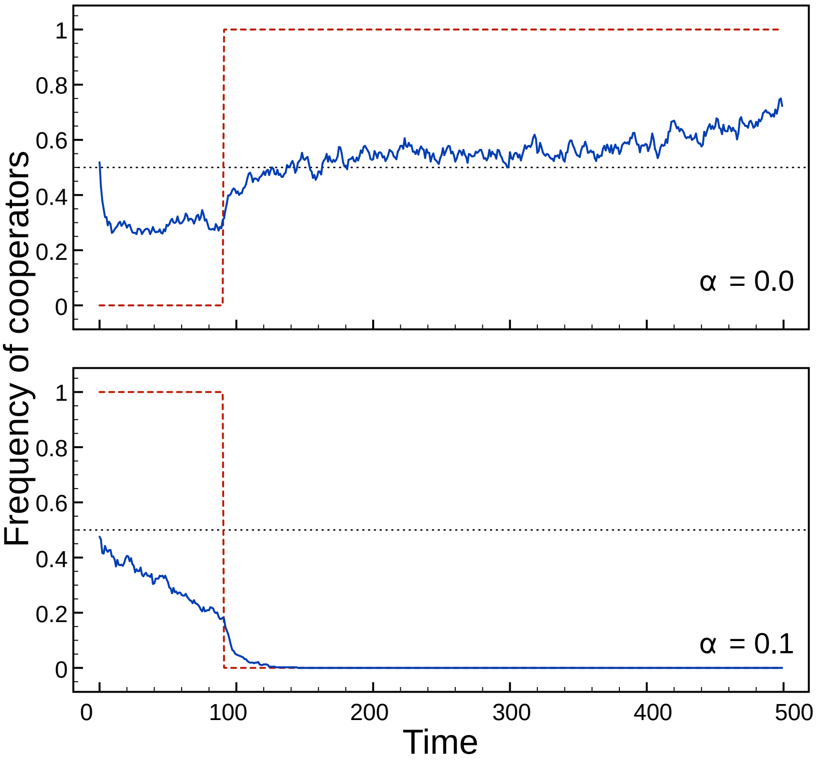

Figure 3.10: Evolution of cooperation around the most connected hub of a scale-free network with $\bar{k} = 8$. The game is a rescaled PD with $b = 1.35$ for $\alpha = 0$ (upper panel) and $\alpha = 0.1$ (lower panel). The fraction of C neighbors is shown in solid lines and the strategy of the hub in dashed lines (D corresponds to 0; C to 1). As a reference, the level of 50% cooperation is depicted in dotted lines. The most connected hub is initially set to D (upper panel) or to C (lower panel). The rest of the population is initialized to around 50% Cs.

accumulated payoffs than cold players. Under pure pay-off biased imitation ($\alpha = 0$) this implies that hot players are also more successful in being imitated and in disseminating their strategies (Masuda, 2007).

Both Cs and Ds do better when they are surrounded by Cs. By spreading defective behavior, hot Ds become less and less successful, since the number of their C neighbors decreases. Hot Cs, on the contrary, see their pay-off increased by spreading their own strategy. The more hot Cs are imitated the more they earn and the more difficult it is for a surrounding D to invade. A typical example of such "hub dynamics" is illustrated in Fig. 3.10 (upper panel) for the most connected hub of a scale-free network. The hub is D at the beginning of the simulation, while the rest of the population is initialized to around 50% Cs.

Many C neighbors imitate the defective hub (or other surrounding Ds) during the first steps of simulation, so that the proportion of C neighbors is reduced to approximately 30%. As a consequence, the total pay-off of the hub is reduced, and the hub becomes vulnerable to invasion from a neighboring C. When the hub becomes a C, more and more of its D neighbors also switch their strategies. Consequently, the proportion of C neighbors (and the total pay-off to the hub) increases and is maintained at a high level afterwards. The presence of such positive feedback mechanism, and the fact that it only works for Cs, greatly enhances cooperation in degree-heterogeneous graphs and, particularly, in scale-free networks (Santos & Pacheco, 2006).

The introduction of conformity decreases the bias in the flow of information in degree-heterogeneous graphs, making hubs vulnerable to invasion from their cold neighbors. While hubs are unlikely to imitate their low connected neighbors when using a pay-off biased rule, nothing prevents them from imitating a cold surrounding player if it holds the strategy of the local majority (see Fig. 3.1(d)). Since the fraction of Cs generally decreases at the outset of the simulation (see the first time steps of the curves shown in Fig. 3.9), conformity further favors Ds, which become predominant in the population. An example of this dynamics is shown in Fig. 3.10 (lower panel). Initially, the hub is a C. Many of the hub's neighbors turn to defection during the first time steps, making cooperation the less common strategy in the hub's neighborhood. Around the 100th time step, the hub imitates by conformity one of its defector neighbors, leading to a quicker decrease in the proportion of Cs in its neighborhood. Shortly after, Cs completely vanish around the most connected hub. During those first time steps, hubs imitating according to a conformist bias will have many chances of becoming Ds. When Cs are not initially in the large majority, such initial asymmetry in the strategies of the hubs can account for the negative effects of conformity in the evolution of cooperation in scale-free networks. Conformity partly reverses the flow of information on degree-heterogeneous networks so that hubs no longer conduct the dynamics and instead quickly conform to the general trend of the whole population.

3.6 Conclusions

To sum up, we have investigated the effects of conformity in the evolution of cooperation on regular one-dimensional lattices (rings) and scale-free networks. This was done by proposing an updating rule that is a stochastic average of the traditional local replicator dynamics, which models pay-off biased imitation, and a conformist biased rule of transmission favoring the most common variants around focal individuals. We explored rings and scale-free networks with different average degrees, as well as different values of the propensity to conform α. Two games representing social dilemmas were studied: the rescaled versions of the PD, and the SG. In addition to Monte Carlo simulations, we also used an extended pair-dynamics model to predict the average fraction of cooperators in equilibrium, and compare them with the results obtained from our simulations.

The results presented in this paper show that whether conformity strengthens or weakens the evolution of cooperation depends on the intrinsic characteristics of the underlying graph. In the PD, conformity favors cooperation on rings by allowing clusters of Cs forming more easily. Conversely, it can hinder cooperation in scale-free networks for medium to large values of b, due to the exposure of hubs to the opinions of the local majority in their neighborhoods. In particular, and already for small amounts of conformity in the imitation rules of the players, scale-free networks do not show the great improvement over regular structures that has been previously reported in the literature. In the SG, conformity fosters cooperation on rings in the case $k = 4$ for all values of the cost-to-benefit ratio r, and for low to medium values of r in the case $k = 8$. In scale-free networks, conformity is rather detrimental for large values of r. Thus, for both the PD and the SG, conformity often hinders the evolution of cooperation on scale-free networks for the cultural evolutionary dynamics described in this paper.

It is worth pointing out that other factors dismissing the advantage of scale-free networks in the evolution of cooperation have been identified, such as participation costs (Masuda, 2007), other positive affine transformations of the pay-off matrix (Luthi et al., 2009; Tomassini et al., 2007), and the use of average instead of accumulated pay-offs (Santos et al., 2006). While these factors are extrinsic to the imitation rules of the agents, conformity is a simple mechanism undoubtedly present in our social learning psychology and central to better understand cultural dynamics and the way cooperation evolves on real social networks.

Acknowledgments

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3.7 Appendix. Pair approximation

An analytical approximation of the dynamics of evolutionary games on graphs can be obtained by means of pair approximation (Matsuda et al., 1992; van Baalen & Rand, 1998). For detailed surveys of this technique, and its applications to games on graphs, we refer the interested reader to Hauert & Doebeli (2004); Hauert & Szabó (2005); Szabó & Fáth (2007). We limit ourselves to briefly introduce the pair approximation and to explain how we have extended it for taking into account conformity in the imitation rules of the players.

Pair approximation is a method for constructing a system of ordinary differential equations for the global frequencies of strategies by tracking the changes in the frequencies of strategy pairs. In our case, we are interested in determining the global frequency ρ of Cs by tracking the fluctuations in $p_{c,c}$, $p_{c,d}$, $p_{d,c}$ and $p_{d,d}$, where $p_{s,s'}$ is the probability of having an individual playing strategy s connected to an individual playing strategy s'. For pair approximation to be consistent with the mean-field approach, it is assumed that $p_s = \sum_{s'} p_{s,s'}$. Furthermore, and in order to "close" the set of equations, configurations of triplets and more complicated configurations are approximated by the configuration probabilities of strategy pairs. For example, the configuration probability of the triplet s, s', s'' is approximated by $p_{s,s',s''} = p_{s,s'}p_{s',s''}/p_{s'}$. It is important to note that pair approximation (i) requires regular graphs and (ii) corrections arising from loops are ignored. Finally, note that the predictions of the pair approximation for any two regular graphs with the same degree k are exactly the same. This allows us to compare our results to those of Hauert & Doebeli (2004) when $\alpha = 0$.

Let us consider individuals sitting on the vertices of a graph of degree k. Whenever a randomly chosen site A updates its strategy, a random neighbor B is selected as A's cultural model. Common neighbors of any pair of vertices are considered to be independent by pair approximation (i.e. loops are neglected). Thus, let us denote by $a_1, \ldots, a_{k-1}$ (resp. $b_1, \ldots, b_{k-1}$) the $k-1$ the neighbors of A (resp. B) other than B (resp. A). The probability of a generic configuration (see Fig. 3.11) is given by:

$$p_{A,B} \frac{\prod_{i=1}^{k-1} p_{a_i,A} p_{b_i,B}}{p_A^{k-1} p_B^{k-1}}.$$

The probability that the pair A, B becomes B, B is calculated by multiplying the transition probability $\sigma_{A\to B}$ by the configuration probability and summing over all possible configurations, so that:

$$p_{A,B\to B.B} = \sum_{a_1,\ldots,a_{k-1}} \sum_{b_1,\ldots,b_{k-1}} \sigma_{A\to B} \times p_{A,B} \frac{\prod_{i=1}^{k-1} p_{a_i,A} p_{b_i,B}}{p_A^{k-1} p_B^{k-1}}.$$

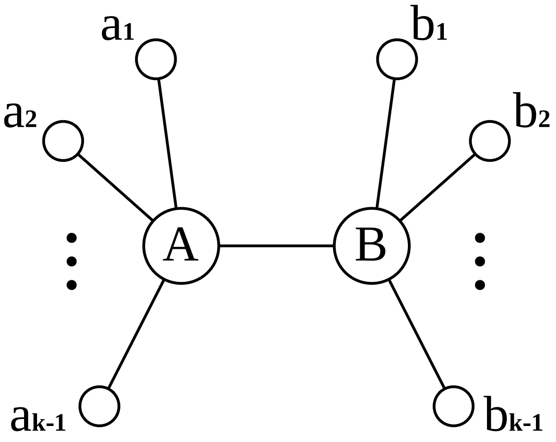

Figure 3.11: A generic configuration for pair approximation. A is the focal individual, B is A's cultural model, $a_1, a_2, \ldots, a_{k-1}$ are A's neighbors other than B, and $a_1, a_2, \ldots, a_{k-1}$ are B's neighbors other than A. A and B are assumed to have no common neighbors, i.e. triangles and loops are neglected.

In our model, the transition probability $\sigma_{A\to B}$ depends not only on the payoffs of A and B but also on α (the probability to imitate according to a conformist bias) and on the number of players among $a_1, \ldots, a_{k-1}$ playing the same strategy of A and B. The transition probability is given by:

$$\begin{aligned}\sigma_{A\to B} &= (1-\alpha) f\left(\frac{\Pi_B(b_1,\ldots,b_{k-1}) - \Pi_A(a_1,\ldots,a_{k-1})}{k\theta}\right) + \\ &\quad \alpha f\left(\frac{n_B(a_1,\ldots,a_{k-1},B) - n_A(a_1,\ldots,a_{k-1},B)}{k}\right),\end{aligned}$$

where $\Pi_B(x_1,\ldots,x_{k-1})$, $\Pi_A(x_1,\ldots,x_{k-1})$ denote the payoffs of B (A) interacting with $x_1,\ldots,x_{k-1}$ plus A (B), and $n_B(a_1,\ldots,a_{k-1},B)$, $n_A(a_1,\ldots,a_{k-1},B)$ specify the number of players with strategy B (A) among $a_1,\ldots,a_{k-1}$ and B. The definitions of the parameter θ and the function f are given in Section 3.2.

Whenever A imitates B, the pair configuration probabilities change so that $p_{B,B}$, $p_{B,a_i}, \ldots, p_{B,a_{k-1}}$ increase, while $p_{A,B}$, $p_{A,a_i}, \ldots, p_{A,a_{k-1}}$ decrease. All these changes lead to a set of ordinary differential equations governing the dynamics of

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the system:

$$
\begin{aligned}
\dot{p}_{c,c} \quad = \quad & \sum_{a_1,\ldots,a_{k-1}} (n_c(a_1,\ldots,a_{k-1})+1) \prod_{i=1}^{k-1} p_{d,a_i} \sum_{b_1,\ldots,b_{k-1}} \prod_{j=1}^{k-1} p_{c,b_j} \times \\
& \left\{(1-\alpha) f\left(\frac{\Pi_c(b_1,\ldots,b_{k-1}) - \Pi_d(a_1,\ldots,a_{k-1})}{k\theta}\right) + \alpha f\left(\frac{2n_c(a_1,\ldots,a_{k-1}) + 2 - k}{k}\right)\right\} \\
& - \sum_{a_1,\ldots,a_{k-1}} n_c(a_1,\ldots,a_{k-1}) \prod_{i=1}^{k-1} p_{c,a_i} \sum_{b_1,\ldots,b_{k-1}} \prod_{j=1}^{k-1} p_{d,b_j} \times \\
& \left\{(1-\alpha) f\left(\frac{\Pi_d(b_1,\ldots,b_{k-1}) - \Pi_c(a_1,\ldots,a_{k-1})}{k\theta}\right) + \alpha f\left(\frac{k - n_c(a_1,\ldots,a_{k-1})}{k}\right)\right\}
\end{aligned}
$$

$$
\begin{aligned}
\dot{p}_{c,d} \quad = \quad & \sum_{a_1,\ldots,a_{k-1}} \left(\frac{k}{2} - 1 - n_c(a_1,\ldots,a_{k-1})\right) \prod_{i=1}^{k-1} p_{d,a_i} \sum_{b_1,\ldots,b_{k-1}} \prod_{j=1}^{k-1} p_{c,b_j} \times \\
& \left\{(1-\alpha) f\left(\frac{\Pi_c(b_1,\ldots,b_{k-1}) - \Pi_d(a_1,\ldots,a_{k-1})}{k\theta}\right) + \alpha f\left(\frac{2n_c(a_1,\ldots,a_{k-1}) + 2 - k}{k}\right)\right\} \\
& - \sum_{a_1,\ldots,a_{k-1}} \left(\frac{k}{2} - n_c(a_1,\ldots,a_{k-1})\right) \prod_{i=1}^{k-1} p_{c,a_i} \sum_{b_1,\ldots,b_{k-1}} \prod_{j=1}^{k-1} p_{d,b_j} \times \\
& \left\{(1-\alpha) f\left(\frac{\Pi_d(b_1,\ldots,b_{k-1}) - \Pi_c(a_1,\ldots,a_{k-1})}{k\theta}\right) + \alpha f\left(\frac{k - n_c(a_1,\ldots,a_{k-1})}{k}\right)\right\},
\end{aligned}
$$

where $n_c(a_1,\ldots,a_{k-1})$ gives the number of Cs among $a_1,\ldots,a_{k-1}$ and $\Pi_c(x_1,\ldots,x_{k-1})$, $\Pi_d(x_1,\ldots,x_{k-1})$ denote the payoffs of a C (D) interacting with $x_1,\ldots,x_{k-1}$ plus a D (C). Because of the symmetry condition $p_{c,d} = p_{d,c}$ and the constraint $p_{c,c}+p_{c,d}+p_{d,c}+p_{d,d} = 1$ these two differential equations are sufficient to describe the system. Note that whenever $\alpha = 0$ the system of equations is equivalent to that derived in the supplementary information of Hauert & Doebeli (2004) and the appendix of Hauert & Szabó (2005). Following those works, the above equations also omit the common factor $2p_{c,d}/(\rho^{k-1}p_d^{k-1})$, which has no influence in the equilibria of the system. The equilibrium values $\hat{p}_{c,c}$, $\hat{p}_{c,d}$, were obtained by numerically integrating the equations after specifying initial conditions for 10^{10} time steps. In all cases, $p_{c,c}(0) = (\rho(0))^2$, $p_{c,d}(0) = \rho(0)(1-\rho(0))$. The equilibrium frequency of Cs was then approximated by $\hat{p}_c = \hat{p}_{c,c} + \hat{p}_{c,d}$.

Part II

Upstream reciprocity

> Show no pity: life for life, eye for eye, tooth for tooth, hand for hand, foot for foot.
>
> Deuteronomy 19:21

Cooperation in the prisoner's dilemma may evolve through reciprocity if individuals interact repeatedly. Models of *direct reciprocity* suggest that cooperation can arise if individuals repeatedly interact with the same partner (Axelrod, 1984; Axelrod & Hamilton, 1981). A strategy such as tit-for-tat (TFT), which starts cooperating and then continues to cooperate as long as the co-player cooperates but defects if the co-player do so, can be evolutionarily stable with respect to unconditional defection. TFT implements the biblical *lex talionis*: cooperation for cooperation, defection for defection, eye for an eye.

Alexander (1987) proposed that networks of *indirect reciprocity*, in which A helps or refuses to help B even though B does not directly reciprocate to A, are crucial for understanding large-scale human cooperation. How should we reinterpret the principle of an eye for an eye when thinking of indirect reciprocity? Two answers have been given in the literature (Alexander, 1987; Boyd & Richerson, 1989; Nowak & Sigmund, 2005). The first is that I shall do to A whatever he did to B: in the case of defection, the wrongdoer's eye for the victim's eye. This has been called *downstream reciprocity* (Boyd & Richerson, 1989; Nowak & Sigmund, 2005), *vicarious reciprocity* (Sigmund, 2010) or simply *indirect reciprocity* (Nowak & Sigmund, 1998b). Downstream reciprocity has been shown to be evolutionarily stable against defection and to constitute a robust mechanism for the evolution of cooperation. Incidentally, downstream reciprocity is also what at least another writer of the Hebrew Bible thought of the indirect implementation of *lex talionis*: 'if anyone injures his neighbor, whatever he has done must be done to him'[2].

The second interpretation of indirect reciprocity has been called *upstream reciprocity* (Boyd & Richerson, 1989; Nowak & Sigmund, 2005), *generalized reciprocity* (Pfeiffer et al., 2005) or *misguided reciprocity* (Sigmund, 2010). According to it, whatever A has done to me I shall do to B: in the case of defection, an inocent's eye for mine. In stark contrast to direct or downstream reciprocity, upstream reciprocity *per se* does not work as a correlation device and thus as a primary mechanism for the evolution of cooperation under the prisoner's dilemma. Indeed, upstream reciprocity alone does not select for cooperation in infinite well-mixed populations (Nowak & Roch, 2007; Rankin & Taborsky, 2009; Sigmund, 2010). The moral virtues of such a social norm are also questionable.

Despite these gloomy prospects, recent models suggest that, if some assumptions hold true, upstream reciprocity may evolve and resist invasion by defectors (Barta et al., 2011; Hamilton & Taborsky, 2005; Pfeiffer et al., 2005; Rankin

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[2] Leviticus 24:19.

& Taborsky, 2009). Moreover, it has been proposed that upstream reciprocity can promote cooperation when it is modeled as random walks of gratitude taking place in a structured population (Iwagami & Masuda, 2010; Nowak & Roch, 2007; van Doorn & Taborsky, 2011). Chapters 4 and 5 present two contributions to the study of upstream reciprocity. Chapter 4 is a critical re-examination of Nowak & Roch (2007)'s use of 'random walks of gratitude' to model upstream reciprocity. It is shown that the assumptions of such model lead to non-uniform and strategy-dependent interaction rates, which greatly limit the generality of the obtained results. In particular, accounting for participation costs can completely suppress the evolution of upstream reciprocity in structured populations. In chapter 5, we get rid of several of the assumptions of Nowak & Roch (2007) and model upstream reciprocity in a population structured as a one-dimensional lattice. Analytical results are obtained by solving a particular instance of the discrete heat equation, a partial difference equation used to model diffusion processes. The results show that, even in the case where the evolving population is structured as a cycle, upstream reciprocity is not evolutionarily stable against both unconditional cooperators and unconditional defectors.

Chapter 4

Participation costs can suppress the evolution of upstream reciprocity[†]

Abstract

Indirect reciprocity, one of the many mechanisms proposed to explain the evolution of cooperation, is the idea that altruistic actions can be rewarded by third parties. Upstream or generalized reciprocity is one type of indirect reciprocity in which individuals help someone if they have been helped by somebody else in the past. Although empirically found to be at work in humans, the evolution of upstream reciprocity is difficult to explain from a theoretical point of view. A recent model of upstream reciprocity, first proposed by Nowak & Roch (2007) and further analyzed by Iwagami & Masuda (2010), shows that while upstream reciprocity alone does not lead to the evolution of cooperation, it can act in tandem with mechanisms such as network reciprocity and increase the total level of cooperativity in the population. We argue, however, that Nowak & Roch's model systematically leads to non-uniform interaction rates, where more cooperative individuals take part in more games than less cooperative ones. As a result, the critical benefit-to-cost ratios derived under this model in previous studies are not invariant with respect to the addition of participation costs. We show that accounting for these costs can hinder and even suppress the evolution of upstream reciprocity, both for populations with non-random encounters and graph-structured populations.

[†] J. Peña, E. Pestelacci, A. Berchtold and M. Tomassini. *Journal of Theoretical Biology*, **273**, 197-206 (2011).

4.1 Introduction

In addition to kin selection (Hamilton, 1964) and group selection (Wilson, 1975), different types of reciprocity have been proposed for explaining altruistic behavior from an evolutionary perspective (Nowak, 2006b). In this paper, we focus on upstream indirect reciprocity and network reciprocity. Contrastingly to direct reciprocity (Axelrod & Hamilton, 1981; Trivers, 1971), which can induce cooperation when individuals base their decision to cooperate on the outcome of previous encounters with the same partner, indirect reciprocity is said to occur when 'the return is expected from someone other than the recipient of the beneficence' (Alexander, 1987). This can happen in one of two ways. In downstream indirect reciprocity (Brandt & Sigmund, 2004, 2006; Leimar & Hammerstein, 2001; Nowak & Sigmund, 1998a,b, 2005; Ohtsuki et al., 2006; Ohtsuki & Iwasa, 2004; Ohtsuki et al., 2007; Panchanathan & Boyd, 2003; Uchida & Sigmund, 2010) or vicarious reciprocity (Sigmund, 2010), first individual A helps individual B and then C helps A. Downstream reciprocity is based on reputation: A acquires a good reputation by helping B, thereby increasing its chances of receiving help by C. In upstream indirect reciprocity (Boyd & Richerson, 1989; Iwagami & Masuda, 2010; Nowak & Roch, 2007; Nowak & Sigmund, 2005), also known as generalized reciprocity (Hamilton & Taborsky, 2005; Pfeiffer et al., 2005; Rankin & Taborsky, 2009; Rutte & Taborsky, 2007) or misguided reciprocity (Sigmund, 2010), first individual A helps individual B and then B helps C. Upstream reciprocity is based on gratitude or moral elevation: individuals who receive help are more inclined to help others in the future. Finally, network reciprocity (Ohtsuki et al., 2006) is at work when the population structure takes the form of a spatial or social network in which clusters of cooperators can help each other and resist invasion from surrounding defectors. Network reciprocity is the generalization of spatial reciprocity (Nowak & May, 1992) to general network models. Under some conditions other mechanisms are also at work in heterogeneous networks, where highly connected individuals can play an important role in promoting cooperation (Gómez-Gardeñes et al., 2007; Pacheco et al., 2009; Santos & Pacheco, 2005, 2006; Szabó & Fáth, 2007).

A simple and general explanation of the evolution of cooperation is the positive assortment between cooperative genotypes and cooperative phenotypes (Fletcher & Doebeli, 2009). In stark contrast with direct, downstream and network reciprocity, upstream reciprocity per se fails to provide such assortment. Thus, strategies based on upstream reciprocity go to extinction in well-mixed populations when competing with defectors (Nowak & Roch, 2007; Rankin & Taborsky, 2009; Sigmund, 2010). Despite this fact, models of upstream reciprocity are worth studying for several reasons. Firstly, there is ample empirical evidence of upstream reciprocity occurring in humans (Bartlett & DeSteno, 2006; Berkowitz

& Daniels, 1964; Dufwenberg et al., 2001; Güth et al., 2001; Isen, 1987; Stanca, 2009) and some evidence in non-human animals such as Norwegian rats (Rutte & Taborsky, 2007). Secondly, it has been theoretically shown that upstream reciprocity can evolve if there is some pre-existent assortment among strategies (Rankin & Taborsky, 2009). Such assortment can be provided, for instance, by the random formation of small groups (Boyd & Richerson, 1989; Pfeiffer et al., 2005), by incorporating group-leaving behavior when experiencing defection (Hamilton & Taborsky, 2005), or by the simultaneous presence of another cooperation-promoting mechanism, such as direct reciprocity (Nowak & Roch, 2007) or network reciprocity (Iwagami & Masuda, 2010; Nowak & Roch, 2007). Finally, when acting in tandem with these mechanisms, the presence of upstream reciprocity seems to lead to higher levels of cooperation and/or lower critical cost-to-benefit ratios than those obtained by direct or network reciprocity alone (Iwagami & Masuda, 2010; Nowak & Roch, 2007).

Usually, indirect reciprocity is theoretically studied in the framework of the Donation game. Each round of the game, two players are chosen at random from the population. One is assigned the role of the donor and the other the role of the recipient. The donor has the option of either helping the recipient or not. If the donor chooses to help, the donor will incur a cost c while the recipient obtains a benefit b, with $b > c > 0$. If the donor refuses to help, payoffs are left unchanged. In Nowak & Roch (2007) and Iwagami & Masuda (2010), Donation games are played along 'chains of altruism' leading to random walks in the population of players. Each player can start a chain of altruism by helping a second player in the population, who can in turn help a third player, and so on and so forth. Such sampling of donors and recipients differs from the one normally used in standard models of indirect reciprocity (cf. Nowak & Sigmund, 1998a) in which interaction partners are randomly and independently sampled from the population. In particular, whereas in standard models individuals interact in average the same number of times (half of the times as donors, half of the times as recipients) in Nowak & Roch's model more cooperative players end up interacting more often than less cooperative players.

Whenever an evolutionary game model leads to non-uniform interaction rates, some questions arise regarding the generality of the obtained results. It is not clear, for instance, whether a given strategy is successful because it 'plays well' against competitors or because it plays more often, nor if the assumption of having individuals with no limitations regarding the number of interactions they engage in per generation is biologically or socially grounded. It is reasonable to think that a number of extrinsic constraints limit the interacting capacity of individuals or that participation in a game can have a non-negligible cost. This is an issue that has been dealt with in the context of evolutionary games on heterogeneous networks (Masuda, 2007; Santos & Pacheco, 2006; Santos et al., 2006; Tanimoto

& Yamauchi, 2010; Tomassini et al., 2007). Different methods have been introduced in order to control for the non-uniformity of interaction rates, such as imposing cutoffs in the interaction distributions (Santos et al., 2006), using the average payoff instead of the accumulated payoff when defining fitness (Santos & Pacheco, 2006; Tomassini et al., 2007; see also Taylor & Nowak, 2006) and introducing participation costs (Masuda, 2007; Tanimoto & Yamauchi, 2010). All these studies have shown that adding such limits can hinder and even suppress the evolution of cooperation based on network reciprocity in heterogeneous networks.

In this paper, we re-examine the model of upstream reciprocity first proposed by Nowak & Roch (2007) and further investigated by Iwagami & Masuda (2010). Nowak & Roch (2007) showed that upstream reciprocity is viable when acting in tandem with direct reciprocity or when the population is arranged in a one-dimensional array. Iwagami & Masuda (2010) extended the model to more complex network structures and showed that heterogeneous networks can be important amplifiers of upstream reciprocity. We show that non-uniform interaction rates naturally arise in the original model by Nowak & Roch (2007) and that when population structure favors some assortment of strategies more cooperative players end up playing more often as recipients than less cooperative players, i.e. that interaction rates are strategy-dependent. We find that the evolutionary dynamics of upstream reciprocity are modified when controlling for such non-uniformity by introducing participation costs, to the extent that whether or not upstream reciprocity is able to hitch-hike on mechanisms such as direct or network reciprocity depends on the cost of participation in the game.

4.2 Upstream reciprocity with participation costs

We briefly describe Nowak & Roch's model and its extension to include participation costs. A population V of n individuals plays the upstream reciprocity game. The strategy implemented by player v is denoted by $S_v(p_v, q_v)$, where q_v is the probability to initiate a chain of gratitude and p_v is the probability to pass a chain initiated by another player. Consider the random walk originated in player v. The random walk ends with probability $1 - q_v$ or moves to another player $w \in V - \{v\}$ with probability q_v. Then the walk ends with probability $1 - p_w$ or is passed to another player in $V - \{w\}$ with probability p_w. The process is repeated until the random walk ends. Each time the random walk enters a player it brings a benefit b to that player. Each time the random walk exits a player (without ending) it costs c to that player. In order for the game to be a social dilemma, $b > c > 0$.

Let us denote by N_v^{in} the number of times the random walk started by any player reaches v and by N_v^{out} the number of times such walk exits v without ending. In other words, N_v^{in} and N_v^{out} are, respectively, the number of times player v has acted as recipient and the number of times it has acted as donor. Finally, denote by N_v the total number of participations in a game by player v, i.e. $N_v := N_v^{in} + N_v^{out}$. With these definitions, the accumulated payoff to player v is given by

$$\pi_v = N_v^{in} b - N_v^{out} c. \tag{4.1}$$

This expression assumes that participation in a game is free. Let us now suppose that both the donor and the recipient pay a fee $d > 0$ for participating in the game. With participation costs, every time the random walk of gratitude reaches a player, it brings a net profit $b - d$ to that player, whereas every time the walk exits a player, it costs $c + d$ to that player. In order to analyze the effects of the introduction of participation costs in the game it thus suffices to make the replacements $b \to b - d$ and $c \to c + d$ in Eq. 4.1. We will make use of this simple fact in the next sections.

Consider now the evolutionary competition between individuals v and w when fitness is equated with the accumulated payoff. The difference in fitness can be expressed as

$$\Delta\pi := \pi_v - \pi_w = \left(N_v^{in} - N_w^{in}\right) b - \left(N_v^{out} - N_w^{out}\right) c - \left(N_v - N_w\right) d.$$

When $N_v = N_w$, the third term vanishes and the difference in fitness between players v and w is independent of the cost of participation d. When $N_v \neq N_w$, however, the difference in fitness depends on the participation cost d. Evolutionary game dynamics based on the fitness difference, such as the replicator equation (Hofbauer & Sigmund, 1998; Taylor & Jonker, 1978; Weibull, 1995), are thus influenced by the participation cost d when interaction rates are non-uniform.

Consider a random walk entering and exiting a player (i.e. an individual participating as recipient and immediately as donor) so that the increase in payoff for such player is equal to $\delta\pi := b - c - 2d$. One can identify two regimes in terms of the participation cost d: (i) $d < (b - c)/2$, and (ii) $d > (b - c)/2$. In regime (i), $\delta\pi > 0$. In this case, gratitude-related altruists can prevail by maximizing the number of waves of generosity being initiated and passed, as long as some mechanism of assortment makes such waves return more often to gratitude-related altruists than to other strategists. In regime (ii), $\delta\pi < 0$, and the optimal strategy is now to minimize the number of participations in a game. Defectors never initiate nor pass waves of generosity. Thus, they are expected to perform better than gratitude-related altruists in this regime, and to be evolutionarily stable.

In the following, we confirm these predictions in two models of upstream reciprocity, each one providing assortment of strategies in a different way: (i) by assuming non-random encounters, and (ii) by incorporating network reciprocity. The last model extends the results by Nowak & Roch (2007) and Iwagami & Masuda (2010) to cases when participation is costly.

4.3 Upstream reciprocity under assortment of encounters

Consider a population of size n and the interaction between strategy $S_1 = S(p_1, q_1)$, of relative frequency x, and strategy $S_2 = S(p_2, q_2)$, of relative frequency $1-x$. The cooperativity s_i of strategy S_i, defined as 'the expected number of secondary altruistic acts induced by a single player per time-step' (Nowak & Roch, 2007), is given by $s_i = q_i/(1-p_i)$. The expected fitnesses of S_1 and S_2 are given by their expected accumulated payoffs $\pi_1(x)$ and $\pi_2(x)$, and the evolutionary dynamics by the replicator equation, so that the frequency of S_1 in an infinite population evolves according to

$$\dot{x} = x(1-x)\Delta\pi(x), \tag{4.2}$$

where $\Delta\pi(x) := \pi_1(x) - \pi_2(x)$.

We introduce assortment of strategies in a simple manner (Boyd & Richerson, 1989; Eshel & Cavalli-Sforza, 1982; Rankin & Taborsky, 2009). We suppose that, once a player of type S_i has decided to initiate or pass a random walk of gratitude, the probability that the recipient is of type S_j is given by $\sigma_{ij} = \sigma_{ij}(x)$, with

$$\begin{aligned}\sigma_{11} &= \sigma + x(1-\sigma),\\ \sigma_{22} &= \sigma + (1-x)(1-\sigma),\end{aligned}$$

and $\sigma_{i1}+\sigma_{i2} = 1$, for $i = 1, 2$. The parameter $\sigma \in [0, 1]$ is the degree of assortment: when $\sigma = 0$ interactions are random and we recover the well-mixed limit; when $\sigma > 0$ strategies help their own type more often than what is expected by chance.

In this section we investigate the number of participations in a game by a player, and show that this quantity depends on the cooperativity of its strategy and on the degree of assortment. We also derive the conditions under which a given strategy is favored by natural selection in the framework of the replicator dynamics.

4.3.1 Number of participations

In order to calculate N_v^{in} and N_v^{out} for each $v \in V$, we follow closely the derivation presented in the supplementary material of Nowak & Roch (2007). For the sake of clarity, we also try to adopt their notation as much as possible. Notice, however, that the following results are for the general case of upstream reciprocity under assortment of encounters imposed by population structure, whereas Nowak & Roch targeted the link between direct and upstream reciprocity.

By a slight abuse of notation, let us denote by N_i^{out} (resp. N_i^{in}) the average number of times that an individual of type S_i acts as donor (resp. recipient) in a

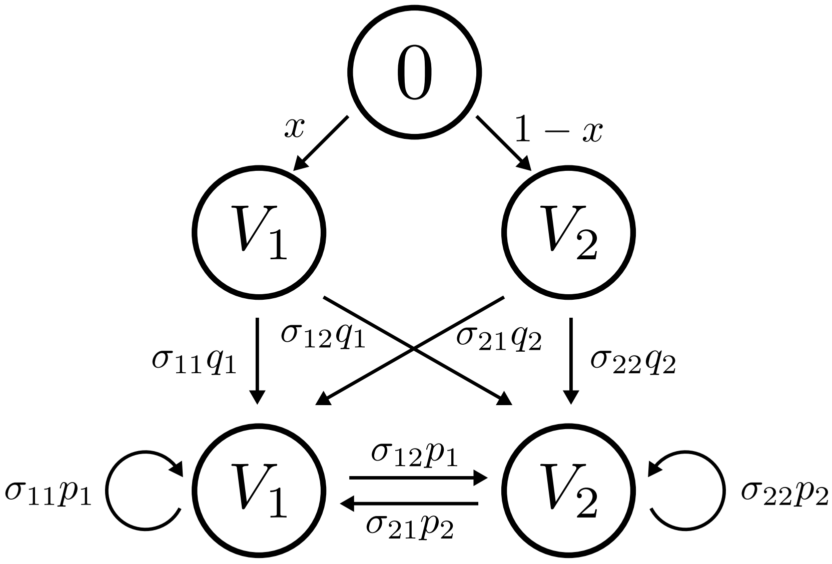


Figure 4.1: Transition graph of the Markov chain describing random walks of upstream reciprocity in the population of players. 0 is the initial state.

Donation game. Let us also denote by V_i the set of S_i players, so that $V = V_1 \cup V_2$. It is possible to compute N_2^{out} by counting the number of donations originating in V_2 and dividing by the total number of individuals of type S_2. Likewise to compute the number of times a player of type S_2 has acted as recipient. Finally, one can get N_1^{out} and N_1^{in} from N_2^{out} and N_2^{in} by permuting the strategy parameters and the proportions of the two strategies.

Let us first calculate N_2^{in}. In order to calculate this quantity we consider the Markov chain model shown in Fig. 4.1. With a probability x the random walk starts in a player belonging to V_1; with a probability $1-x$, in a player belonging to V_2. If we define M_{ij} as the number of times the walk enters any S_2 player when the walk starts on V_i and is conditioned to move to V_j at the first step, we can write

$$\begin{aligned}
N_2^{in} &= \frac{\sum_{v \in V_2} N_v^{in}}{n(1-x)} && (4.3)\\
&= \frac{nx\left(\sigma_{11}q_1M_{11} + \sigma_{12}q_1M_{12}\right) + n(1-x)\left(\sigma_{21}q_2M_{21} + \sigma_{22}q_2M_{22}\right)}{n(1-x)} && (4.4)\\
&= \frac{q_1x\left(\sigma_{11}M_{11} + \sigma_{12}M_{12}\right) + q_2(1-x)\left(\sigma_{21}M_{21} + \sigma_{22}M_{22}\right)}{1-x}. && (4.5)
\end{aligned}$$

In order to calculate M_{ij}, and for mathematical convenience, we expand the state space and consider all pairs of consecutive states, such that

$$U = \{u_1 = (V_1, V_1), u_2 = (V_1, V_2), u_3 = (V_2, V_1), u_4 = (V_2, V_2)\}$$

is the new extended space state, where the state (V_i, V_j) denotes the transition between the previous state V_i to the present state V_j. Thus, the substochastic transition matrix of the Markov chain excluding the first step (i.e. describing the transitions between the two lowest states in Fig. 4.1) is given by

$$\mathbf{P} = \begin{pmatrix} p_1\sigma_{11} & p_1\sigma_{12} & 0 & 0 \\ 0 & 0 & p_2\sigma_{21} & p_2\sigma_{22} \\ p_1\sigma_{11} & p_1\sigma_{12} & 0 & 0 \\ 0 & 0 & p_2\sigma_{21} & p_2\sigma_{22} \end{pmatrix}.$$

Now, defining

$$m_{11} = m_{21} = 0, m_{12} = m_{22} = 1,$$

so that m_{ij} is 1 if the walk moves from V to V_2 and 0 otherwise, we have, by the Markov property:

$$\begin{pmatrix} M_{11} \\ M_{12} \\ M_{21} \\ M_{22} \end{pmatrix} = \begin{pmatrix} m_{11} \\ m_{12} \\ m_{21} \\ m_{22} \end{pmatrix} + \mathbf{P} \begin{pmatrix} M_{11} \\ M_{12} \\ M_{21} \\ M_{22} \end{pmatrix}.$$

Solving this system of equations, we obtain the values M_{ij}. Plugging them in Eq. 4.5, we obtain after simplifying:

$$N_2^{in} = \frac{x(1-\sigma)(q_1 - q_2) + q_2(1 - \sigma p_1)}{\omega}, \tag{4.6}$$

with

$$\omega = 1 - [\sigma(1 - p_2) + x(1 - \sigma)]\, p_1 - [1 - x(1 - \sigma)]\, p_2. \tag{4.7}$$

We can use the same procedure to compute N_2^{out}. It suffices to reinterpret M_{ij} as the number of times the walk exits any S_2 player when the walk starts on V_i and is conditioned to move to V_j at the first step. In other words, M_{ij} is now the number of times that a single random walk initiated at V_i and that moves to V_j at the first step exits any S_2 player. Thus, we redefine

$$m_{11} = m_{12} = 0, m_{21} = m_{22} = 1,$$

i.e. m_{ij} is now 1 if the walk moves from V_2 to V to and 0 otherwise. Following the same procedure used before for N_2^{in}, we obtain:

$$N_2^{out} = \frac{q_2(1 - \sigma p_1) + x(1 - \sigma)(p_2 q_1 - p_1 q_2)}{\omega} \tag{4.8}$$

with ω given by Eq. 4.7.

Finally, we can get N_1^{in} and N_1^{out} from N_2^{in} and N_2^{out} by permuting the parameters and the proportions of the two strategies, i.e. by taking $p_1 \leftrightarrow p_2$, $q_1 \leftrightarrow q_2$, and $x \leftrightarrow (1-x)$. Thus we obtain

$$\begin{aligned} N_1^{in} &= \frac{(1-x)(1-\sigma)(q_2-q_1)+q_1(1-\sigma p_2)}{\omega}, && (4.9) \\ N_1^{out} &= \frac{q_1(1-\sigma p_2)+(1-x)(1-\sigma)(p_1 q_2 - p_2 q_1)}{\omega}. && (4.10) \end{aligned}$$

When the degree of assortment is zero, it is easy to show that $N_1^{in} = N_2^{in}$ and that the inequality $N_2^{out} > N_1^{out}$ simplifies to $s_2 > s_1$. Thus, when the population is well mixed, all individuals interact the same number of times as recipients, and individuals of the more cooperative strategy interact as donors more times than individuals of the less cooperative strategy. When the degree of assortment is greater than zero, it can be shown that both $N_2^{in} > N_1^{in}$ and $N_2^{out} > N_1^{out}$ simplify to $s_2 > s_1$. This means that if S_2 is more cooperative than S_1, S_2 individuals interact in more Donation games than S_1 individuals and that, by construction, more cooperative players play more rounds of the game than less cooperative players. In summary, for any value of σ, $s_1 > s_2 \Rightarrow N_1 > N_2$, i.e. an individual of the more cooperative strategy takes part in more games. This fact makes the replicator dynamics dependent on the participation cost d.

4.3.2 Difference in accumulated payoffs

The difference in accumulated payoffs between S_1 and S_2 is given by

$$\begin{aligned} \Delta\pi(x) &= \left[N_1^{in}(b-d) - N_1^{out}(c+d)\right] - \left[N_2^{in}(b-d) - N_2^{out}(c+d)\right] \\ &= (N_1^{in} - N_2^{in})(b-d) - (N_1^{out} - N_2^{out})(c+d). \end{aligned}$$

Replacing Eq. 4.6, 4.8, 4.9 and 4.10 in this formula and simplifying, we obtain

$$\Delta\pi(x) = \chi\psi/\omega,$$

where

$$\begin{aligned} \chi &= (b-d)\sigma - (c+d), \\ \psi &= q_1(1-p_2) - q_2(1-p_1), \\ \omega &= 1 - \left[\sigma(1-p_2) + x(1-\sigma)\right] p_1 - \left[1 - x(1-\sigma)\right] p_2. \end{aligned}$$

Selection favors S_1 over S_2 if $\Delta\pi(x) > 0$. As long as $p_1, p_2 < 1$, ω is always greater than 0. Thus, the condition $\Delta\pi(x) > 0$ only depends on the values of

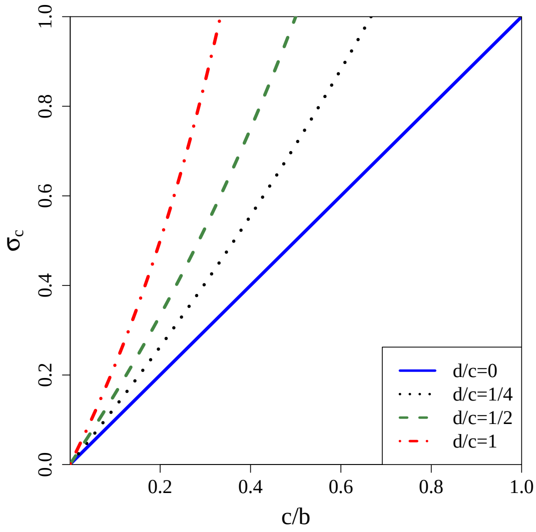


Figure 4.2: Critical degree of assortment σ_c as a function of the cost-to-benefit ratio c/b for different values of the ratio between the participation cost and the cost of cooperation d/c. Each curve divides the plane into two regions. If we assume that strategy S_1 is more cooperative than strategy S_2 and $d < (b-c)/2$, then S_1 dominates S_2 above the curve and S_1 dominates S_2 below the curve. For a fixed cost of cooperation c, increasing the cost of participation d reduces the region of dominance of the more cooperative strategy.

χ and ψ, which are independent of x. Furthermore, $\Delta\pi(x)$ adds no additional equilibria to the replicator equation given by Eq. 4.2, so that the only equilibria of the replicator equation are given by $x = 0$ and $x = 1$. If $\chi\psi > 0$, $x = 1$ is stable and S_1 dominates S_2. If $\chi\psi < 0$, $x = 0$ is stable and S_2 dominates S_1. Let us suppose that S_1 is more cooperative than S_2, i.e. $s_1 > s_2$. Then, ψ is also always greater than 0, and the condition $\Delta\pi(x) > 0$ reduces to $\chi > 0$. If $d < (b-c)/2$ selection favors the more cooperative strategy S_1 if $\sigma > \sigma_c$ and the less cooperative strategy if $\sigma < \sigma_c$, where

$$\sigma_c = \frac{c+d}{b-d} = \frac{1+d/c}{(c/b)^{-1} - d/c} \tag{4.11}$$

is the critical degree of assortment. σ_c is a monotonically increasing function of the cost of participation d, as we illustrate in Fig. 4.2 with some numerical examples. If $d > (b-c)/2$ selection always favors the less cooperative strategy S_2 irrespective of the degree of assortment and upstream reciprocity is doomed to extinction.

4.4 Upstream and network reciprocity

As a second model, we consider the evolution of upstream reciprocity when network reciprocity is also at work. Individuals are embedded in a social network of contacts represented by a simple graph. Interaction and competition are constrained to nearest neighbors in the network. The link between upstream and network reciprocity has been investigated analytically by Nowak & Roch (2007) for the case of the one-dimensional array and numerically by Iwagami & Masuda (2010) for the cases of regular lattices, random graphs and scale-free networks. Both studies report a synergistic interaction between upstream and network reciprocity. In the following we show that participation costs can suppress such synergy.

4.4.1 Analytical results

Let us first consider the analytical treatment reported by Nowak & Roch (2007). Strategies are still denoted by $S(p, q)$, where p is the probability of passing on and q the probability of initiating altruistic acts. Strategists with $p = 0$ do not implement upstream reciprocity, since they do not pass chains of gratitude. In particular, $S(0, 0)$ gives classical defectors (CDs) and $S(0, 1)$ gives classical cooperators (CCs). In contrast, when $p > 0$ we obtain strategies such $S(p, 0)$, passers-on (POs), that pass but not initiate and $S(p, 1)$, generous cooperators (GCs), that both pass and initiate. Players are arranged in a one-dimensional array and 'imitation updating' (Ohtsuki et al., 2006) is used as evolutionary dynamics. For this evolutionary dynamics, a player is randomly chosen from the entire population. Then it will either keep its strategy or imitate one of its neighbors' strategies proportional to fitness.

As shown by Nowak & Roch (2007) for the case of costless participation, GCs win against both CDs and CCs when

$$b/c > h(p) = \frac{8 + 2p + 8\sqrt{1 - p^2}}{3 + 4p + \sqrt{1 - p^2}}. \tag{4.12}$$

The function h is monotonically decreasing with the probability to pass p so that the larger the probability of passing p the lower the benefit-to-cost ratio b/c necessary for GCs to prevail in the population. With $p = 1$, $h(p)$ attains its minimum, $h(1) = 10/7$. The condition $b/c > 10/7$ is less stringent than the condition $b/c > 4$, obtained when only network reciprocity is at work (Ohtsuki et al., 2006; Ohtsuki & Nowak, 2006a). Thus, upstream reciprocity makes the evolution of cooperation by network reciprocity easier when participation is costless.

Let us consider a population comprising GCs and CDs arranged in a one-dimensional array, with players indexed with integer values, so that $v \in \{0, -1, -2, \ldots\}$

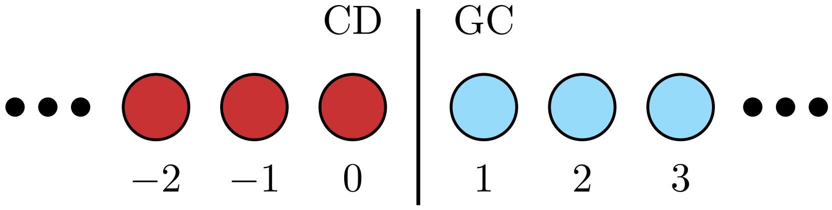


Figure 4.3: Classical defectors (CDs) and generous cooperators (GCs) arranged in a one-dimensional array.

play CD and $v \in \{1, 2, \ldots\}$ play GC (Fig. 4.3). Whether the GC−CD boundary will move to the left or to the right as result of the evolutionary dynamics depends only on the fitnesses of players $-1, 0, 1$ and 2, which depend in turn on the number of games played by those players. Fig. 4.4 plots the number of participations in a game by players $-1, 0, 1$ and 2 as functions of the probability p that a GC passes on a chain of gratitude (see 4.6 for the mathematical expressions). As in the model with assortment of encounters presented in Sec. 4.3, interaction rates are non-uniform such that more cooperative players tend to play more games than less cooperative players. The number of games played by an individual also depends on its position in the array. Thus, GCs farther from the GC−CD boundary interact more often than GCs closer to the boundary. Player 0 interacts exclusively as recipient, receiving but not passing random walks arriving from player 1. Players $-1, -2, \ldots$ do not interact at all and can actually be considered as loners that do not take part in any social interaction (Hauert et al., 2002).

Since interaction rates are non-uniform, evolutionary dynamics are modified when participation in the game has a cost d. The new results are obtained by making the replacements $b \to b - d$ and $c \to c + d$. The condition for the establishment of altruism thus changes to $(b - d)/(c + d) > h(p)$ or, equivalently, to

$$b/c > d/c + (1 + d/c) \times h(p) \tag{4.13}$$

with $h(p)$ as given in Eq. 4.12. Eq. 4.13 is harder to fulfill than Eq. 4.12 for any $d > 0$. This is shown in Fig. 4.5 for some numerical examples.

4.4.2 Simulation results

We now turn to the interaction between upstream and network reciprocity in less simple graph-structured populations. Such investigation has been recently pioneered by Iwagami & Masuda (2010), who in addition to confirm the synergistic interaction between upstream and network reciprocity, also point out the

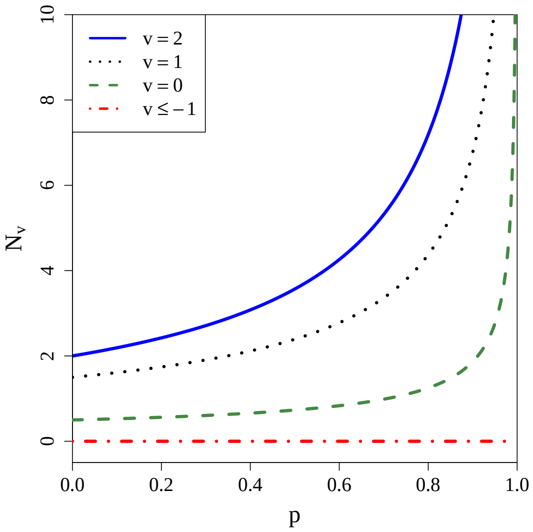


Figure 4.4: Number of participations in a game N_v by a player v as a function of the probability to pass p in the one-dimensional array. The GC–CD boundary is located between players 0 and 1, so that $v \in \{0, -1, -2, \ldots\}$ play CD and $v \in \{1, 2, \ldots\}$ play GC (see Fig. 4.3).

importance of heterogeneous networks as amplifiers of cooperation when fitness is given by the accumulated payoff and participation in the game is costless. Here, we study the cases when participation has some non-negligible cost.

We use different types of networks as population structures: rings (one-dimensional lattices), random regular networks, and Barabási-Albert scale-free networks (Barabási & Albert, 1999) (see 4.7 for more details on the construction of the random and scale-free networks). All the networks are of size $n = 10^4$. We use rings of degree $k = 2$ and $k = 8$, regular random networks with $k = 8$, and scale-free networks of average degree $\langle k \rangle = 8$. For the sake of comparison, we follow the setup considered by Iwagami & Masuda (2010) and described in the following. A simulation step comprises two phases. During the first phase each player in turn attempts to start an independent random walk. Players are assigned a payoff as a result of the interactions with neighboring players along the trajectories of the random walks. In the second phase, when all the random walks have ended, individuals update their strategies according to the obtained payoff. The evolutionary dynamics is the one suggested by Iwagami & Masuda (2010): n_u out of the n players are randomly selected each generation for strategy updating. They synchronously adopt the strategy of the individual with the highest payoff in their neighborhoods (including themselves). We consider the

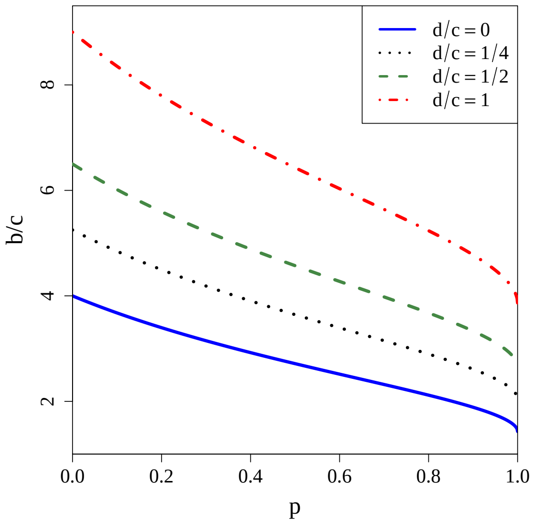


Figure 4.5: Critical benefit-to-cost ratio b/c for different values of the ratio between the participation cost and the cost of cooperation d/c in the one-dimensional array. Each curve divides the plane into two regions. Above the curve, GCs win against CDs; below the curve, GCs lose against CDs. For a fixed cost of cooperation c, increasing the cost of participation d reduces the region of dominance of GCs.

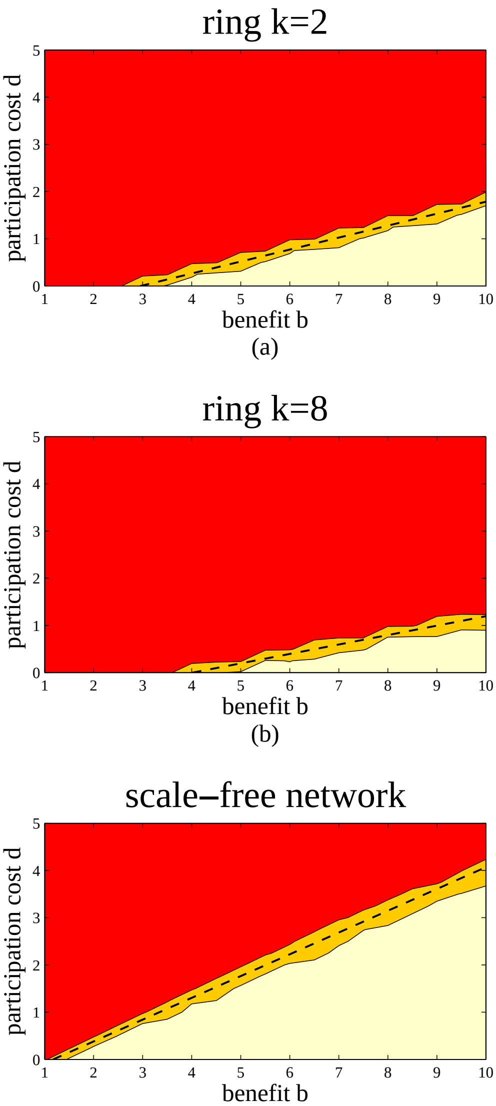
four strategies previously introduced: CDs, CCs, POs and GCs. For the strategies based on upstream reciprocity (POs and GCs) we set $p = 0.8$, and $n_u = 200$ for the evolutionary dynamics. Without loss of generality, we assume $c = 1$. We set the maximum number of rounds to 50000 for the scale-free networks, regular random graphs and the rings with $k = 2$, and to 150000 rounds for the rings with $k = 8$.

We found no qualitative differences in the results when we run simulations for other values of n_u (20 and 2000), p (0.7 and 0.9) and $\langle k \rangle$ (6 and 14). For reasons of space, we stick to the baseline model and show the results only for $n_u = 200$, $p = 0.8$ and $\langle k \rangle = 8$.

4.4.2.1 Populations comprising GCs and CDs

Before considering the competition among the four strategies, we first investigate the outcome of the evolutionary dynamics when only GCs and CDs are present in the population, for random initial configurations of 50% GCs. We found essentially the same results as those reported by Iwagami & Masuda (2010), namely, that network reciprocity can favor GCs over CDs, that degree-heterogeneous topologies are strong amplifiers of cooperation under both upstream and network reciprocity, and that CDs prevail in random regular structures, presumably because of the low clustering coefficient of this topology. Results are, however, dependent on the participation cost d. Fig. 4.6 shows the final fraction of GCs for different values of the benefit b and the participation cost d. The results for regular random graphs are not shown as defection always prevails in these structures for the region of parameters we considered. For the other population topologies, the higher the participation cost, the more difficult for gratitude-related altruists to be selected against pure defectors. In particular, GCs completely vanish if $d > (b - c)/2$ for all population structures. If $d < (b - c)/2$ the detrimental effect of participation costs in the evolution of upstream reciprocity is far less pronounced for scale-free networks than for the other population topologies.

The exact threshold value of the participation cost d above which CDs prevail can be approximated by making use of Eq. 4.13. In this case, it is reasonable to expect that h depends not only on p, but also on the network topology, the updating rule and the population size. In the absence of theoretical results, h can be numerically approximated by the value of the critical benefit-to-cost ratio when $d = 0$, which can be found by linearly interpolating the average final fraction of GCs resulting from the simulations. Following this procedure we obtained $h = 2.95$ for the rings with $k = 2$, $h = 4.01$ for the rings with $k = 8$, and $h = 1.17$ for the scale-free networks. We show the approximated critical values of d for each network with dashed lines in Fig. 4.6.



(a)

(b)

(c)

Figure 4.6: Average final fraction of GCs ρ for different networks when players initially adopt either GC or CD. We distinguish three zones: $\rho \leq 0.1$, $0.1 < \rho < 0.9$ and $\rho \geq 0.9$. Regions with smaller ρ are shown in darker tones. The dashed lines give the estimated critical values of d for the transition between evolutionary dynamics favoring GCs and evolutionary dynamics favoring CDs. We set $c = 1$ and, for GCs, $p = 0.8$.

4.4.2.2 Populations comprising CDs, CCs, POs and GCs

Fig. 4.7 shows the final fraction of the four strategies for the different networks when fitness is given by the accumulated payoff and participation is free or when it has a cost $d = 1$. The costless case is included for the sake of comparison and completeness, since the results are essentially the same as those found by Iwagami & Masuda (2010).

When participation is free, GCs are able to invade all population structures for sufficiently high values of b, except for the regular random graphs, in which CDs dominate for all the tested values of b. In the rings, the steady state makes a transition between a population dominated by CDs or POs to a population dominated by GCs at a given threshold value of b. Such threshold is higher for $k = 8$ than for $k = 2$. Scale-free networks are even more favorable to cooperation in general. In this case neither CDs nor POs go to extinction for all values of b. There is a coexistence of CCs and GCs, with the fraction of GCs increasing with b. With the addition of a participation cost $d = 1$ the point at which GCs statistically dominate the outcome of the simulations establishes at sensibly higher values of b. Additionally, CDs can now prevail in the scale-free networks for very low values of b.

4.5 Discussion

The main conclusion of Nowak & Roch (2007) is that 'upstream reciprocity alone does not select for cooperation, but can promote cooperation if it is linked to a mechanism for the evolution of cooperation', that is, a mechanism providing positive assortment of strategies. Such promotion seems to be a consequence of specific modeling choices, particularly the sampling of donor–recipient pairs along random walks in the population of individuals, and the fact that such sampling leads to non-uniform interaction rates in which more cooperative strategies engage in more rounds of the game per generation than less cooperative strategies. Hence, in Nowak & Roch's model, upstream reciprocity plays a role analogous to that of degree-heterogeneity in network reciprocity. In this sense upstream reciprocity does not constitute an independent mechanism for the evolution of cooperation, but can further enhance the levels of cooperation by inducing non-uniform interaction rates. However, while in evolutionary games on networks such non-uniformity in interaction rates is *strategy-independent* (e.g. some individuals interact more because they are placed in the hubs of a network of contacts), in Nowak & Roch (2007) it is *strategy-dependent*, which implies that more cooperative players end up interacting more times than less cooperative ones.

In this paper, we investigated one way of controlling such non-uniformity in the interaction rates of the players: the introduction of participation costs. Par-

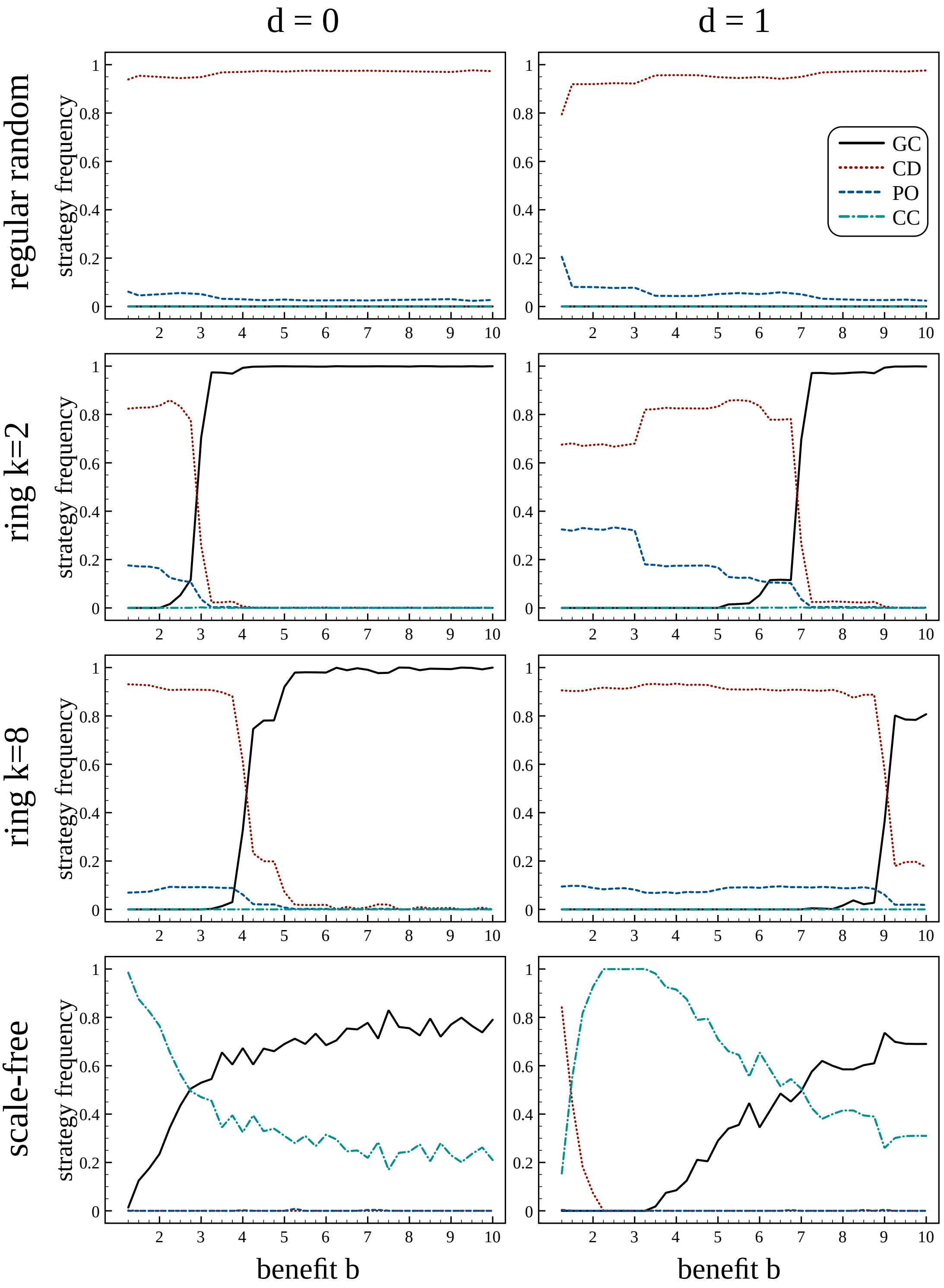


Figure 4.7: Final fractions of CDs, CCs, POs and GCs when the four strategies are initially present in the population. We set $c = 1$ and, for POs and GCs, $p = 0.8$.

ticipation costs implement the idea that there is often no free lunch when it comes to social interaction. Even players in the role of recipients have to be available to eager donors in order to get the benefit of altruistic acts directed towards them, and this availability may have a cost. We found that participation costs can have an important effect on the the evolution of upstream reciprocity. Gratitude-related altruism can be unbeatable with respect to defection when participation is free and there is some degree of assortment of strategies, provided for instance by population structure. However, defection can turn out to be the dominant strategy when participation is expensive. Specifically, the higher the participation cost, the higher the degree of assortment and/or the benefit-to-cost ratio needed for upstream reciprocity to evolve. Finally, when participation is so costly that $d > (b-c)/2$, the evolution of upstream reciprocity is totally suppressed. Similar results can be readily obtained if we consider direct reciprocity instead of network reciprocity as the mechanism responsible for building up assortment (see Section 4.8).

These results bear resemblance to those obtained by Masuda (2007), who found that participation costs influence the outcome of evolutionary games on degree-heterogeneous networks. In the case studied in this paper, the evolutionary dynamics under Nowak & Roch's model are found to be dependent on the participation cost not only for heterogeneous graphs, but also for any population structure, including well-mixed populations. In the case of networked games of upstream reciprocity, and contrastingly to the results obtained by Masuda (2007) regarding participation costs in network reciprocity alone, heterogeneous networks are more successful than homogeneous networks at promoting upstream reciprocity. Furthermore, scale-free networks were found to promote gratitude-based cooperation for practically all of the region out of the costly regime, i.e. for $d < (b-c)/2$. These highly heterogeneous networks greatly amplify even small positive payoffs resulting from passing along chains of gratitude.

A different but related way to control for the non-uniformity of interaction rates is by using the average payoff instead of the accumulated payoff when defining fitness (Santos & Pacheco, 2006; Tomassini et al., 2007). In this case, the fitness of player v is given by the accumulated payoff divided by the total number of interactions, that is

$$\pi_v = (N_v^{in} b - N_v^{out} c)/N_v. \tag{4.14}$$

Selection based on the average payoff can be justified when evolutionary dynamics emerge from imitation processes, where it is reasonable to think of individuals looking not at the accumulated payoff over many interactions but at typical or average outcomes of social interactions as the appropriate guidelines when targeting cultural models for imitation. It is easy to see that upstream reciprocity cannot evolve in Nowak & Roch's model when selection is based on the average payoff. Indeed, defectors act only as recipients in this model. Their average payoff (when interacting with a cooperative strategy that initiates and passes chains of gratitude) is thus always equal to b, which is the maximum possible value of Eq. 4.14. This fact is the direct result of two additional features of Nowak & Roch's model. First, participation in a game as a donor (i.e. initiating or passing chains of altruistic acts) is not compulsory but voluntary, and players can refrain from taking part in a game. Second, once a player has entered the game as donor it never refuses to help the recipient. Thus, defection is never actually experienced by recipients and only helping acts are passed and reciprocated. Hence, defection is interpreted as the refusal to participate in a game. All of this makes defection the obvious outcome of selection when fitness is given by the average payoff. A slightly different definition of the average payoff when the upstream reciprocity game is played on networks is to normalize the accumulated payoff by the degree of each player instead of by the total number of participations in a game (Iwagami & Masuda, 2010). The evolution of upstream reciprocity is also expected to be hampered when selection is based on this alternative definition of the average payoff.

We note that interaction rates are uniform in other models of upstream or generalized reciprocity (Boyd & Richerson, 1989; Pfeiffer et al., 2005; Hamilton & Taborsky, 2005; Rankin & Taborsky, 2009; Sigmund, 2010, pg. 82). Thus, the evolutionary dynamics in these models are invariant with respect to the introduction of participation costs (or to the replacement of the accumulated payoff by the average payoff). This means that the invasion conditions and the effective critical cost-to-benefit ratios derived in these papers are, in contrast to those derived by Nowak & Roch (2007) and Iwagami & Masuda (2010), unaffected by the replacements $b \to b - d$, and $c \to c + d$. Additionally, all of these models assume that participation is compulsory and, when considering Donation games, that participation as a donor does not equate with Donation. Donors can refrain from giving and recipients can experience defection. Strategists implementing upstream or generalized reciprocity can thus base their actions on whether they have been helped or have been refused help in the past. This last scenario is missing in the model of upstream reciprocity investigated by Nowak & Roch (2007) and Iwagami & Masuda (2010), where only altruistic acts can be passed and reciprocated. We think that this is a fundamental feature that cannot be omitted in models of reciprocity. When participation is compulsory and acts of defection are allowed to be passed and reciprocated, upstream reciprocity seems to be harder to explain from an evolutionary perspective, even in structured populations. This has already been shown for a model of non-random encounters, where it was found that generalized reciprocity is not evolutionarily stable against both unconditional cooperators and unconditional defectors under a Prisoner's dilemma equivalent to the Donation game (Rankin & Taborsky, 2009).

Acknowledgements

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4.6 Appendix. Upstream and spatial reciprocity: number of participations for GCs and CDs

Consider a population comprising GCs and CDs, arranged in a one-dimensional array. Players are indexed with integer values so that players $v \in \{0, -1, -2, \ldots\}$ play CD and players $v \in \{1, 2, \ldots\}$ play GC. The number of participations in the game can be found by making the replacements $b \to 1$ and $c \to -1$ in the expression for the fitness of player v (Eq. 8 in the supplementary material of Nowak & Roch (2007)). By plugging the values $p_0 = q_0 = 0$, $p_1 = p$ and $q_1 = 1$ in the formulas given by Nowak & Roch (2007), we obtain the following values for N_v:

$$
\begin{aligned}
N_2 &= 1 + \frac{(1+p)\left\{4H + (H-p)\left[H(2+p)+2p\right]\right\}}{(H-p)\left[4H - p^2(2+H)\right]}, \\
N_1 &= 1 + \frac{(1+p)\left[p(H-p)+2H\right]}{(H-p)(2H-p^2)}, \\
N_0 &= \frac{1}{2} + \frac{p\left[p(H-p)+2H\right]}{2(H-p)(2H-p^2)}, \\
N_{-1} &= 0,
\end{aligned}
$$

where

$$H = 1 + \sqrt{1-p^2}.$$

4.7 Appendix. Network models

Regular random networks In these networks every node has the same degree k, but its neighbors are randomly scattered in the graph. To build the networks we start from a one-dimensional lattice with degree k and apply the following algorithm, proposed by Szabó et al. (2004). A randomly selected link AB is removed from the network. A new link is then created going from B, which has lost one link, to a randomly selected node C, which has now one excess link. To maintain the same degree in C one of its edges, for example CD, is deleted. This process of creating a random link starting from the new less-connected node and removing an edge starting from the new more-connected node is repeated $2kn$ times to assure that the neighborhood is completely random. At this point a link between the less-connected player and the first player A, which also lacked one link, is created.

Scale-free networks Among the several available models for constructing scale-free networks (Newman, 2003), we use the one by Barabási & Albert (1999). Barabási–Albert networks are grown starting from a small clique of m_0 nodes. At each successive time step a new node is added such that its $m \leq m_0$ edges link it to m nodes already present in the graph. It is assumed that the probability p that a new node will be connected to node i depends on the current degree k_i of the latter. This is called the *preferential attachment* rule. The probability $p(k_i)$ of node i to be chosen is given by $p(k_i) = k_i / \sum_j k_j$, where the sum is over all nodes already in the graph. The model evolves into a network with power-law probability distribution for the vertex degree $P(k) \sim k^{-\gamma}$, with $\gamma \sim 3$ and $\langle k \rangle = 2m$. For the simulations, we used $m_0 = m = \langle k \rangle / 2$.

4.8 Appendix. Upstream and direct reciprocity

In addition to spatial reciprocity, Nowak & Roch (2007) also considered allowing some level of direct reciprocity in the strategies of players as means of introducing assortment of strategies and pave the way for the evolution of upstream reciprocity. Strategies are now given by $S(p, q, r)$ where r is the probability that help is immediately returned to the donor. Recipients reciprocate to the donor with probability r and help a random player with probability $(1 - r)p$. The cooperativity s_i of strategy S_i is now given by $s_i = q_i / [(1 - r_i)(1 - p_i)]$.

Consider the competition between strategies $S_1 = S(p_1, q_1, r_1)$ and $S_2 = S(p_2, q_2, r_2)$. If fitness is given by the accumulated payoff with $d = 0$, then the fitness difference is given by

$$\Delta\pi(x) := \pi_1(x) - \pi_2(x) = (N_1^{in} - N_2^{in})b - (N_1^{out} - N_2^{out})c.$$

According to Nowak & Roch (2007), such fitness difference is given by

$$\Delta\pi(x) = \alpha\beta/\gamma,$$

with

$$\begin{aligned}
\alpha &= q_1(1-r_2)(1-p_2) - q_2(1-r_1)(1-p_1), \\
\beta &= (br_2 - c)(1-r_1) - x(b-c)(r_2-r_1), \\
\gamma &= [x(1-p_1)(1-r_1(p_2(1-r_2)+r_2)) + (1-x) \\
&\quad \times (1-p_2)(1-r_2(p_1(1-r_1)+r_1))] \times (1-r_1)(1-r_2).
\end{aligned}$$

We can easily derive an expression for the difference in the number of times players of the two types have interacted $N(x) := N_1(x) - N_2(x)$, by making $b \to 1$ and $c \to -1$ in the expressions above. We thus obtain

$$N(x) = \alpha\widetilde{\beta}/\gamma,$$

where

$$\widetilde{\beta} = (1+r_2)(1-r_1) - 2x(r_2-r_1).$$

As long as $p_1, p_2 < 0$, γ is always greater than zero and as long as $0 < r_1, r_2 < 1$, $\widetilde{\beta}$ is always greater than zero. Thus, the condition $N(x) > 0$ reduces to $\alpha > 0$. We conclude that $s_1 > s_2$, with $s_i = q_i/\left[(1-r_i)(1-p_i)\right]$, implies $N_1 > N_2$.

Results are similar to those obtained with the model of non-random encounters analyzed in Sec. 4.3 of the present paper. If $s_1 > s_2$, then $N_1 > N_2$. Interaction rates are thus non-uniform and strategy-dependent. With non-zero participation costs the results presented by Nowak & Roch (2007) are valid up to the replacements $b \to b - d$ and $c \to c + d$. If $d > (b-c)/2$, selection always favors the strategy with lower cooperativity. If $d < (b-c)/2$, the critical ratio r_c defining phase transitions in the evolutionary dynamics is given by Eq. 4.11. Thus, for increasing values of the participation cost d, larger values of r are required for more cooperative strategies to win over less cooperative strategies and for upstream reciprocity to hitch-hike on direct reciprocity.

Chapter 5

Evolutionary dynamics of upstream reciprocity on cycles[†]

Abstract

Upstream reciprocity is one type of reciprocity according to which individuals help someone if they have been helped by somebody else in the past. Here, I study the evolutionary dynamics of upstream reciprocity on the simplest network structure (a cycle) by solving particular instances of the discrete heat equation, a partial difference equation used to model diffusion processes, e.g. the diffusion of heat on a rod. I find that, even when linked to population structure, upstream reciprocity is not evolutionarily stable against both unconditional cooperators and unconditional defectors. The obtained results cast some doubts on the generality of results previously obtained suggesting a synergistic interaction between upstream reciprocity and population structure.

5.1 Introduction

Why should an individual help another at a personal cost? Answers to this question, once regarded as a major theoretical problem faced by the theory of evolution by natural selection, broadly fall into two categories (Lehmann & Keller, 2006; West et al., 2007): (i) indirect fitness benefits, whereby there is a gain in fitness by aiding relatives, and (ii) direct fitness benefits, whereby the act of helping feeds back to the actor so that the resulting personal benefit outweighs the cost of the cooperative act. Indirect fitness benefits basically hinges on kin selection (Hamilton, 1964; Maynard Smith, 1964), alternatively viewed as group selection (Hamilton, 1975; Wilson, 1975) or, in the special case of limited dis-

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[†] J. Peña. *Working paper.*

persal in graph-structured populations, as network reciprocity (Nowak, 2006b; Ohtsuki et al., 2006). Direct fitness benefits can be brought about by a plethora of different mechanisms (West et al., 2007). Among these, direct and downstream indirect reciprocity have attracted much theoretical attention and are believed to play a key role in humans. Direct reciprocity is based on repeated interactions with the same partner (Axelrod & Hamilton, 1981; Trivers, 1971) and is said to occur if individuals preferentially help those that have helped them in the past, i.e. if they act as if according to the motto 'help those who helped you'. Downstream indirect reciprocity (Boyd & Richerson, 1989; Nowak & Sigmund, 1998b, 2005), is based on reputation. It can be understood as 'a consequence of direct reciprocity occurring in the presence of interested audiences' (Alexander, 1987), where individuals behave as if their maxim was to 'help those who have helped someone in the past'.

Yet a third type of reciprocity, known alternatively as upstream (indirect) reciprocity (Boyd & Richerson, 1989; Iwagami & Masuda, 2010; Nowak & Roch, 2007; Peña et al., 2011), generalized reciprocity (Barta et al., 2011; Hamilton & Taborsky, 2005; Pfeiffer et al., 2005; Rankin & Taborsky, 2009; van Doorn & Taborsky, 2011) or misguided reciprocity (Sigmund, 2010), has been also considered in theoretical models of the evolution of cooperation. Upstream reciprocity happens if individuals help third parties after they have been helped, as if implementing the heuristic 'help someone, if you have been helped' (see Figure 5.1 for a graphical comparison of direct, downstream and upstream reciprocity). Upstream reciprocity has been the focus of some attention during the last years for two reasons. First, it does not require partner recognition, memory of previous encounters or language and social norms (Pfeiffer et al., 2005; Rutte & Taborsky, 2007). Thus, if viable, cooperation based on upstream reciprocity should in principle be more common in nature than that based on direct or downstream reciprocity. Second, there is empirical evidence showing that upstream reciprocity occurs not only in humans (Bartlett & DeSteno, 2006; Berkowitz & Daniels, 1964; Dufwenberg et al., 2001; Güth et al., 2001; Isen, 1987; Stanca, 2009), but also in other animals, as demonstrated by a recent study on Norwegian rats (Rutte & Taborsky, 2007). In spite of this, and in stark contrast to what happens with direct and downstream reciprocity, upstream reciprocity has proved to be more difficult to explain from an evolutionary perspective (Nowak & Roch, 2007; Pfeiffer et al., 2005; Rankin & Taborsky, 2009; Sigmund, 2010). Indeed, it is unclear how the act of helping could feed back again to the original donor when supplied randomly, unless interactions are carried out in small groups (Hamilton & Taborsky, 2005; Pfeiffer et al., 2005), structured populations (Iwagami & Masuda, 2010; Nowak & Roch, 2007; Rankin & Taborsky, 2009; van Doorn & Taborsky, 2011) or in the presence of other mechanisms such as direct reciprocity (Nowak & Roch, 2007).

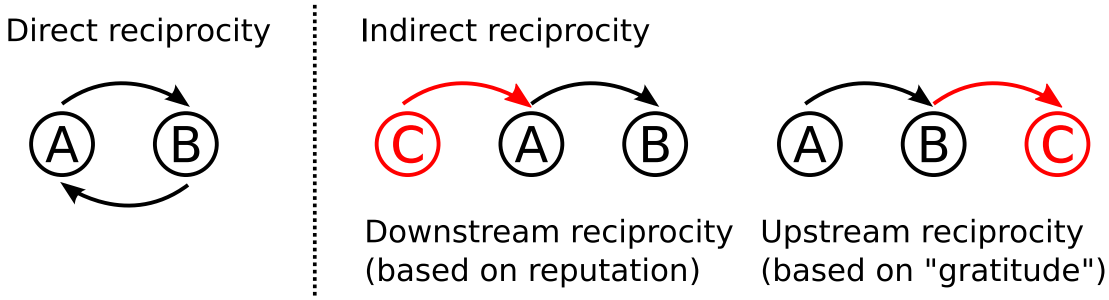

Figure 5.1: Three flavors of reciprocity. In direct reciprocity, if A helps B, B helps A. In downstream reciprocity, if C observes that A helps B, C helps A. In upstream reciprocity (also called generalized reciprocity) if A helps B, B helps C.

In Nowak & Roch (2007), a way of modeling social interactions as random walks of cooperative acts in a networked population was introduced and used to show that upstream reciprocity could evolve if linked to limited dispersal on a simple one-dimensional array, i.e. ‘spatial reciprocity’. This result has been recently extended to other network topologies by Iwagami & Masuda (2010) and van Doorn & Taborsky (2011), who have shown that the heterogeneity, sparseness and modularity of interaction networks can further promote cooperation based on upstream reciprocity. The model by Nowak & Roch (2007), however, is based on particular assumptions that can lead to confusion and misunderstandings (Peña et al., 2011). First, interaction rates are heterogeneous and strategy-dependent so that, by construction, more cooperative players end up playing more often than less cooperative ones. This makes difficult to evaluate whether upstream reciprocators fare well because of the merits of their strategy or just because they interact more often than other players, hence accumulating larger payoffs. Second, individuals never experience actual defection from donors refusing to help. Rather, ‘defection’ is equated to opting out of playing the next round as donor. This makes confusing the distinction between unconditional and conditional strategies. For instance, classical cooperators, *sensu* Nowak & Roch (2007), initiate waves of gratitude but do not reciprocate them. This is in stark contrast to unconditional cooperators in models of direct and downstream reciprocity, who *always* help.

Here, I investigate a model of upstream reciprocity where the population is structured as a cycle, i.e. a one-dimensional array, much in the same spirit as in Nowak & Roch (2007). Contrastingly to Nowak & Roch’s model, however, interaction rates are homogeneous and participation in a game is compulsory, as in other models of upstream or generalized reciprocity (Boyd & Richerson, 1989; Hamilton & Taborsky, 2005; Pfeiffer et al., 2005; Rankin & Taborsky, 2009;

Sigmund, 2010). I consider three strategies: *cooperators*, *defectors* and *upstream reciprocators*. In the model presented in this study, upstream reciprocators can experience defection from refused donations, and guide their behavior accordingly, whereas cooperators (defectors) always (never) help, irrespective of the actions of their neighbors in previous time steps. In this sense, the strategies considered here are equivalent to those used in previous models of upstream reciprocity (Rankin & Taborsky, 2009; Sigmund, 2010). Conditions for the evolutionary replacement of clusters of one strategy by clusters of another strategy are derived by solving particular instances of the discrete heat equation, a partial difference equation usually used to model diffusion processes in discrete time and space, such as heat on a rod (Cheng, 2003; Lawler, 2010).

5.2 Model

5.2.1 Population structure and game dynamics

Imagine a population structured as a one-dimensional array or a cycle, so that individual i interacts with two neighbors: its left neighbor $(i-1)$ and its right neighbor $(i+1)$. Social interactions are modeled as a repeated Donation game (Sigmund, 2010). Each round of the game every player plays once as donor with a randomly chosen neighbor (either the left or the right) as recipient. The donor can opt to help the recipient or not. If the donor helps, its payoff is reduced by c and the recipient's payoff is increased by b, with $b > c > 0$. If the donor decides not to help, the payoffs of both donor and recipient are left unchanged. Note that, since recipients are chosen randomly, each round a given player interacts on average once as recipient (0 times with probability $1/4$, once with probability $1/2$ and twice with probability $1/4$). Finally, with probability $0 < w < 1$, another round of the game is played. Thus, the number of interaction rounds follows a geometric distribution with parameter w and the average number of rounds per generation is given by $1/(1-w)$.

5.2.2 Strategies and average payoffs

I consider three different strategies: *cooperators* (Cs) who always donate, *defectors* (Ds) who never donate, and *upstream reciprocators* (Rs) who donate only if they experienced a succesful donation the last time they interacted as recipients. Each strategy can be thought of as implemented by means of an automaton with two states: the helping state and the defecting state. If an individual is in his helping state, he will help when acting as donor, if he is in the defecting state, he will refuse to help. Let us denote by $h_n(i)$ the probability that player i is in the helping state at time step n. By definition, $h_n(i) = 1\ \forall n$ if i is a C and $h_n(i) = 0\ \forall n$ if i is a D. If i is a R, the probability of being in the helping state at time step $n+1$ depends on the recursion[1]

$$h_{n+1}(i) = \frac{1}{4} h_n(i) + \frac{3}{8}\left[h_n(i-1) + h_n(i+1)\right], \tag{5.1}$$

It will be assumed that all Rs start with the same probability ρ in the helping state, i.e. $h_0(i) = \rho\ \forall i$.

It then follows that the expected payoff of player i in the n-th round, $P_n(i)$, is given by

$$P_n(i) = \frac{1}{2}\left[h_n(i-1) + h_n(i+1)\right] b - h_n(i)c,$$

and the expected value of the total payoff by

$$\begin{aligned} P_i &= \sum_{n=0}^{+\infty} w^n P_n(i) \\ &= \frac{1}{2}\left[\left(\sum_{n=0}^{+\infty} w^n h_n(i-1)\right) + \left(\sum_{n=0}^{+\infty} w^n h_n(i+1)\right)\right] b - \left(\sum_{n=0}^{+\infty} w^n h_n(i)\right) c. \end{aligned}$$

Now, defining

$$h_i^* := \sum_{n=0}^{+\infty} w^n h_n(i) \tag{5.2}$$

as the expected value of the helping state of individual i, we can finally write

$$P_i = \frac{1}{2}(h_{i-1}^* + h_{i+1}^*)b - h_i^* c. \tag{5.3}$$

Note that, if i is a D, $h_i^* = 0$ and if i is a C, $h_i^* = 1/(1-w)$.

5.2.3 Evolutionary dynamics

As in Nowak & Roch (2007), assume that there are two contiguous infinite clusters of related players on the line, C_0 and C_1, so that individuals $i \in \{0, -1, -2, \ldots\}$ play strategy A and individuals $i \in \{1, 2, 3, \ldots\}$ play strategy B (see Fig. 5.2). Payoffs accumulated during the rounds of the iterated Donation game translate into fitness. More specifically, let the fitness f_i of player i be given by $f_i = 1 + sP_i$, where P_i is the expected payoff of individual i (given by Eq. 5.3) and s is the strength of selection.

---

[1] Here, I assume that if i is recipient of both $i-1$ and $i+1$ at time step n, the probability that i will be in the helping state at time step $n+1$ is 0 if neither $i-1$ nor $i+1$ helped, 1/2 if only $i-1$ or $i+1$ helped and 1 if both $i-1$ and $i+1$ helped.

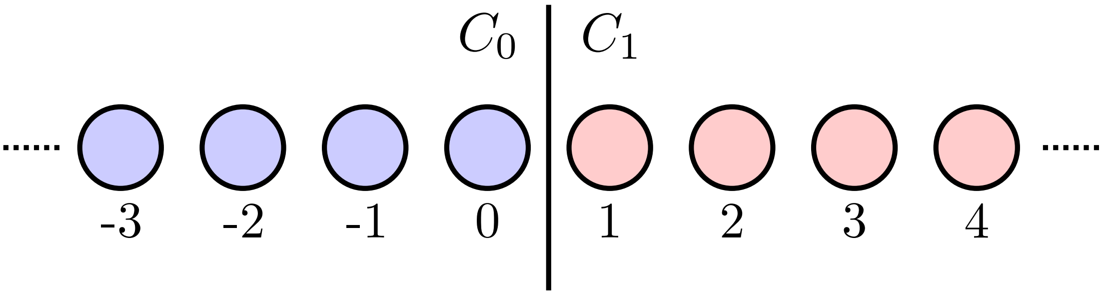

Figure 5.2: The simplest population structure. Players are arranged on a cycle (one-dimensional lattice). They can interact only with their left and right neighbors. Consider an infinite cluster C_0 of individuals of type A next to an infinite cluster C_1 of individuals of type B. Players play the iterated donation game and accumulate payoffs. Payoffs are translated to fitness and evolution is modeled by means of a given stochastic process. Which cluster will expand at the expenses of the other and win the evolutionary race?

For the evolutionary dynamics, and in order to be able to compare the results with those by Nowak & Roch (2007), I consider 'imitation updating' (IM): each time step a random individual is chosen to update its strategy so that she will either stay with her own strategy or adopt one of her neighbors proportional to fitness (Ohtsuki et al., 2006). In section 5.7, I derive the same results for other two stochastic processes: 'birth-death' (BD) and 'death-birth' (DB). In any case, it is clear that the population changes if and only if individuals at the $C_0 - C_1$ boundary are involved in the reproduction/death or imitation stages. In this case, it is also obvious that the configuration stays the same up to a translation. The final fate of the population thus simply depends on whether the C_0 cluster is more likely to invade the C_1 cluster at the initial state, or vice versa. It is easy to show that, in the limit of weak selection ($s \ll 1$) C_1 is more likely to invade C_0 for IM updating when (Nowak & Roch, 2007)

$$3P_1 + P_2 > P_{-1} + 3P_0. \tag{5.4}$$

5.3 Results

5.3.1 Populations comprising upstream reciprocators and defectors

Let us first consider the case where C_0 is a cluster of Ds and C_1 a cluster of Rs. Replacing Eq. 5.3 into Eq. 5.4 and simplifying, we obtain that Rs invade Ds more easily than the converse if

$$b/c > \frac{6h_1^* + 2h_2^*}{h_3^* + 3h_2^* - 2h_1^*}. \tag{5.5}$$

Hence, in order to evaluate the critical benefit-to-cost ratio above which Rs win over Ds, one needs to compute h_1^*, h_2^* and h_3^*, as given by Eq. 5.2. This would in turn require us to solve Eq. 5.1 under the initial condition

$$h_0(i) = \rho, \ i \geq 1$$

and the boundary condition

$$h_n(i) = 0, \ i = 0.$$

Here, I proceed in a different but at the same time more general way. Consider a cluster of j Rs in the middle of a population of Ds so that individuals $i \in \{1, 2, \dots j\}$ are Rs and individuals $i \leq 0$ and $i \geq j+1$ are Ds. In this case, the initial condition becomes

$$h_0(i) = \rho, \ 1 \leq i \leq j \tag{5.6}$$

and the boundary condition,

$$h_n(i) = 0, \ i = 0, i = j+1. \tag{5.7}$$

The solution for the two contiguous, infinite clusters can be recovered by taking the limit when $j \to \infty$ of the solution of Eq. 5.1 under the initial condition given by Eq. 5.6 and the boundary condition given by Eq. 5.7.

A trivial solution is found if $\rho = 0$. In this case, $h_n(i) = 0 \ \forall i$: Rs start and continue for ever in the defecting state, thus behaving effectively as Ds. As a result, nobody helps, Rs are neutral with respect to Ds and evolution proceeds completely by random drift. For $0 < \rho \leq 1$, the dynamics of $h_n(i)$ are a particular case of the discrete heat equation analyzed in section 5.5 with parameters $\alpha = 1/4$, $\beta = 3/8$, $a = \rho$ and $d = 0$. In this case, and in the limit when $j \to \infty$ and $w \to 1$, h_i^* is equivalent to u_i^* as calculated in section 5.6 and given by Eq. 5.34.

Let us write $\theta = \pi/(j+1)$. Then replacing Eq. 5.34 into Eq. 5.5 and simplifying we can write

$$b/c > \frac{6\sin\theta + 2\sin 2\theta}{\sin 3\theta + 3\sin 2\theta - 2\sin\theta}. \tag{5.8}$$

Making use of trigonometric identities we can simplify the previous expression to

$$\begin{aligned} b/c \ &> \ \frac{6\sin\theta + 4\sin\theta\cos\theta}{3\sin\theta - 4\sin^3\theta + 6\sin\theta\cos\theta - 2\sin\theta} \\ &= \ \frac{6 + 4\cos\theta}{3 - 4\sin^2\theta + 6\cos\theta - 2}. \end{aligned}$$

In the limit when $j \to \infty$, $\theta \to 0$, we can finally write

$$b/c > \frac{10}{7}. \tag{5.9}$$

Thus, upstream reciprocators win against defectors when $b/c > 10/7$. Interestingly, this is the same condition found by Nowak & Roch (2007) for 'upstream cooperators' $S(p, 1)$ winning against defectors $S(0, 0)$ when $p = 1$.

5.3.2 Populations comprising upstream reciprocators and cooperators

Let us now consider the case where C_0 is a cluster of Cs and C_1 a cluster of Rs. It turns out that this case is easier to analyse if we keep track, not of the probability of being in the helping state, $h_n(i)$, but of the probability of being in the defective state, $d_n(i) = 1 - h_n(i)$. In this case, it is easy to show that the recursion we need to solve is

$$d_{n+1}(i) = \frac{1}{4} d_n(i) + \frac{3}{8} \left[d_n(i-1) + d_n(i+1) \right], \tag{5.10}$$

with the initial condition

$$d_0(i) = 1 - \rho, \ 1 \leq i \leq j \tag{5.11}$$

and the boundary condition

$$d_n(i) = 0, \ i = 0, i = j + 1, \tag{5.12}$$

in the limit of large j.

Note the similarity between this case and the case analyzed in the previous section. The trivial solution is now when $\rho = 1$: in this case we have $d_n(i) = 0 \ \forall i$, so that Rs behave effectively as Cs, everybody helps, Rs are neutral with respect to Cs and evolution proceeds completely by random drift. For $0 < \rho \leq 1$, the dynamics of $d_n(i)$ are again a particular case of the discrete heat equation analyzed in section 5.5, now with parameters $\alpha = 1/4$, $\beta = 3/8$, $a = 1 - \rho$ and $d = 0$.

It is also easy to show that

$$h_i^* = \frac{1}{1 - w} - d_i^*, \tag{5.13}$$

so that, from Eq. 5.3, Eq. 5.4 and Eq. 5.13 we obtain that Rs invade Cs more easily than the converse if

$$b/c < \frac{6d_1^* + 2d_2^*}{d_3^* + 3d_2^* - 2d_1^*}. \tag{5.14}$$

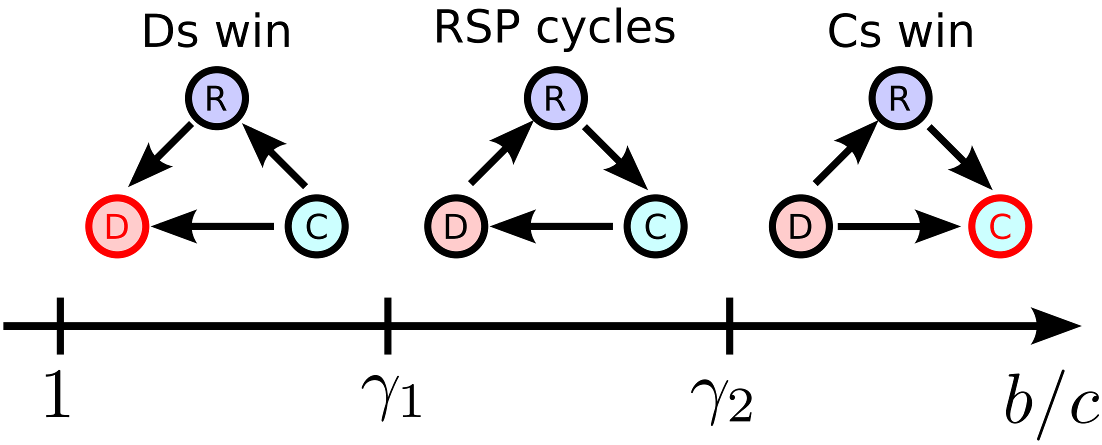

Figure 5.3: ‘Invasion’ analysis. In the limit $w \to 1$ and for all of the studied evolutionary dynamics, if $1 < b/c < \gamma_1$, clusters of Ds expand against clusters of Cs and of Rs; if $\gamma_1 < b/c < \gamma_2$, there is a rock-scissors-paper dynamics with clusters of Ds losing against clusters of Rs, clusters of Rs losing against clusters of Cs, and clusters of Cs losing against clusters of Ds; if $b/c > \gamma_2$ then unconditional cooperation beats both unconditional defection and upstream reciprocity. See Table 5.1 for the values of γ_1 and γ_2 for the different updating rules.

Once more, and in the limit when $j \to \infty$ and $w \to 1$, d_i^* is equivalent to u_i^* as calculated in section 5.6 and given by Eq. 5.34. Making use of this we finally arrive at the condition $b/c < 10/7$. Note that from this result and that obtained in the preceding subsection, upstream reciprocators win against Ds when they lose against Cs and vice versa.

5.3.3 Populations comprising cooperators and defectors

Let us finally consider the case where C_0 is a cluster of Ds and C_1 a cluster of Cs. In this case it is easy to show that the condition for Cs to win over Ds is the same as that given in Eq. 5.5, only that in this case $h_i^* = 1/(1-w)$ for $i \geq 1$. The condition becomes

$$b/c > 4, \tag{5.15}$$

as it has been derived previously in other works (Nowak & Roch, 2007; Ohtsuki et al., 2006).

5.3.4 Summary

In summary, the evolutionary dynamics of upstream reciprocity on cycles in the limit of infinitely repeated interactions ($w \to 1$) and infinitely large populations

Table 5.1: Critical benefit-to-cost ratios.

updating rule	γ_1	γ_2
IM	10/7	4
DB	6/5	2
BD	2	∞

The table shows the critical benefit-to-cost ratio below which defectors dominate (γ_1) and above which cooperators dominate (γ_2) for three different updating rules: 'imitation updating' (IM), 'death-birth' (DB) and 'birth-death' (BD).

is governed by two benefit-to-cost ratios γ_1 and γ_2 so that (see Fig. 5.3)

1. For $1 < b/c < \gamma_1$ clusters of Ds expand against clusters of Cs and Rs.
2. For $\gamma_1 < b/c < \gamma_2$ there is a rocks-scissors-paper dynamics so that clusters of Rs win against clusters of Ds, which win against clusters of Cs, which finally win against clusters of Rs.
3. For $b/c > \gamma_2$ clusters of Cs expand against clusters of Ds and Rs.

The values for γ_1 and γ_2 are shown in Table 5.1 for IM, DB and BD updating (see section 5.7 for the derivation of the results for DB and BD updating). Note that upstream reciprocators are never advantageous over Ds and Cs at the same time. Note also that IM updating is the less disfavoring evolutionary dynamics, as the region of the parameter space where rock-scissors-paper dynamics are present is the largest. For BD, Cs are never advantageous.

5.4 Conclusions

In the model investigated in this study, and in contrast to the model by Nowak & Roch (2007), upstream reciprocity does not select for cooperation when linked to population structure in the form of a one-dimensional array. Upstream reciprocators, who help if previously helped and defect otherwise, are never simultaneously advantageous to both cooperators and defectors. For intermediate benefit-to-cost ratios, the evolutionary dynamics displays a rock-scissors-paper cycle, in which defectors are replaced by upstream reciprocators, upstream reciprocators by cooperators, and cooperators by defectors. This is reminiscent of the cycles featured by defectors, loners and cooperators in models of public good games with voluntary participation (Hauert et al., 2002).

The results presented in this study can be extended in several ways. First, finite populations can be considered. Indeed, expressions for the expected total payoff of different strategists in different configurations are readily available from the solutions to the heat equation presented in sections 5.5 and 5.6, which are valid for any number j of individuals. Second, the effect of w on the evolutionary dynamics should be investigated in detail. Finally, the model shall be extended to take into account the possibility that individuals are prone to implementing errors, i.e. failing to give intended donations.

Acknowledgements

I would like to thank Daniel J. Rankin for discussion and his comments on the model.

5.5 Appendix. Discrete heat equation

Consider the following discrete heat equation

$$u_{n+1}(i) = \alpha u_n(i) + \beta\left[u_n(i-1) + u_n(i+1)\right],\ 1 \le i \le j, \tag{5.16}$$

with $\alpha + 2\beta \le 1$, under the initial condition

$$u_0(i) = a,\ 1 \le i \le j, \tag{5.17}$$

and the periodic boundary condition

$$u_n(i) = d,\ i = 0,\ i = j+1. \tag{5.18}$$

This equation can be readily solved using techniques of partial difference equations (Cheng, 2003). Defining

$$\mathbf{u}_n := \left(u_n(1), u_n(2), \ldots, u_n(j)\right)^T,$$

and

$$\mathbf{q} := (\beta d, 0, \ldots, 0, \beta d)$$

we can rewrite Eq. 5.16 and 5.18 as the vector equation

$$\mathbf{u}_{n+1} = \mathbf{A}\mathbf{u}_n + \mathbf{q},$$

where $\mathbf{A}$ is the tridiagonal matrix

$$\mathbf{A} = \begin{pmatrix} \alpha & \beta & 0 & 0 & \ldots & 0 & 0 \\ \beta & \alpha & \beta & 0 & \ldots & 0 & 0 \\ 0 & \beta & \alpha & \beta & \ldots & 0 & 0 \\ & & & & \vdots & & \\ 0 & 0 & 0 & 0 & \ldots & \alpha & \beta \\ 0 & 0 & 0 & 0 & \ldots & \beta & \alpha \end{pmatrix}.$$

Now, by induction

$$\mathbf{u}_{n+1} = \mathbf{A}^{n+1}\mathbf{u}_0 + \sum_{k=0}^{n} \mathbf{A}^k \mathbf{q}. \tag{5.19}$$

Moreover, the eigenvalues of $\mathbf{A}$ can be shown to be given by

$$\lambda_l = \alpha + 2\beta \cos\left(\frac{l\pi}{j+1}\right),\ l = 1, \ldots, j, \tag{5.20}$$

and the corresponding eigenvectors by

$$\mathbf{v}_l = \frac{2}{j+1}\left[\sin\left(\frac{l\pi}{j+1}\right), \sin\left(\frac{2l\pi}{j+1}\right), \ldots, \sin\left(\frac{jl\pi}{j+1}\right)\right]^T \tag{5.21}$$

where $2/(j+1)$ is chosen as scaling factor in order for the set of eigenvectors to form an orthonormal basis.

We can now express $\mathbf{A}$ as the spectral decomposition

$$\mathbf{A} = \sum_{l=1}^{j} \lambda_l \mathbf{v}_l \mathbf{v}_l^T, \tag{5.22}$$

so that the general solution to the discrete heat equation can now be formulated as

$$\begin{aligned} \mathbf{u}_{n+1} &= \sum_{l=1}^{j} \lambda_l^{n+1} \mathbf{v}_l \mathbf{v}_l^T \mathbf{u}_0 + \sum_{l=1}^{j}\sum_{k=0}^{n} \lambda_l^k \mathbf{v}_l \mathbf{v}_l^T \mathbf{q} && (5.23) \\ &= \sum_{l=1}^{j} \lambda_l^{n+1} \mathbf{v}_l \mathbf{v}_l^T \mathbf{u}_0 + \sum_{l=1}^{j} \frac{1-\lambda_l^{n+1}}{1-\lambda_l} \mathbf{v}_l \mathbf{v}_l^T \mathbf{q}. && (5.24) \end{aligned}$$

Writing the previous formula explicitly in non-matrix form

$$\begin{aligned} u_{n+1}(i) &= \frac{2}{j+1}\sum_{l=1}^{j} \lambda_l^{n+1} \sin\left(\frac{il\pi}{j+1}\right)\sum_{m=1}^{j} \sin\left(\frac{ml\pi}{j+1}\right) u_0(m) && (5.25) \\ &+ \frac{2}{j+1}\sum_{l=1}^{j} \frac{1-\lambda_l^{n+1}}{1-\lambda_l} \sin\left(\frac{il\pi}{j+1}\right)\sum_{m=1}^{j} \sin\left(\frac{ml\pi}{j+1}\right) q(m). && (5.26) \end{aligned}$$

Replacing the values of $\mathbf{u}_0$ and $\mathbf{q}$:

$$\begin{aligned} u_{n+1}(i) &= \frac{2a}{j+1}\sum_{l=1}^{j} \lambda_l^{n+1} \sin\left(\frac{il\pi}{j+1}\right)\sum_{m=1}^{j} \sin\left(\frac{ml\pi}{j+1}\right) && (5.27) \\ &+ \frac{2\beta d}{j+1}\sum_{l=1}^{j} \frac{1-\lambda_l^{n+1}}{1-\lambda_l} \sin\left(\frac{il\pi}{j+1}\right) \times && (5.28) \\ &\left[\sin\left(\frac{l\pi}{j+1}\right) + \sin\left(\frac{jl\pi}{j+1}\right)\right]. && (5.29) \end{aligned}$$

Now, making use of the trigonometric identities

$$\sum_{k=1}^{n} \sin kx = \sin \frac{nx}{2} \sin \frac{(n+1)x}{2} \csc \frac{x}{2}$$

and

$$\sin x + \sin y = 2 \sin \frac{x+y}{2} \cos \frac{x-y}{2},$$

we obtain after simplifying

$$\begin{aligned} u_{n+1}(i) &= \frac{2a}{j+1} \sum_{l=1}^{j} \lambda_l^{n+1} \sin\left(\frac{il\pi}{j+1}\right) \sin\left(\frac{l\pi}{2}\right) \sin\left(\frac{jl\pi}{2(j+1)}\right) \csc\left(\frac{l\pi}{2(j+1)}\right) \\ &\quad + \frac{4\beta d}{j+1} \sum_{l=1}^{j} \frac{1-\lambda_l^{n+1}}{1-\lambda_l} \sin\left(\frac{il\pi}{j+1}\right) \sin\left(\frac{l\pi}{2}\right) \cos\left(\frac{(j-1)l\pi}{2(j+1)}\right). \end{aligned}$$

Defining

$$\nu_l := \frac{2a}{j+1} \sin\left(\frac{l\pi}{2}\right) \sin\left(\frac{jl\pi}{2(j+1)}\right) \csc\left(\frac{l\pi}{2(j+1)}\right) \tag{5.30}$$

and

$$\xi_l := \frac{4\beta d}{j+1} \sin\left(\frac{l\pi}{2}\right) \cos\left(\frac{(j-1)l\pi}{2(j+1)}\right), \tag{5.31}$$

we can finally write

$$u_n(i) = \sum_{l=1}^{j} \left(\lambda_l^n \nu_l + \frac{1-\lambda_l^n}{1-\lambda_l} \xi_l\right) \sin\left(\frac{il\pi}{j+1}\right). \tag{5.32}$$

5.6 Appendix. Total discounted heat

Expressions of the form

$$u_i^* = \sum_{n=0}^{+\infty} w^n u_n(i), \tag{5.33}$$

with $u_n(i)$ given by Eq. 5.32 often appear in the expressions for the total expected payoffs of players in the model presented in this paper. In the following, I derive a closed form formula for this expression for general j and w and find a simple expression of it when $d = 0$ and in the limit of $j \to \infty$ and $w \to 1$.

First, note that we can write

$$\begin{aligned}
u_i^* &= \sum_{n=0}^{+\infty} w^n u_n(i) \\
&= \sum_{n=0}^{+\infty} w^n \sum_{l=1}^{j} \left(\lambda_l^n \nu_l + \frac{1-\lambda_l^n}{1-\lambda_l} \xi_l \right) \sin\left(\frac{il\pi}{j+1} \right) \\
&= \sum_{l=1}^{j} \left(\sum_{n=0}^{+\infty} w^n \lambda_l^n \nu_l + \sum_{n=0}^{+\infty} w^n \frac{1-\lambda_l^n}{1-\lambda_l} \xi_l \right) \sin\left(\frac{il\pi}{j+1} \right) \\
&= \sum_{l=1}^{j} \left[\sum_{n=0}^{+\infty} (w\lambda_l)^n \nu_l + \frac{1}{1-\lambda_l} \left(\sum_{n=0}^{+\infty} w^n - \sum_{n=0}^{+\infty} (w\lambda_l)^n \right) \xi_l \right] \sin\left(\frac{il\pi}{j+1} \right) \\
&= \sum_{l=1}^{j} \left[\frac{1}{1-w\lambda_l} \nu_l + \frac{1}{1-\lambda_l} \left(\frac{1}{1-w} - \frac{1}{1-w\lambda_l} \right) \xi_l \right] \sin\left(\frac{il\pi}{j+1} \right) \\
&= \frac{1}{1-w} \sum_{l=1}^{j} \frac{(1-w)\nu_l + w\xi_l}{(1-w\lambda_l)} \sin\left(\frac{il\pi}{j+1} \right).
\end{aligned}$$

Now, if $d = 0$, $\xi_l = 0\ \forall l$ (see Eq. 5.31) and the previous expression further simplifies to

$$u_i^* = \sum_{l=1}^{j} \frac{\nu_l}{(1-w\lambda_l)} \sin\left(\frac{il\pi}{j+1} \right).$$

In the limit when $j \to \infty$ and $w \to 1$, the term corresponding to the eigenvalue λ_1 dominates the sum, so that we can finally write

$$u_i^* = \frac{\nu_1}{1-\lambda_1} \sin\left(\frac{i\pi}{j+1} \right). \tag{5.34}$$

5.7 Appendix. Results for 'death-birth' and 'birth-death'

5.7.1 Death-birth (DB)

For DB updating, a random individual is eliminated and the neighbors compete for the empty site proportional to their fitness. In this case it is easy to show that, in the limit of weak selection ($s \ll 1$), C_1 is more likely to invade C_0 if

$$P_1 + P_2 > P_0 + P_{-1}. \tag{5.35}$$

Let us consider the case where C_1 are Rs and C_0 are Ds. By replacing Eq. 5.3 into Eq. 5.38 and simplifying, it can be shown that Rs invade Ds more easily than the converse if

$$b/c > \frac{2(h_1^* + h_2^*)}{h_2^* + h_3^*}. \tag{5.36}$$

Making use of Eq. 5.34, and writing $\theta = \pi/(j+1)$, the previous expression leads to

$$b/c > \frac{2(\sin\theta + \sin 2\theta)}{\sin 2\theta + \sin 3\theta},$$

which can be simplified to

$$\begin{aligned} b/c &> \frac{2(\sin\theta + 2\sin\theta\cos\theta)}{\sin 2\theta + \sin 3\theta} \\ &= \frac{2 + 4\cos\theta}{3 + 2\cos\theta - 4\sin^2\theta}. \end{aligned}$$

In the limit $j \to \infty$, $\theta \to 0$ and we finally obtain

$$b/c > \frac{6}{5}. \tag{5.37}$$

Thus, clusters of Rs invade more easily clusters of Ds than the converse when $b/c > 6/5$. It can be shown, similarly as it was done for IM updating, that this is also the condition for clusters of Cs to replace clusters of Rs. Finally, Cs win over Ds when $b/c > 2$ (Ohtsuki et al., 2006).

5.7.2 Birth-death (BD)

For BD updating, an individual is selected for reproduction from the whole population proportional to fitness and the offspring replaces a randomly chosen neighbor. In the limit of weak selection ($s \ll 1$), it can be shown that C_1 is more likely to invade C_0 if

$$P_1 > P_0. \tag{5.38}$$

Consider the case where C_1 are Rs and C_0 are Ds. By replacing Eq. 5.3 into Eq. 5.38 and simplifying, we get that Rs invade Ds more easily than the converse if

$$b/c > \frac{2h_1^*}{h_2^* - h_1^*}. \tag{5.39}$$

Using Eq. 5.34 and writing $\theta = \pi/(j+1)$, the previous expression becomes

$$b/c > \frac{2\sin\theta}{\sin 2\theta - \sin\theta},$$

which can be simplified to

$$\begin{aligned} b/c &> \frac{2\sin\theta}{2\sin\theta\cos\theta - \sin\theta} \\ &= \frac{2}{2\cos\theta - 1}. \end{aligned}$$

In the limit $j \to \infty$, $\theta \to 0$ and we finally obtain

$$b/c > 2. \tag{5.40}$$

Hence, clusters of Rs invade more easily clusters of Ds than the converse when $b/c > 2$. Again, this is also the condition for clusters of Cs to replace clusters of Rs. Finally, it can be shown that under BD updating, Cs never win over Ds (Ohtsuki et al., 2006).

Part III

Social diversity

> For to everyone who has, more shall be given, and he will have an abundance; but from the one who does not have, even what he does have shall be taken away.
>
> Matthew 25:29

'The rich get richer and the poor get poorer' is a catchphrase that often appears in discussions on economic, political and social inequality, from Marxist critiques of capitalism to sociology of science. American sociologist Robert K. Merton used it to describe the fact that an eminent researcher gets more credit than a relatively unknown one, even if their work is similar (Merton, 1968). Merton called this phenomenon 'the Matthew effect', taking its name from the line of the gospel of Matthew quoted above.

The Matthew effect and the more general 'rich get richer' phenomenon is the simple idea of autocatalysis or positive feedback in a social context: those who have (social or economic) power can use such resources to gain even more power. Thus, often cited papers or scientists are more likely to be cited in a new study, popular people is more likely to get new friends, and rich companies are more likely to win telecom auctions (thus getting richer). In 1999, Barabási & Albert made use of the concept (that they called 'preferential attachment') in their famous procedure for constructing networks having highly heterogeneous degree distributions, i.e. scale-free networks. Later on, in 2005, Santos & Pacheco showed that the evolution of cooperation under the two-person prisoner's dilemma can be significantly promoted on scale-free graphs, suggesting that heterogeneity in population structure was 'a new route to cooperation' (Santos & Pacheco, 2006). Finally, in 2008, Santos et al. extended these results to the case of the linear public goods game (a version of the N-person prisoner's dilemma) finding that the combination of heterogeneity and asymmetric interactions again promoted cooperation. Their conclusion, summarized in the title of their paper, is that 'social diversity promotes the emergence of cooperation in public goods games'.

The following chapters present three contributions to the study of the effects of social diversity (heterogeneity) in the evolution of cooperation. Chapter 6 focuses on the effects of group diversity in both linear and non-linear public goods games. In this chapter I make use of the standard formalism of infinite well-mixed populations and the replicator dynamics, in order to study the effects of group-size diversity in the absence of any kind of assortment. Chapter 7 introduces the use of bipartite graphs as population structures, showing how they allow for a neat separation between two different types of social diversity, indistinguishable from one another in the model by Santos et al. (2008): *individual diversity* and *group diversity*. Individual diversity refers to heterogeneity at the level of the number of interactions per individual; group diversity, to heterogeneity at the level of the number of individuals taking part in a social interaction. Finally, in chapter 8, the interplay between individual diversity and asymmetric interactions is studied in more detail. Using a new model based on the sampling of interaction partners according to different rules, it is shown how inequality can promote cooperation and vice versa. It is also shown, however, how a supposedly ideal world where everybody cooperates can be nothing more than a swindle from the rich to control and exploit the poor, similar to that theorized by Rousseau in *A Discourse of Inequality*.

Chapter 6

Group-size diversity in public goods games[†]

Abstract

Public goods games are models of social dilemmas where cooperators pay a cost for the production of a public good while defectors free ride on the contributions of cooperators. In the traditional framework of evolutionary game theory, the payoffs of cooperators and defectors result from interactions in groups formed by binomial sampling from an infinite population. Despite empirical evidence showing that group-size distributions in nature are highly heterogeneous, most models of social evolution assume that the group size is constant. In this paper, I remove this assumption and explore the effects of having random group sizes on the evolutionary dynamics of public goods games. By a straightforward application of Jensen's inequality, I show that the outcome of general nonlinear public goods games depend not only on the average group size but also on the variance of the group-size distribution. This general result is illustrated with two nonlinear public goods games (the public goods game with discounting or synergy and the N-person volunteer's dilemma) and three different group-size distributions (Poisson, geometric, and Waring). The results suggest that failing to acknowledge the natural variation of group sizes can lead to an underestimation of the actual level of cooperation exhibited in evolving populations.

6.1 Introduction

Social dilemmas are situations in which there is a conflict between individual and collective interests. In game theory terms, social dilemmas are defined as

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games with at least one Pareto inefficient Nash equilibrium (Archetti & Scheuring, 2011b; Kollock, 1998): an alternative outcome making at least one player better off without reducing any other player's payoff is possible, but no player has the incentive to change their behavior. Such tension between the individual and the collective interest is encountered at all levels of biological organization, from the production of enzymes in microorganisms (Gore et al., 2009; Turner & Chao, 1999) to predator inspection (Pitcher, 1991), sentinel behavior (Clutton-Brock et al., 1999) and cooperative hunting (Packer & Ruttan, 1988) in social vertebrates. Pollution, human overpopulation, overexploitation of fisheries (Hardin, 1968), the use of public transportation (van Vugt et al., 1996), and the production of open-source software (von Hippel & von Krogh, 2003) are typical examples of the kind of social dilemmas faced by contemporary human societies.

Many social dilemmas are related to the production of public goods, defined as common resources that are simultaneously non-excludable (no individual can be excluded from its consumption) and non-rivalrous (one individual's use of the public good does not diminish its availability to another individual) (Pindyck & Rubinfeld, 2001; Samuelson, 1954). Public goods games (PGGs) are simple models of public goods dilemmas, used by both experimental economists (Kagel & Roth, 1995) and theoreticians (Fox & Guyer, 1978; Hamburger, 1973; Sigmund, 2010). In general, a PGG can be described by a benefit function $B(i, N)$ and a cost function $C(i, N)$, where i is the number of cooperators (Cs) in a group of size N (Archetti & Scheuring, 2011b). Only Cs pay the cost $C(i, N)$ while both Cs and defectors (Ds) get the benefit $B(i, N)$. This leads to payoffs for Ds and Cs being respectively given by $P_D(i, N) = B(i, N)$ and $P_C(i, N) = B(i, N) - C(i, N)$.

By far, the most well known PGG is the N-person Prisoner's Dilemma, hereafter NPD (Hamburger, 1973). The NPD involves a group of N individuals where Cs contribute a cost $c > 0$ to the public good, whereas Ds contribute nothing. All contributions are added together, multiplied by an enhancement factor $1 < r < N$, and then shared among all the individuals of the group. This gives $B(i, N) = rci/N$ for the benefit function and $C(i, N) = c$ for the cost function. The NPD is the archetypal example of a social dilemma because its only Nash equilibrium (all players defect) is evidently Pareto inefficient: everybody ends up getting nothing, but if everybody had cooperated, each individual would have obtained $c(r - 1) > 0$. Moreover, defection is dominant, so that each individual is better off defecting no matter what their co-players do, i.e. $P_D(i, N) > P_C(i + 1, N)$. The fact that defection is dominant prevents cooperation from evolving when groups form randomly (Nunney, 1985). (Note, however, that if $r > N$ cooperation dominates defection, there is no social dilemma, and cooperation evolves).

A great deal of effort in evolutionary biology has been devoted to the study of mechanisms allowing for the evolution of cooperation in the NPD, such as kin selection (Frank, 1998; Grafen, 1985, 2009; Hamilton, 1964) and reciprocity (Axelrod & Hamilton, 1981; Nowak & Sigmund, 2005; Trivers, 1971), which can all be understood as different ways of creating and maintaining positive assortment between Cs (Fletcher & Doebeli, 2009; Lehmann & Keller, 2006). Voluntary participation (Hauert et al., 2002), punishment of non-contributors (Boyd & Richerson, 1992) and rewards to contributors (Hauert, 2010) have also been proposed as alternative mechanisms to promote cooperation in the NPD.

Despite its theoretical importance, it is clear that the NPD is only a very specific case of PGG, characterized by a linear benefit function and by the fact that defection is the dominant strategy. Other social dilemmas may depart from these assumptions, as it has been well understood in the social sciences (Hirshleifer, 1983; Kollock, 1998; Schelling, 1978; Taylor & Ward, 1982) and recognized in theoretical evolutionary biology (Boyd & Richerson, 1988; Charnov & Krebs, 1975; Cohen & Eshel, 1976; Dugatkin, 1990; Matessi & Jayakar, 1976; Maynard Smith, 1965; Motro, 1991) for decades. Recently, several works in evolutionary game theory have focused on PGGs with nonlinear payoff functions, bringing to the fore alternatives to the NPD for modeling social dilemmas (Archetti, 2009a,b; Archetti & Scheuring, 2011a,b; Bach et al., 2006; Hauert et al., 2006; Pacheco et al., 2009; Souza et al., 2009; Zheng et al., 2007). The most important result from this heterogeneous collection of works is that removing the assumptions of dominant defection and linearity on which the NPD is based has important consequences on the resulting evolutionary dynamics. Stable and unstable interior fixed points may appear in the replicator dynamics of nonlinear PGGs, leading to the coexistence of Cs and Ds or to bistability between cooperative and defective equilibria. In these cases, cooperation can be maintained without the need of invoking reciprocity, punishment, voluntary participation, rewards or any of the mechanisms generally proposed to generate assortment in the NPD (Archetti & Scheuring, 2011b).

For reasons of parsimony, it is common to consider the group size N as constant when investigating the evolutionary dynamics of PGGs. Natural and social systems, however, often exhibit high levels of group-size heterogeneity. Indeed, the group-size distributions of several species, including social amoeba (Fortunato & Queller, 2003), tuna fish and sardinellas (Bonabeau & Dagorn, 1995), buffaloes (Sinclair, 1977), antelopes (Wirtz & Lörscher, 1983), bisons (Lott & Minta, 1983), lions (Schaller, 1972), wolves (Rodman, 1981), killer whales (Baird & Dill, 1996), and humans (James, 1953; Newman, 2001; Zipf, 1949) have been reported to be heavily skewed, and in many cases well approximated by power-law distributions (Bonabeau & Dagorn, 1995; Bonabeau et al., 1999; Newman, 2001; Niwa, 2003; Sjöberg et al., 2000). Heterogeneous group-size distributions are also expected to arise from simple stochastic models of aggregation and grouping (Bonabeau et al., 1999; Cohen, 1971; Duerr & Dietz, 2000; Niwa, 2003; Okubo, 1986).

In this paper I study the effects of introducing variable group sizes in the replicator dynamics of PGGs. I do so by assuming that group size is a random variable with a prescribed probability distribution. In contrast to other models of social evolution featuring diverse group sizes, the model presented here does not involve (1) changes in group size caused by changes in behavior (Lehmann et al., 2006), (2) individual group size preferences (Avilés, 2002; Powers et al., 2011; van Veelen et al., 2010), (3) time-varying group-size distributions with fluctuating mean values (Eshel, 1977; Hauert et al., 2002, 2006, 2008; Mathew & Boyd, 2009; Parvinen, 2010; Szathmáry, 1993) nor (4) network-structured populations (Santos & Pacheco, 2011; Santos et al., 2008). Rather, it is based on the following assumptions: (1) group-size distributions are exogenously determined, (2) Cs and Ds have the same tendency to aggregate (no particular preference for a given group size), (3) group-size distributions are static, and (4) the population is well-mixed. The motivation behind these simpler assumptions is to explore to which extent the sole fact of having diverse but static group-size distributions can affect the evolutionary dynamics of PGGs in the absence of assortment of strategies resulting from differential grouping tendencies or population structure.

With the above-mentioned assumptions, the general model presented in this paper is closely related to the models of intrademic group selection by Cohen & Eshel (1976) and Matessi & Jayakar (1976), who also studied evolutionary PGGs with constant and random group sizes. However, my approach contrasts with these works in various respects. Firstly, I make explicit use of a general result in probability theory (Jensen's inequality) for investigating when and how the evolutionary dynamics under random group sizes are expected to be different from those under constant group sizes. Secondly, I consider group-size distributions going beyond the Poisson distribution used by Cohen & Eshel (1976). Finally, I illustrate the general results with different social dilemmas, namely the public goods with discounting or synergy (Hauert et al., 2006) and the N-person volunteer's dilemma (NVD) (Archetti, 2009a,b; Diekmann, 1985).

My model is also related to recent work by Brännström et al. (2011), who studied the consequences of fluctuating group sizes for the evolution of cooperation in continuous PGGs. The authors analyzed general classes of PGGs with payoff functions that do not explicitly depend on group size and derived general conditions for group-size diversity to promote/hinder cooperation in the framework of adaptive dynamics (Metz et al., 1996). In this work, I focus instead on the effects of group-size diversity on PGGs with payoff functions that explicitly depend on group size, in the framework of the replicator dynamics for two discrete strategies: Ds that contribute $c = 0$ and Cs that contribute $c > 0$. This choice allows direct comparison with recent works on evolutionary PGGs which consider the same setup (replicator dynamics of Cs and Ds), but assume that the group size is constant (Archetti, 2009a,b; Archetti & Scheuring, 2011a; Hauert et al., 2006; Pacheco et al., 2009; Souza et al., 2009; Zheng et al., 2007).

6.2 The model

Consider a very large and well-mixed population consisting of a fraction x of Cs and $1-x$ of Ds, where groups of N individuals are formed randomly by binomial sampling. For now, assume that the group size N is constant, so that $N = n$ with probability equal to one. Then, the probability that a given individual finds itself in a group where j of the other $n-1$ individuals are Cs is given by

$$\binom{n-1}{j} x^j (1-x)^{n-1-j}.$$

In each group with j other Cs, Cs receive a payoff $P_C(j+1, n)$ and Ds a payoff $P_D(j, n)$. Therefore, the average payoff of a C and a D are given respectively by

$$f_C(x,n) = \sum_{j=0}^{n-1} \binom{n-1}{j} x^j (1-x)^{n-1-j} P_C(j+1, n),$$

and

$$f_D(x,n) = \sum_{j=0}^{n-1} \binom{n-1}{j} x^j (1-x)^{n-1-j} P_D(j, n).$$

In the framework of evolutionary game theory, the change in frequency of cooperators can be described by the replicator dynamics (Hofbauer & Sigmund, 1998; Taylor & Jonker, 1978)

$$\dot{x} = x(1-x) f(x,n), \tag{6.1}$$

where $\dot{x} = dx/dt$ and

$$f(x,n) = f_C(x,n) - f_D(x,n).$$

As mentioned above, the analysis of equation 6.1 for different PGGs has been extensively carried out for the case of constant group sizes (Archetti, 2009a,b; Archetti & Scheuring, 2011a; Boyd & Richerson, 1988; Dugatkin, 1990; Hauert et al., 2006; Pacheco et al., 2009; Souza et al., 2009; Zheng et al., 2007).

In order to introduce group-size diversity, suppose now that N is no longer a constant but a random variable with support $n \in \{n_{min}, n_{min}+1, \ldots, n_{max}\}$ and probability mass function $p_n = \Pr(N = n)$, so that $\sum_{n_{min}}^{n_{max}} p_n = 1$. The mean value of N is given by $\mu_N = \mathbb{E}[N] = \sum_n p_n n$ and its variance by σ_N^2. Assume that $n_{min} \geq 2$ as to exclude "groups" of size one where by definition there is no social dilemma. Finally, denote by $\mathbb{E}\left[g(N)\right] = \sum_n p_n g(n)$ the expected value of the function $g(N)$. Then, by the law of total probability, the average payoff of a C and a D can be written as

$$F_C(x, N) = \sum_n q_n f_C(x, n),$$

and

$$F_D(x, N) = \sum_n q_n f_D(x, n),$$

where $q_n = np_n/\mu_N$ is the probability that an individual joins a group of size n. The replicator dynamics becomes

$$\dot{x} = x(1-x)F(x, N), \tag{6.2}$$

where

$$F(x, N) = F_C(x, N) - F_D(x, N) = \sum_n q_n f(x, n) = \frac{1}{\mu_N}\mathbb{E}\left[N f(x, N)\right]. \tag{6.3}$$

Notice that the standard case where group size is constant is recovered from equation 6.2 by assuming that N is distributed according to the degenerate distribution, i.e. a distribution with probability mass function $p_n = \delta(n, \mu_N)$, where $\delta(x, y)$ is the Kronecker delta function, so that $\delta(x, y) = 1$ if $x = y$ and $\delta(x, y) = 0$ otherwise. In this case, the replicator dynamics reduces to

$$\dot{x} = x(1-x)f(x, \mu_N). \tag{6.4}$$

Let us now assume that N is distributed according to a non-degenerate distribution, so that $\sigma_N^2 > 0$. Then, it is clear from equations 6.2, 6.3 and 6.4 that, for a given x, group-size diversity will lead to a dynamical scenario which is more favorable to cooperation than the one obtained if N is constant whenever $F(x, N) > f(x, \mu_N)$. This last expression leads to

$$\mathbb{E}\left[N f(x, N)\right] > \mu_N f(x, \mu_N). \tag{6.5}$$

I now make use of Jensen's inequality (see Jensen (1906) for the original paper, Gillespie (1977) for a classic application to evolutionary biology, and Ruel & Ayres (1999) for a review and applications to ecology), a well-established result in probability theory stating that the average of a nonlinear function $\mathbb{E}[g(X)]$ is different from the function evaluated at the average $g(\mathbb{E}\left[X\right])$. In particular, $\mathbb{E}[g(X)] > g(\mathbb{E}\left[X\right])$ if $g(x)$ is strictly convex ($d^2g(x)/dx^2 > 0$) and

$\mathbb{E}[g(X)] < g(\mathbb{E}[X])$ if $g(x)$ is strictly concave ($d^2g(x)/dx^2 < 0$). By a straightforward application of Jensen's inequality, the condition given by equation 6.5 is true if

$$h(x,n) \equiv nf(x,n)$$

is strictly convex in n, i.e. if $\partial^2 h/\partial n^2 > 0$.

From this, it is clear that the NPD is essentially unaffected by group-size diversity. Indeed, it can be easily shown that for this game $h(x,n)$ reduces to $c(r-n)$, which is a linear function of n. Thus, $F(x,N) = f(x,\mu_N)$ so that the replicator dynamics of the NPD is invariant with respect to changes of the group-size distribution preserving its average value.

A different picture emerges in the case of nonlinear PGGs, since nonlinearities in payoff functions translate into functions h that are nonlinear in n and, by Jensen's inequality, into $F(x,N) \neq f(x,\mu_N)$. In particular, the more diverse the group-size distribution and the more nonlinear the function h, the larger the deviation of the gradient of selection of the replicator dynamics from its mean-value approximation $F(x,N) \approx f(x,\mu_N)$. Indeed, we can write (see Section 6.4)

$$F(x,N) \approx \underbrace{f(x,\mu_N)}_{\text{mean-value approximation}} + \frac{1}{2} \times \underbrace{\frac{\partial^2 h(x,\mu_N)}{\partial n^2}}_{\text{nonlinearity}} \times \underbrace{\sigma_N^2/\mu_N}_{\text{group-size diversity}} . \quad (6.6)$$

Equation 6.6 neatly shows the combined effects of nonlinearity and group-size diversity on the replicator dynamics and further clarifies the predictions of Jensen's inequality: for a given x, group-size diversity favors cooperation if and only if h is strictly convex in n ($\partial^2 h(x,\mu_N)/\partial n^2 > 0$). Whenever h is nonlinear, so that $\partial^2 h(x,\mu_N)/\partial n^2 \neq 0$, the promotion or hindering of cooperation is more important the larger the nonlinearity of h (as measured by $|\partial^2 h(x,\mu_N)/\partial n^2|$) and the larger the diversity of the group-size distribution (as measured by the variance-to-mean ratio σ_N^2/μ_N).

In the following I illustrate this general result with two particular cases of nonlinear PGGs: the PGGDS and the NVD (Archetti, 2009a,b). I explicitly model the group-size distributions by making use of (truncated) Poisson, geometric and Waring distributions, which greatly differ in their variance-to-mean ratios (see Figure 6.1). These distributions frequently arise as the result of simple aggregation processes (Cohen, 1971; Coleman & James, 1961; Duerr & Dietz, 2000; Okubo, 1986) and are good models of animal group-size distributions. The Waring distribution (Irwin, 1968) exhibits power-law behavior for large values of the random variable (i.e. if N is a Waring variate, $\Pr(N=n) \propto n^{-\alpha}$ for large values of n), hence it can be used to model grouping based on preferential attachment (Barabási & Albert, 1999), whereby larger groups are preferentially chosen by joining individuals. A mathematical description of these probability distributions is given in Section 6.5.

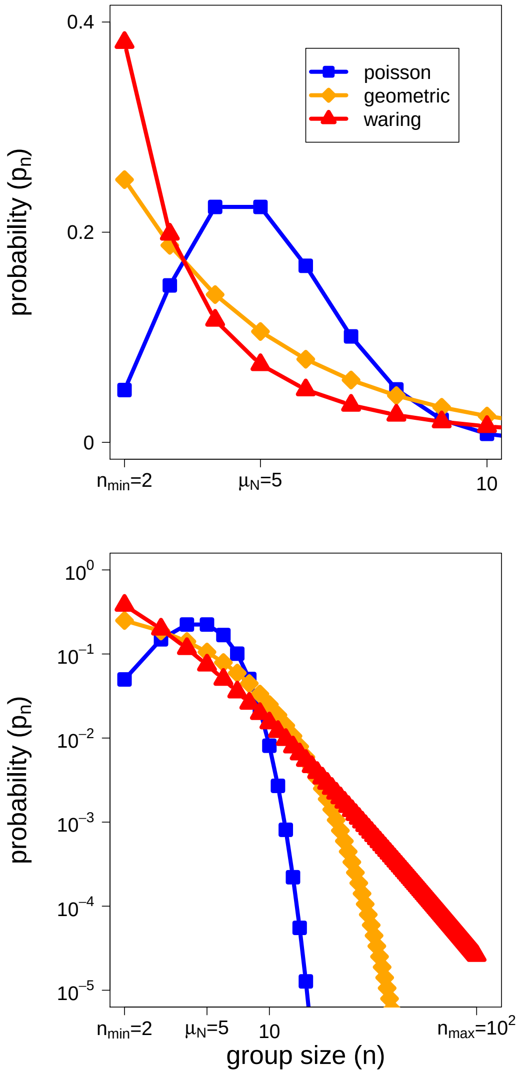

Figure 6.1: Examples of the non-degenerate group-size distributions used in this study: Poisson, geometric and Waring. Parameters: $n_{min} = 2$, $n_{max} = 100$, and $\mu_N = 5$. **Top panel.** Plots of the probability mass functions. **Bottom panel.** Log-log plots of the probability mass functions. For large values of n, the Waring distribution used in this study exhibits power-law behavior with exponent $\alpha = 3$, i.e. $p_n \propto n^{-\alpha}$ with $\alpha = 3$.

6.2.1 Public goods game with discounting or synergy (PGGDS)

In the PGGDS (Hauert et al., 2006), the first C in the group contributes a value b to produce a public good, the second C contributes wb and so on, to the i-th C which contributes $w^{i-1}b$. The public good is then shared equally among the members of the group. The benefit function is thus given by

$$B(i,n) = \frac{b\,(1+w+w^2+\ldots+w^{i-1})}{n} = \frac{b\,(1-w^i)}{n\,(1-w)},$$

while the cost function is given by $C(i,n) = c$ (each C pays a fixed cost c). For $w = 1$, the NPD is recovered as a special case when $b = rc < nc$. If $0 < w < 1$ the benefit function is decelerating (benefits are discounted) while if $w > 1$ it is accelerating (benefits are synergistically enhanced).

With these definitions we obtain after little algebra:

$$f(x,n) = \frac{b}{n}(1-x+wx)^{n-1} - c, \tag{6.7}$$

and

$$F(x,N) = \frac{b}{\mu_N}\mathbb{E}\left[(1-x+wx)^{N-1}\right] - c. \tag{6.8}$$

Let us denote by $\gamma = c/b$ the cost-to-benefit ratio, and define $\gamma_1 = 1/\mu_N$ and

$$\gamma_2 = \mathbb{E}\left[w^{N-1}\right]/\mu_N. \tag{6.9}$$

Then, as shown in the left panel of Figure 6.2, four different dynamical scenarios can be distinguished (see Section 6.6 for the derivation):

1. If $\gamma > \gamma_1$ and $\gamma > \gamma_2$, the only stable fixed point is $x_0 = 0$, and defection is dominant.

2. If $\gamma_2 < \gamma < \gamma_1$, there is an interior fixed point x_F, which is stable, while both $x_0 = 0$ and $x_1 = 1$ are unstable. Cs and Ds coexist at a polymorphic equilibrium with a proportion x_F of Cs.

3. If $\gamma < \gamma_1$ and $\gamma < \gamma_2$ the only stable fixed point is $x_1 = 1$, and cooperation is dominant.

4. If $\gamma_1 < \gamma < \gamma_2$, the interior fixed point x_F is unstable and both $x_0 = 0$ and $x_1 = 1$ are stable. There is bistability: Cs and Ds cannot invade each other and the population evolves either to $x_0 = 0$ or $x_1 = 1$ depending on the initial conditions.

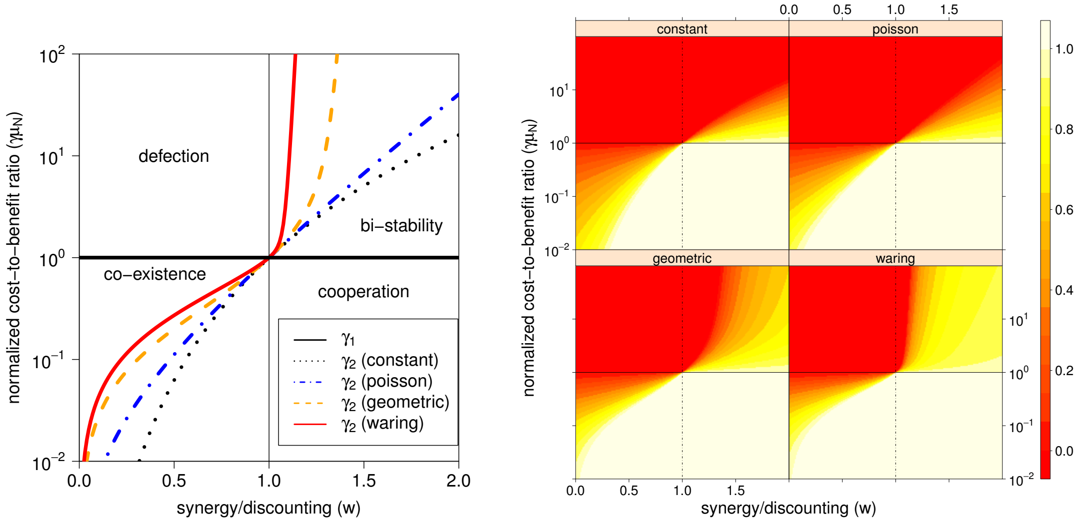

Figure 6.2: Phase diagram and degree of cooperation in the public goods game with discounted or synergistic benefits for the different group-size distributions. **Left panel.** Phase diagram illustrating the four different dynamical regimes (defection, co-existence, cooperation, and bistability). **Right panel.** Degree of cooperation for the different group-size distributions. The degree of cooperation is given by the fraction of Cs at equilibrium, except in the bistability region where it is given by the size of the basin of attraction of the cooperative equilibrium. Parameters: $n_{min} = 2$, $n_{max} = 100$, $\mu_N = 5$.

For constant group sizes, the conditions found by Hauert et al. (2006) are recovered, namely, $\gamma_2 = w^{\mu_N - 1}/\mu_N$, and $x_F = x_f$, with

$$x_f = \frac{1 - (\gamma\mu_N)^{1/(\mu_N - 1)}}{1 - w}.$$

For random group sizes, we have

$$\frac{\partial^2 h(x,n)}{\partial n^2} = b(1 - x + wx)^{n-1} \ln^2(1 - x + wx),$$

which is greater than zero for all $x \in (0,1)$, for all $w \neq 1$ and for all n. Hence, by Jensen's inequality, $F(x,N) \geq f(x,\mu_N)$ for all x, with strict equality only in the case where the group-size distribution is degenerate or when $w = 1$. This means that group-size diversity systematically promotes cooperation in the PGGDS with respect to the case of constant group sizes for both discounted and synergistically enhanced benefits. In particular, since w^n is a convex function of n, Jensen's inequality gives $\gamma_2 = \mathbb{E}\left[w^{N-1}\right]/\mu_N > w^{\mu_N - 1}/\mu_N$. As a result, the introduction of group-size diversity makes the regions of dominant cooperation and of bistability grow at the expense of the regions of coexistence and dominant defection, respectively. Moreover, it is clear that $F(x,N) > f(x,\mu_N)$ for all x implies that $x_F > x_f$ for $w < 1$ and $x_F < x_f$ for $w > 1$. Hence, group-size diversity translates into a larger fraction of Cs when there is coexistence (see the top panel of Figure 6.3), and into a larger basin of attraction for the C equilibrium when cooperation and defection are bistable (see the bottom panel of Figure 6.3). Overall, the degree of cooperation (given by the fraction of Cs at equilibrium or by the size of the basin of attraction of $x_1 = 1$) in the case of random group sizes is always greater than or equal to the respective degree of cooperation in the case of constant group sizes, for any point in the parameter space (see the right panel of Figure 6.2).

For an arbitrary n_{max}, the critical value γ_2 can be directly calculated from its defining series $\gamma_2 = \frac{1}{w\mu_N}\sum_n p_n w^n$, and the fixed point x_F can be found by numerically solving $F(x_F,N) = \frac{1}{\mu_N}\sum_n p_n n f(x_F,n) = 0$. This is the approach I used for calculating the data shown in Figure 6.2 and Figure 6.3. These calculations can be cumbersome for large values of n_{max}. In such cases, it is more convenient to have closed-form expressions for γ_2 and $F(x,N)$. These can be obtained exactly in the limit $n_{max} \to \infty$ if the expected values converge (see Section 6.7) or approximated using equation 6.6 to obtain

$$\gamma_2 \approx \frac{w^{\mu_N - 1}}{\mu_N}\left[1 + \frac{\ln^2(w)\sigma_N^2}{2}\right],$$

and

$$F(x,N) \approx \frac{b}{\mu_N}(1 - x + wx)^{\mu_N - 1}\left[1 + \frac{\ln^2(1 - x + wx)\sigma_N^2}{2}\right] - c.$$

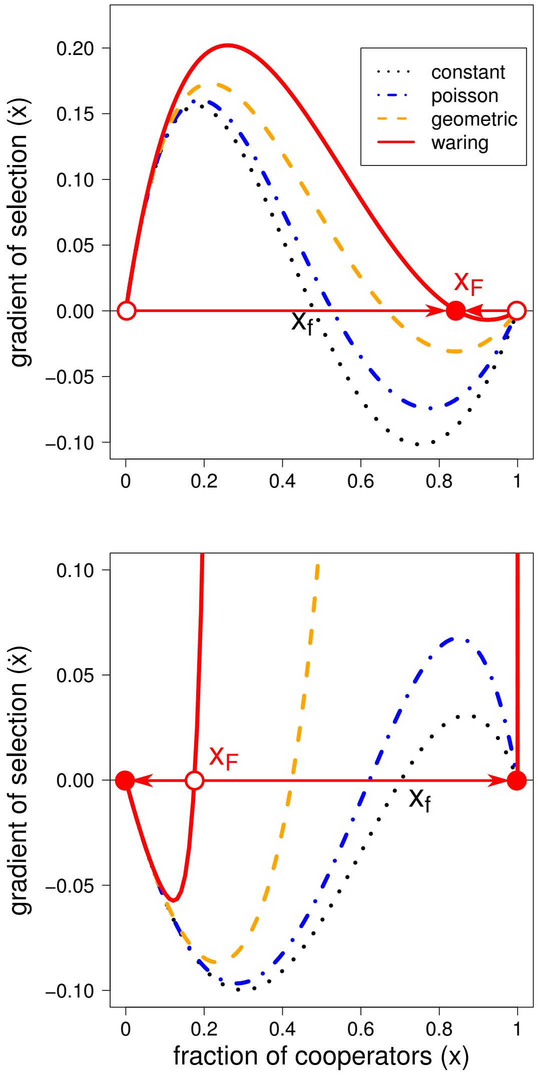

Figure 6.3: Effects of group-size diversity in the PGGDS. **Top panel.** Evolutionary dynamics for $w = 0.5$, $c = 1$ and $b = 15$ ($\gamma\mu_N = 1/3$). Coexistence: $x_F > x_f$. **Bottom panel.** Evolutionary dynamics for $w = 0.5$ $c = 1$ and $b = 1.5$ ($\gamma\mu_N = 10/3$). Bistability: $x_F < x_f$. Parameters: $n_{min} = 2$, $n_{max} = 100$, $\mu_N = 5$.

6.2.2 N-person volunteer's dilemma (NVD)

In the NVD (Archetti, 2009a,b; Diekmann, 1985), each individual in a group of size n must decide whether to volunteer to provide a public good or not. If at least k players volunteer to pay a cost c, everyone receives a benefit b. Thus $B(i, n) = b\theta(i - k)$, where $\theta(x)$ is the Heaviside step function, such that $\theta(x < 0) = 0$ and $\theta(x \geq 0) = 1$, and $C(i, n) = c$. Here I explore the simple case where $k = 1$. Note that this case has sometimes been called N-person snowdrift game (van Veelen & Nowak, 2012).

With $k = 1$ we find

$$f(x, n) = b(1 - x)^{n-1} - c,$$

and

$$F(x, N) = \frac{b}{\mu_N}\mathbb{E}\left[N(1 - x)^{N-1}\right] - c.$$

Note that f is a monotonically decreasing function of x for $n \geq 1$, which implies that $F = \sum_n q_n f(x, n)$ is also a monotonically decreasing function of x, since $q_n \geq 0\ \forall n$. Additionally, since $F(0, N) = b - c > 0$ and $F(1, N) = -c < 0$, the only stable state of the replicator dynamics is the fixed point $x_F \in (0, 1)$, so that Cs and Ds coexist at a polymorphic equilibrium with a proportion x_F of Cs. In the general case of random group sizes, x_F can be found by numerically solving $F(x_F, N) = 0$. In the case of constant group sizes, x_F reduces to (Archetti, 2009b)

$$x_F = x_f = 1 - \gamma^{1/(\mu_N - 1)}, \tag{6.10}$$

where $\gamma = c/b$ is the cost-to-benefit ratio. Note that the proportion of Cs at equilibrium is inversely proportional to the cost-to-benefit ratio.

For random group sizes we have

$$\frac{\partial^2 h(x, n)}{\partial n^2} = b(1 - x)^{n-1}\ln(1 - x)\left[n\ln(1 - x) + 2\right], \tag{6.11}$$

which is less than zero if $n < \eta(x)$ and greater than zero if $n > \eta(x)$, with $\eta(x) = -2/\ln(1 - x)$. Figure 6.4 shows a plot of $\eta(x)$. Note that $\eta(x) \to \infty$ as $x \to 0$ and $\eta(x) \to 0$ as $x \to 1$. Thus, the domain of convexity of h in n decreases as $x \to 0$ and increases as $x \to 1$. Moreover, n_{min} and n_{max} determine values $x_R = 1 - e^{-2/n_{min}}$ and $x_L = 1 - e^{-2/n_{max}}$ such that h is concave in n for all $n \in [n_{min}, n_{max}]$ if $x < x_L$ and convex in n for all $n \in [n_{min}, n_{max}]$ if $x > x_R$. Hence, by Jensen's inequality, $F(x, N) \leq f(x, \mu_N)$ for $x \leq x_L$ and $F(x, N) \geq f(x, \mu_N)$ for $x \geq x_R$. Intuitively, this should translate into more cooperation than in the constant group size case for low cost-to-benefit ratios (where Cs are common at equilibrium) and less cooperation than in the constant

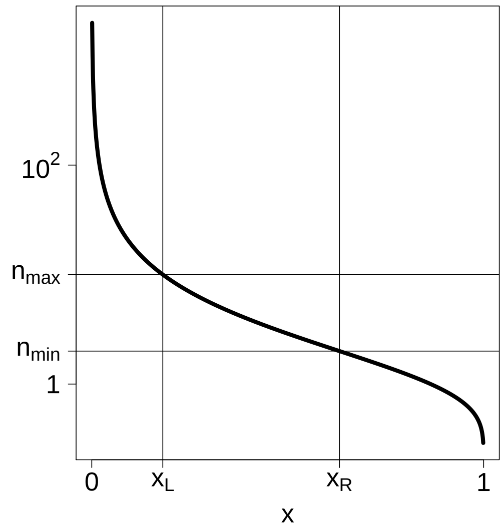

Figure 6.4: Plot of $\eta(x) = -2/\ln(1-x)$. Note that n_{min} and n_{max} determine values $x_R = 1 - e^{-2/n_{min}}$ and $x_L = 1 - e^{-2/n_{max}}$ such that $n < \eta(x)$ for all $n_{min} < n < n_{max}$ if $x < x_L$ and $n > \eta(x)$ for all $n_{min} < n < n_{max}$ if $x > x_R$. Note the logarithmic scale of the y axis. Here, $n_{min} = 2$ and $n_{max} = 10$.

group size case for high cost-to-benefit ratios (where Cs are rare at equilibrium). This prediction is confirmed in Figure 6.5, which shows the stable equilibrium x_F for different group-size distributions with $\mu_N = 5$, $n_{min} = 2$ and $n_{max} = 100$, and the replicator dynamics for $\gamma = 1/20$ and $\gamma = 2/5$. It is clear from these results that group-size diversity favors cooperation up to a critical cost-to-benefit ratio γ^*, above which cooperation is disfavored. Note, however, that the effect of group-size diversity seems to be more pronounced when promoting than when hindering cooperation. The exact value of γ^* depends on the particular group-size distribution, but it can be well approximated (see Section 6.8) by

$$\gamma^* \approx e^{-2(\mu_N - 1)/\mu_N},$$

which leads to $\gamma^* \approx 0.2019$ for $\mu_N = 5$, in good agreement with the results shown in Figure 6.5.

Section 6.9 gives closed-form expressions for $F(x, N)$ in the limit when $n_{max} \to \infty$. In this limit, and in the particular case of the geometric distribution, an analytical expression for x_F can also be derived (see equation 6.18 in Section 6.9). Finally, and for general n_{max}, $F(x, N)$ can also be approximated using equation 6.6 so that

$$F(x, N) \approx b(1-x)^{\mu_N - 1} \left\{ 1 + \ln(1-x) \left[\mu_N \ln(1-x) + 2 \right] \frac{\sigma_N^2}{2\mu_N} \right\} - c.$$

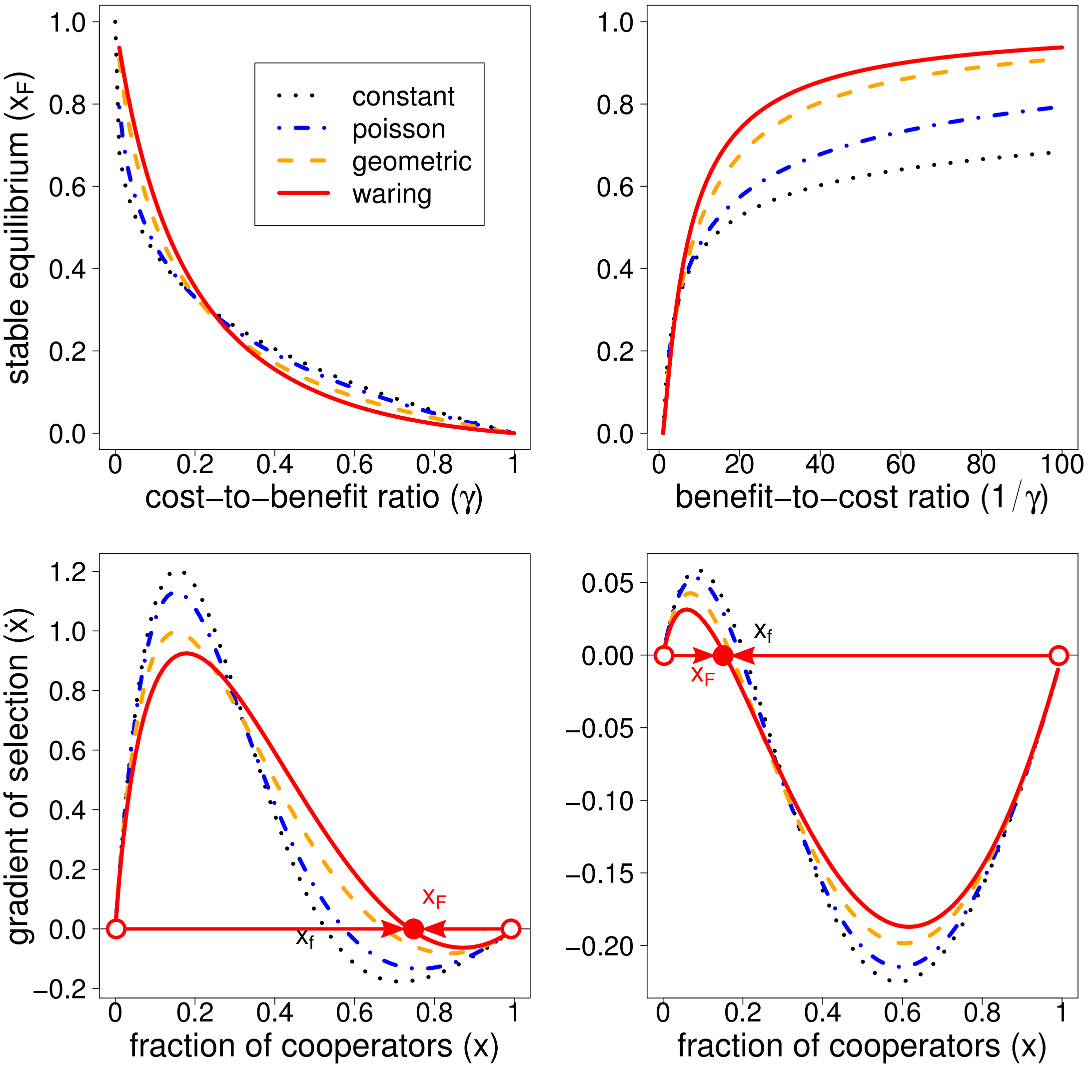

Figure 6.5: Effects of group-size diversity in the NVD. Stable equilibria shown as a function of the cost-to-benefit ratio $\gamma = c/b$ (**top left**) are also shown as a function of the benefit-to-cost ratio b/c (**top right**) in order to emphasize the promotion of cooperation for low values of γ. **Bottom left:** Evolutionary dynamics for $c = 1$ and $b = 20$ ($\gamma = 0.05$). **Bottom right:** Evolutionary dynamics for $c = 1$ and $b = 2.5$ ($\gamma = 0.4$). Parameters: $n_{min} = 2$, $n_{max} = 100$, $\mu_N = 5$.

6.3 Discussion

The evolution of cooperation in sizable groups has been traditionally studied by investigating the evolutionary dynamics of the NPD and other PGGs under the assumption that the group size is constant. In the research presented in this paper, I relaxed this assumption and show that although group-size diversity leaves the linear NPD , it can lead to qualitative and quantitative changes in the evolutionary dynamics of more general, nonlinear PGGs.

I showed that the replicator dynamics of nonlinear PGGs depend not only on the average group size but also on the variance of the group-size distribution and on the convexity of the function $h = nf(x, n)$ (see equation 6.6). Indeed, the evolution of cooperation is promoted with respect to the case of constant group sizes when h is convex and hindered when h is concave in the group size n, the more the larger the variance of the group-size distribution. In the PGGDS, h is always strictly convex and, consequently, group-size diversity systematically leads to dynamical scenarios more favorable to the evolution of cooperation than what is obtained under the assumption of constant group sizes. Specifically, the introduction of variable group sizes enlarges the zones of the parameter space where the cooperative equilibrium is stable, increases the proportion of Cs at stable polymorphic equilibria when Cs and Ds coexist, and leads to larger basins of attraction of the cooperative equilibrium when the replicator dynamics is bistable. In the NVD, h is convex when Cs are common and concave when Cs are rare. As a result, group-size diversity can either promote or hinder cooperation with respect to the case where all groups are of the same size depending on the cost-to-benefit ratio: there is promotion for low cost-to-benefit ratios and hindering for high cost-to-benefit ratios. Overall, I have shown that the degree of cooperation in PGGs can be underestimated by focusing only on the average group size, especially if the group-size distribution is highly heterogeneous.

In the model presented here, the evolutionary dynamics of the NPD is independent of the level of group-size diversity. Consequently, cooperation cannot evolve in the NPD for any group-size distribution. This result, which can be shown to agree with results stemming from patch-structured models where group-size diversity is endogenously determined (Alizon & Taylor, 2008; Lehmann et al., 2006), contrasts with the results of other models of social evolution featuring variable group sizes where cooperation has been shown to be viable under the NPD (Hauert, 2006; Hauert et al., 2002; Santos et al., 2008). The reason behind such seeming discrepancy is to be found in the additional assumptions made in these works, which are not made in the model presented here: (1) fluctuating average group sizes resulting from voluntary participation (Hauert et al., 2002) or ecological feedback (Hauert, 2006) that make the PGG to alternate between an NPD ($1 < r < \mu_N$) and a game with no conflict ($r > \mu_N$), and (2) assortment of strategies via network structure (Santos et al., 2008). Simply introducing variance in the group-size distribution does not make the average group size fluctuate over time nor introduces assortment; as a result, cooperation can not be made possible in the NPD by group-size diversity alone.

Contrastingly, group-size diversity can promote the evolution of cooperation with respect to the case where the group size is constant in nonlinear PGGs. This has been demonstrated here for the specific cases of the PGGDS (cooperation promoted for the whole of the parameter space, except when $w = 1$ where the NPD is recovered) and the NVD (promotion of cooperation for low cost-to-benefit ratios). As mentioned above, the resulting promotion of cooperation does not derive from any kind of assortment, but solely from the interaction between the nonlinearity of public good functions and the variability of group sizes. Such interaction is nicely captured by Jensen's inequality, a somewhat counterintuitive result in probability theory stating that the average of a nonlinear function does not equal the function of the average. This is not the first time that a statistical phenomenon which is apparently paradoxical is associated with models of social evolution. Many readers will be familiar with Simpson's paradox (Bickel et al., 1975; Blyth, 1972; Simpson, 1951): the reversal of a correlation present in different groups when the groups are combined which has been often invoked to explain the evolution of cooperation (Chuang et al., 2009; Hauert, 2006; Hauert et al., 2002; Sober & Wilson, 1998). In the model of nonlinear PGGs with variable group sizes studied here, both Simpson's paradox and Jensen's inequality are at work. Simpson's paradox manifests itself in the fact that, for both the PGGDS and the NVD, cooperation is disfavored in each mixed group ($P_C(i, n) - P_D(i, n) < 0$ for all n and all $0 < i < n$), but it can be favored globally ($f_C(x, n) > f_D(x, n)$ for at least some x) and hence evolutionarily viable. Jensen's inequality is brought about by the variation in group size and the nonlinearity of payoff functions, so that cooperation is promoted with respect to the constant case if $h = nf(x, n)$ is convex in n. Considered together, Simpson's paradox and Jensen's inequality help us understand mathematically the apparent paradox of the evolution of cooperation in variable group-structured populations of individuals facing social dilemmas.

For the sake of parsimony, I have based my analysis on the standard replicator dynamics, which relies on the assumption that the evolving population is of infinite size. Recent work on evolutionary game theory has suggested ways of taking into account the finite nature of real populations, replacing the deterministic replicator equation by frequency-dependent stochastic processes (Nowak et al., 2004; Rousset & Billiard, 2000). Initially developed for studying two-person games, the theory has been extended to take into account multiplayer games as well (Gokhale & Traulsen, 2010; Kurokawa & Ihara, 2009). Preliminary results suggest that the effects of group-size diversity on the evolutionary dynamics of multiplayer games in finite populations can be studied in much the same way as it has been done here for the case of infinite populations, that is, by checking the convexity (in the group size n) of functions of the form $h = nf(n)$, where f is a function ruling the dynamic behavior of the system. It is worth pointing out, however, that the effects of group-size diversity in finite populations can be sometimes qualitatively different from those arising in infinite populations. Further work along these lines is in progress.

In addition to studying finite populations, the work presented in this paper can be extended in several ways. First, more general social dilemmas can be explored. In the case of the NVD, for instance, I limited myself to the case where one volunteer is sufficient for providing the public good. More generally, however, one can assume that the minimal number of volunteers required for providing the public good in a group of size n is any integer $1 \leq k \leq n$. For the extreme case where $k = n$ (a weakest-link N-person stag hunt game (Hirshleifer, 1983; Skyrms, 2004; van Veelen & Nowak, 2012)) one obtains the same results as for the case $k = 1$ analyzed here, up to the replacement $x \leftrightarrow 1-x$. The resulting evolutionary dynamics is one characterized by bistability, with one internal unstable equilibrium standing between the basins of attraction of the two pure stable equilibria. As in the case $k = 1$, group-size diversity can be shown to promote (hinder) cooperation with respect to what is obtained when groups are of equal sizes for low (high) cost-to-benefit ratios. Indeed, the results for $k = n$ can be obtained from those shown in the top panels of Figure 6.4 for $k = 1$ by reinterpreting the y-axis as showing the size of the basin of attraction of the cooperative equilibrium. The cases with $1 < k < n$ are more difficult to analyze, as they can give rise to replicator dynamics with two internal equilibria, and should be addressed in future work.

Yet another possibility is to explore the effects of group-size diversity in games where cost functions are decreasing functions in the number of Cs, as when the cost for providing the public good is assumed to be shared among Cs. Also, augmenting the NPD with reciprocity, punishment or rewarding leads to nonlinear payoff functions and thus to evolutionary game dynamics susceptible of being influenced by group-size diversity. Finally, individual variation resulting from development or ecology can be modeled by letting costs and benefits be random variables with prescribed probability distributions. Such individual variation can be taken into account independently of or together with group-size variation and explored by making use of Jensen's inequality in a similar way as the one proposed in this paper.

Recent theoretical and empirical research has suggested that nonlinear social dilemmas and heterogeneous group-size distributions are the rule rather than the exception in the organization of social and biological systems (Archetti & Scheuring, 2011b; Bonabeau et al., 1999). As demonstrated here, the simultaneous presence of nonlinearity and group-size variance greatly enrich the evolutionary dynamics of N-person games and open up unexpected opportunities for the evolution and maintenance of cooperation in biological and social systems.

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6.4 Appendix: Second order approximation for $F(x, N)$

Expanding $h(x, n) = nf(x, n)$ as a Taylor series about $n = \mu_N$ we obtain

$$h(x, n) = \sum_{k=0}^{\infty} \frac{h^{(k)}(x, \mu_N)}{k!}(n - \mu_N)^k,$$

where $h^{(k)}(x, \mu_N)$ is the k-th partial derivative of h in n evaluated at $n = \mu_N$. Writing this expression as a function of the random variable N, taking the expected value and dividing both sides by μ_N we obtain

$$\begin{aligned} F(x, N) &= \sum_{k=0}^{\infty} \frac{h^{(k)}(x, \mu_N)\mathbb{E}\left[(N - \mu_N)^k\right]}{\mu_N k!} \\ &= f(x, \mu_N) + \frac{h^{(2)}(x, \mu_N)\mathbb{E}\left[(N - \mu_N)^2\right]}{2\mu_N} + \sum_{k=3}^{\infty} \frac{h^{(k)}(x, \mu_N)\mathbb{E}\left[(N - \mu_N)^k\right]}{\mu_N k!}, \end{aligned}$$

which, assuming $\mathbb{E}\left[(N - \mu_N)^k\right] / (\mu_N k!) \approx 0$ for $k \geq 3$, gives equation 6.6 in the main text.

6.5 Appendix: Group-size distributions

I assume that the group size N is a random variable with support

$$n \in \{n_{min}, n_{min} + 1, \dots, n_{max}\}.$$

	ϕ_k	$\sum_{k=0}^{\infty} \phi_k z^k$	μ_K	σ_K^2	σ_K^2/μ_K	parameters
Poisson	$\frac{\lambda^k e^{-\lambda}}{k!}$	$e^{\lambda(z-1)}$	λ	λ	1	$\lambda > 0$
Geometric	$(1-p)^k p$	$\frac{p}{1-(1-p)z}$	$\frac{1-p}{p}$	$\frac{1-p}{p^2}$	$\frac{1}{p} > 1$	$0 < p < 1$
Waring	$\frac{\rho\Gamma(\rho+a)\Gamma(k+a)}{\Gamma(a)\Gamma(k+\rho+a+1)}$	$\frac{\rho}{\rho+a}\ {}_2F_1(a, 1; \rho + a + 1; z)$	$\frac{a}{\rho-1}$	∞	∞	$\rho > 0$, $a > 0$

Table 6.1: Probability mass function (ϕ_k), generating function ($\sum_{k=0}^{\infty} \phi_k z^k$), mean ($\mu_K$), variance ($\sigma_K^2$), variance-to-mean ratio (σ_K^2/μ_K) and parameters for the three choices of K used in this study. For the Waring distribution, $\Gamma(x)$ is the gamma function, and ${}_2F_1(a, b; c; z) = \sum_{k=0}^{\infty} \frac{(a)_k (b)_k z^k}{(c)_k k!}$ is the Gauss hypergeometric function, where $(a)_k = a(a+1)\dots(a+k+1) = \Gamma(a+k)/\Gamma(a)$ is the Pochhammer symbol.

The distribution of N is given by truncating a random variable K distributed according to a Poisson, Geometric or Waring distribution, so that

$$p_n = \Pr(N = n) = \frac{\phi_{n-n_{min}}}{\sum_{n=n_{min}}^{n_{max}} \phi_{n-n_{min}}},$$

with $\phi_k = \Pr(K = k)$. Table 6.1 shows the formulas for the probability mass function ϕ_k, the generating function $\sum_{k=0}^{\infty} \phi_k z^k$, the mean μ_K, the variance σ_K^2, and the variance-to-mean ratio σ_K^2/μ_K, for different choices of the distribution of K. For the Waring distribution, I set $\rho = 2$ so that, for large k, the distribution approximates a power-law $\Pr(K = k) \propto k^{-\alpha}$ with exponent $\alpha = 3$. The free parameters (λ for the Poisson distribution, p for the geometric distribution, and a for the Waring distribution) are calculated in order to set the value μ_N. For finite n_{max}, this means (numerically) solving the equation $\sum_n n p_n = \mu_N$. For $n_{max} \to \infty$ we have $\mathbb{E}[N] = \mathbb{E}[K] + n_{min}$ so that the free parameters can be easily set so that $\mu_K = \mu_N - n_{min}$.

The functions $F(x, N)$ resulting from the two specific cases of nonlinear PGGs analyzed in this paper depend on expressions of the form $\mathbb{E}\left[z^N\right]$ or $\mathbb{E}\left[N z^N\right]$ (see equations 6.8 and 6.2.2) When $n_{max} \to \infty$, $p_n = \phi_{n-n_{min}}$, and we can write such expressions as functions of the generating function of the variable K. Indeed

$$\mathbb{E}\left[z^N\right] = \sum_{n=n_{min}}^{\infty} p_n z^n = \sum_{k=0}^{\infty} p_{k+n_{min}} z^{k+n_{min}} = z^{n_{min}} \sum_{k=0}^{\infty} \phi_k z^k, \tag{6.12}$$

and

$$\begin{aligned}\mathbb{E}\left[Nz^N\right] &= \sum_{n=n_{min}}^{\infty} p_n n z^n && (6.13)\\ &= \sum_{k=0}^{\infty} p_{k+n_{min}}(k+n_{min}) z^{k+n_{min}} && (6.14)\\ &= z^{n_{min}}\left(\sum_{k=0}^{\infty}\phi_k k z^k + n_{min}\sum_{k=0}^{\infty}\phi_k z^k\right) && (6.15)\\ &= z^{n_{min}}\left(z\frac{d}{dz}\sum_{k=0}^{\infty}\phi_k z^k + n_{min}\sum_{k=0}^{\infty}\phi_k z^k\right). && (6.16)\end{aligned}$$

I shall make use of equations 6.12 and 6.16 to write closed-form expressions for $F(x,N)$ for the PGGDS (Section 6.7) and the NVD (Section 6.9).

6.6 Appendix: Dynamical scenarios in the PGGDS

For the PGGDS, $f(x,n)$ is given by equation 6.7 and $F(x,N)$ by equation 6.8. Taking the derivative of $f(x,n)$ with respect to x we obtain

$$\frac{\partial f(x,n)}{\partial x} = \frac{b(n-1)(w-1)\left[1-x+wx\right]^{n-2}}{n},$$

which, for $n>1$, is equal to zero for $w=1$, negative for $w<1$ and positive for $w>1$. Then, for a fixed value of w, $f(x,n)$ is a monotone function of x in $[0,1]$. This means that $F(x,N)=\sum_n q_n f(x,n)$ is also a monotone function of x in $[0,1]$, because $q_n \geq 0\ \forall n$. Moreover, $F(0,N)=b/\mu_N - c$ and $F(1,N) = b\mathbb{E}\left[w^{N-1}\right]/\mu_N - c$. Therefore, the replicator dynamics given by equation 6.2) can have at most one fixed point x_F in $(0,1)$, and this when $F(0,N)$ and $F(1,N)$ are of opposite sign. We thus have the following four scenarios:

1. $F(0,N)<0$ and $F(1,N)<0$. Hence $F(x,N)<0\ \forall x$ (only $x_0=0$ is stable).

2. $F(0,N)>0$ and $F(1,N)<0$. Hence $F(x,N)>0$ for $x<x_F$ and $F(x,N)<0$ for $x>x_F$ ($x_0=0$ and $x_1=1$ are unstable; x_F exists and is stable).

3. $F(0,N)>0$ and $F(1,N)>0$. Hence $F(x,N)>0\ \forall x$ (only $x_1=1$ is stable).

4. $F(0,N) < 0$ and $F(1,N) > 0$. Hence $F(x,N) < 0$ for $x < x_F$ and $F(x,N) > 0$ for $x > x_F$ ($x_0 = 0$ and $x_1 = 1$ are stable; x_F exists and is unstable).

Defining γ, $\gamma_1 = 1/\mu_N$ and $\gamma_2 = \mathbb{E}\left[w^{N-1}\right]/\mu_N$ the scenarios given in the main text are recovered.

6.7 Appendix: Closed-form expressions for γ_2 and $F(x,N)$ in the limit $n_{max} \to \infty$ (PGGDS)

Here, I calculate closed-form expressions for γ_2 and $F(x,N)$ in the limit $n_{max} \to \infty$ for the PGGDS.

6.7.1 Poisson distribution

From equations 6.8, 6.9, 6.12 and the expression for the generating function of the Poisson distribution (see Table 6.1), we obtain after little algebra

$$F(x,N) = \frac{b}{\mu_N}(1-x+wx)^{n_{min}-1}e^{\lambda(w-1)x} - c,$$

and

$$\gamma_2 = \frac{w^{n_{min}-1}}{\mu_N}e^{\lambda(w-1)},$$

with $\lambda = \mu_N - n_{min}$. The previous expressions are valid for all w, since the generating function of the Poisson distribution converges for all z.

Solving $F(x_F,N) = 0$ we obtain

$$x_F = \frac{(n_{min}-1)W\left(\frac{\lambda\left(\gamma\mu_N e^{\lambda}\right)^{1/(n_{min}-1)}}{n_{min}-1}\right) - \lambda}{\lambda(w-1)}, \tag{6.17}$$

where W is the Lambert W-function, i.e. the inverse function of $f(W) = We^W$.

6.7.2 Geometric distribution

We obtain

$$F(x,N) = \frac{bp(1-x+wx)^{n_{min}-1}}{\mu_N\left[1-(1-p)(1-x+wx)\right]} - c,$$

and

$$\gamma_2 = \frac{pw^{n_{min}-1}}{\mu_N\left[1-(1-p)w\right]},$$

with $p = 1/(\mu_N - n_{min} + 1)$. These expressions are valid only for $w < 1/(1-p)$, since the generating function of the geometric distribution converges only for $z < 1/(1-p)$. For $n_{min} = 2$, $F(x_F, N) = 0$ can be solved analytically, yielding

$$x_F = \frac{p(1-\gamma\mu_N)}{(1-w)\left[p(1-\gamma\mu_N) + \gamma\mu_N\right]}.$$

6.7.3 Waring distribution

We obtain

$$F(x,N) = \frac{2b(1-x+wx)^{n_{min}-1}}{\mu_N(a+2)}\, {}_2F_1(a,1;a+3;1-x+wx) - c,$$

and

$$\gamma_2 = \frac{2w^{n_{min}-1}}{\mu_N(a+2)}\, {}_2F_1(a,1;a+3;w),$$

with $a = \mu_N - n_{min}$. ${}_2F_1(a,b;c;z)$ is the Gauss hypergeometric function (see Table 6.1). The previous expressions are valid only for $w < 1$, since the generating function of the geometric distribution converges only for $z < 1$.

6.8 Appendix: An approximation for γ^* in the NVD

Let us define the critical value γ^* as the cost-to-benefit ratio such that $x_F = x_f$. The exact value of γ^* will depend on the particular group-size distribution. However, a useful approximation for γ^* can be found in the following way. From equation 6.6 and equation 6.11, we have that $F(x_F(\gamma^*), N) \approx f(x_f(\gamma^*), \mu_N)$ if

$$\frac{\partial^2 h(x_f, \mu_N)}{\partial n^2} = b(1-x_f)^{\mu_N - 1}\left[\mu_N \ln(1-x_f) + 2\right] = 0.$$

Solving for x_f we obtain $x_f(\gamma^*) \approx 1 - e^{-2/\mu_N}$. Finally, comparing this with equation 6.10 and solving for γ^*, we obtain the approximation given in the main text.

6.9 Appendix: Closed-form expressions for $F(x,N)$ in the limit $n_{max} \to \infty$ (NVD)

Here, I calculate closed-form expressions for $F(x,N)$ in the limit $n_{max} \to \infty$ for the NVD.

6.9.1 Poisson distribution

From equations 6.2.2, 6.16 and the expression for the generating function of the Poisson distribution (see Table 6.1), we obtain after little algebra

$$F(x,N) = \frac{b}{\mu_N}(1-x)^{n_{min}-1}e^{-\lambda x}\left[n_{min}+\lambda(1-x)\right]-c,$$

with $\lambda = \mu_N - n_{min}$.

6.9.2 Geometric distribution

We obtain

$$F(x,N) = \frac{b}{\mu_N}\frac{(1-x)^{n_{min}-1}p\left[n_{min}-(n_{min}-1)(1-p)(1-x)\right]}{\left[1-(1-p)(1-x)\right]^2}-c,$$

with $p = 1/(\mu_N - n_{min} + 1)$. For $n_{min} = 2$, $F(x_F, N) = 0$ can be solved analytically, yielding

$$x_F = \frac{1}{1-p}\left(\sqrt{\frac{p}{p+\gamma\mu_N(1-p)}}-p\right). \tag{6.18}$$

6.9.3 Waring distribution

We obtain

$$\begin{aligned} F(x,N) = {} & \frac{b(1-x)^{n_{min}-1}}{\mu_N}\frac{a(1-x)}{\rho+a+1}\,{}_2F_1(a+1,2;\rho+a+2;1-x) \\ & +\frac{b(1-x)^{n_{min}-1}}{\mu_N}\frac{n_{min}\rho}{\rho+a}\,{}_2F_1(a,1;\rho+a+1;1-x)-c, \end{aligned}$$

with $a = \mu_N - n_{min}$.

Chapter 7

Bipartite graphs as models of population structures in evolutionary multiplayer games[†]

Abstract

By combining evolutionary game theory and graph theory, “games on graphs” study the evolutionary dynamics of frequency-dependent selection in population structures modeled as geographical or social networks. Networks are usually represented by means of unipartite graphs, and social interactions by two-person games such as the famous prisoner’s dilemma. Unipartite graphs have also been used for modeling interactions going beyond pairwise interactions. In this paper, we argue that bipartite graphs are a better alternative to unipartite graphs for describing population structures in evolutionary multiplayer games. To illustrate this point, we make use of bipartite graphs to investigate, by means of computer simulations, the evolution of cooperation under the conventional and the distributed N-person prisoner’s dilemma. We show that several implicit assumptions arising from the standard approach based on unipartite graphs (such as the definition of replacement neighborhoods, the intertwining of individual and group diversity, and the large overlap of interaction neighborhoods) can have a large impact on the resulting evolutionary dynamics. Our work provides a clear example of the importance of construction procedures in games on graphs, of the suitability of bigraphs and hypergraphs for computational modeling, and of the importance of concepts from social network analysis such as centrality, centralization and bipartite clustering for the understanding of dynamical processes occurring on networked population structures.

[†] J. Peña and Y. Rochat. *PLoS ONE*, **7**(9): e44514 (2012).

7.1 Introduction

Since the pioneering work of Maynard Smith & Price (1973), evolutionary game theory (Maynard Smith, 1982) has become a valuable tool to describe and study evolutionary dynamics when fitness is frequency-dependent. Evolutionary game theory builds on the theory of games (Von Neumann & Morgenstern, 1944) by considering populations of individuals whose success or fitness depends on the outcome of social interactions. Behavioral strategies are genetically or culturally inherited, so that the relative abundance of fitter strategies increases over time due to natural selection or social learning. When populations are assumed to be infinite and well-mixed, the replicator dynamics (Hofbauer & Sigmund, 1998; Taylor & Jonker, 1978) offers a deterministic and exact account of the evolutionary dynamics.

In spite of the importance of the replicator dynamics as a mathematical tool for investigating evolutionary dynamics, it is obvious that real populations are never infinite nor perfectly well-mixed. Games on graphs (see Szabó & Fáth (2007) and Roca et al. (2009b) for reviews) go beyond these two simplifying assumptions by considering finite-sized populations embedded in graphs representing geographical isolation or social networks. A graph $G = (V, E)$ consists of a set V of vertices and a set E of edges connecting pairs of vertices. In general models of games on graphs, individuals are placed on two graphs with the same set of vertices (Ohtsuki et al., 2007): the interaction graph $G = (V, E_G)$ and the replacement graph $H = (V, E_H)$. Evolutionary dynamics are specified so that, first, individuals play two-person games with their neighbors in the interaction graph G, and second, strategy updating takes place along the edges of the replacement graph H. Although the set of edges of the replacement graph may differ from the set of edges of the interaction graph, it is usually assumed that $E_H = E_G$ so that G and H effectively coincide.

A perusal of the vast literature on games on graphs highlights the importance of network structure in the evolutionary dynamics of different games. Two particular results are worth mentioning. First, although unconditional cooperation under the one-shot prisoner's dilemma (PD) is not evolutionarily stable in infinite and well-mixed populations, it can be viable in sparse homogeneous networks (Nowak & May, 1992; Ohtsuki et al., 2006; Taylor et al., 2007). "Spatial reciprocity" (Taylor & Nowak, 2007), "network reciprocity" (Nowak, 2006b) and "graph selection" (Nowak & Sigmund, 2007) are different labels that have been coined in order to contrast such effect with other cooperation-promoting mechanisms (see, however, Grafen (2007); Grafen & Archetti (2008); Lehmann et al. (2007); Taylor et al. (2007) for the close connections between network reciprocity and kin selection via limited dispersal, and between games on graphs and inclusive fitness theory). Second, heterogeneous population structures such as scale-free networks (Barabási & Albert, 1999) can significantly promote cooperation under the PD and other social dilemmas (Santos & Pacheco, 2005, 2006), although such promotion strongly depends on several details of the network, the payoff functions and the updating rules (Fu et al., 2009; Masuda, 2007; Peña et al., 2009; Roca et al., 2009b; Rong et al., 2007; Szolnoki et al., 2008; Tomassini et al., 2007).

Notwithstanding the importance of pairwise social interactions, many situations in real social systems require the collective action of groups comprised by more than two individuals. Moreover, interactions within these larger groups can not always be represented as disjointed collections of two-person games (Hamilton, 1975). Public goods games (PGGs) are paradigmatic among such non-decomposable multiplayer games. PGGs are models of situations where individuals face the dilemma of providing and/or maintaining a public good: a common resource that is both non-excludable (no individual can be excluded from its consumption) and non-rivalrous (one individual's use of the public good does not diminish its availability to another individual) (Samuelson, 1954). Digestive enzymes in yeast (Gore et al., 2009), ATP in heterotrophic microorganisms (Pfeiffer et al., 2001), webs in social spiders (Lubin & Bilde, 2007), alarm calls in meerkats (Clutton-Brock et al., 1999), collective hunting in lions (Packer & Ruttan, 1988), and open-source software in contemporary humans (von Hippel & von Krogh, 2003) are typical examples of public goods whose abusive exploitation by non-contributing individuals may lead to the so-called tragedy of the commons (Hardin, 1968): a situation in which nobody contributes and therefore no public good is produced or maintained.

By far, the most well known PGG is the N-person prisoner's dilemma (NPD) (Hamburger, 1973). In this game, each individual in a group of size N has to decide whether to cooperate (by contributing to a common pot) or to defect (by refraining from contributing). The sum of the individual contributions is multiplied by a factor r and then equally distributed among all players, including those who did not contribute. No matter the decisions taken by the other players, it is always better to defect if $1 < r < N$. In infinite well-mixed populations and in the absence of cooperation-promoting mechanisms, defection is evolutionarily stable and the replicator dynamics predicts the ultimate extinction of Cs. However, as it is also the case in the two-person PD, cooperation in the NPD can be sustained in structured populations under particular life-cycle assumptions. Hauert et al. (2002) studied a spatial NPD resulting from placing the individuals in the nodes of a two-dimensional lattice and restricting interactions to nearest neighbors. In this model and for large values of r (but still for $r < N$) Cs are able to survive by minimizing interactions with Ds through cluster formation. Hauert et al.'s model has been extended by Santos et al. (2008), who used scale-free networks instead of regular lattices as population structures. The highly heterogeneous degree distributions of scale-free networks introduce *social diversity* both at the individual level (players vary greatly with respect to the number of games they take part in) and at the group level (different games are played by different numbers of players). Social diversity brings up a moderate promotion of cooperation when Cs pay a fixed cost c per game, but a significant boost when Cs pay a fixed cost c for all the games they play. In the following we use the terminology introduced in Pacheco et al. (2009) and call conventional NPD the former case and distributed NPD the latter.

The way networks are constructed is a common feature of Hauert et al. (2002); Santos et al. (2008) and many other papers dealing with evolutionary multiplayer games on networks (Brandt et al., 2003; Hauert & Szabó, 2003; Helbing et al., 2010; Huang et al., 2008; Lei et al., 2010; Rong & Wu, 2009; Rong et al., 2010; Shi et al., 2010; Szabó & Hauert, 2002; Szolnoki & Perc, 2010; Szolnoki et al., 2009; Yang et al., 2009; Zhang et al., 2010). We refer to this construction procedure as *the graph approach*. According to this framework, nodes of a graph $G = (V, E)$ define both individuals playing a game and games being played by the focal individual plus its direct neighbors, so that an individual with z neighbors takes part in $z+1$ games: the one centered on itself plus z games, each centered on one of its neighbors. Fitness or social success is given by the sum of payoffs collected in these $z+1$ games, and competition or imitation takes place along the edges of the graph.

An alternative way of looking at the population structure resulting from the graph approach is realizing that while the replacement graph is the *original graph* G, the interaction graph is actually a hypergraph (or a bipartite graph) in which hyperedges (or top vertices) correspond to closed neighborhoods of G (see Figure 7.1). A hypergraph is the generalization of a graph for the case where edges (called in this case hyperedges) can connect arbitrarily many vertices. A bipartite graph $B = (\top, \bot, E)$, also called a bigraph, consists of two disjoint sets of vertices, $\top$ (top vertices) and $\bot$ (bottom vertices), and a set of edges, E. The difference between bipartite graphs and standard unipartite graphs is that edges in a bigraph only connect vertices of different kinds. Undirected hypergraphs and bigraphs are mathematically equivalent, but bigraphs are usually easier to implement and to work with. Many real biological and social networks display a natural bipartite structure and can be represented as bigraphs in a straightforward manner. Food webs (Saavedra et al., 2009) and metabolic networks (Jeong et al., 2000) are well known biological examples; social examples include affiliation (Wasserman & Faust, 1994) or collaboration networks (Newman, 2001), such as those connecting co-owners of companies (Davis et al., 2003), film actors (Watts & Strogatz, 1998) and scientists (Newman, 2001). In this paper, we represent groups/games as top vertices and individuals/players as bottom vertices. Three network statistics will be particularly important. First, the *top degree distribution* gives the distribution of the number of games being played by a given individual. Second, the *bottom*

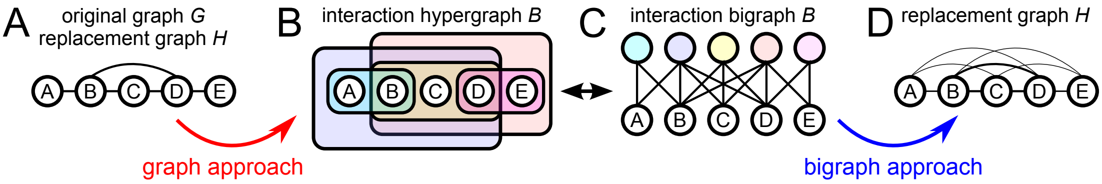

Figure 7.1: **Modeling population structures in evolutionary multiplayer games.** The graph approach consists in first defining the original graph G (Panel A) and then constructing the interaction hypergraph B (Panel B) by associating a hyperedge with each closed neighborhood in G. The interaction hypergraph can be also represented as a bigraph (Panel C), where individuals/players are bottom vertices and groups/games are top vertices. In the graph approach the replacement graph H is assumed to be equal to the original graph G, so that interactions take place along the hyperedges of the hypergraph, but strategy updating occurs along the edges of the original graph. The alternative bigraph approach consists in first defining the interaction bigraph B (Panel C) and then obtaining the replacement graph H (Panel D) as the bottom projection of the interaction bigraph. Weights can be attached to the links of the replacement graph according to different heuristics (here, the "unnormalized weighted projection" method is used; the width of the links is proportional to the links' weights). The interaction bigraph can be constructed from a bipartite graph model or following the graph approach from a simple graph G (Panel A). In this last case, the replacement graphs due to the graph approach (the original graph shown in Panel A) and to the bigraph approach (the projection of the interaction bigraph shown in Panel D) differ, the latter being denser.

degree distribution gives the distribution of the number of individuals playing a given game. Finally, the *bipartite clustering coefficient* captures correlations between the neighborhoods of bottom vertices, i.e. the degree to which groups overlap.

With the previous definitions, the graph approach can be interpreted as one in which (1) the replacement graph is defined, and (2) the interaction bigraph is constructed from the replacement graph. This approach has become the de facto standard for modeling population structures in multiplayer games on graphs. However, it has many important limitations. First, since both players and games are identified with the same set of vertices, the numbers of games and players are exactly the same, i.e. $|\top| = |\bot|$ in the resulting interaction bigraph. Second, and for the same reason, the top degree distribution and the bottom degree distribution coincide. In real systems, however, these distributions are usually very different. In collaboration networks, for example, the number of papers per author has been shown to follow a power-law distribution while the number of authors per paper generally follows an exponential distribution (Newman, 2001). Third, the graph approach automatically leads to a relatively large bipartite clustering coefficient. Although such large coefficient seems to be an intrinsic property of many social and biological networks (Palla et al., 2005), its presence by default in models of games on graphs can be a drawback if the goal is to build null models of connectivity patterns or to study the effects of bipartite clustering. Fourth, while each individual effectively interacts with second-order neighbors in the original graph, strategy updating is posited to occur only between first-order neighbors. As an example of this, consider the graphs depicted in Panels A and B of Figure 7.1. Note that individual A plays with C and D the game centered on B, but A is not connected to C nor D in the replacement graph. Finally, replacement graphs in the graph approach do not reflect encounter rates between two individuals but rather assume that all neighbors in the replacement graph are equally important. Consider again the graphs depicted in Panels A and B of Figure 7.1. On the one hand, individual B plays thrice with C (the games centered on B, C and D) but only twice with A (the games centered on A and B). On the other hand, individual B plays (on average) games of smaller size with A (one two-person game centered on A and one four-person game centered on B) and games of larger size with C (two four-person games centered at B and D, and one three-person game centered on C). In any case, the replacement graph posited by the graph approach fails to take into account these heterogeneities, since the connections between B and A and between B and C are equally (un)weighted in this graph.

A new modeling framework for studying networked multiplayer games, recently proposed by Gómez Gardeñes and co-workers (Gómez-Gardeñes et al., 2011) and further generalized here, is free of these limitations. We call this framework *the bigraph approach.* It consists in (1) defining the interaction bigraph $B = (\top, \bot, E)$ so that top vertices correspond to games and bottom vertices to players, and (2) deriving the replacement graph $H = (\bot, E_H)$ as the (bottom) projection of B (see Panels C and D of Figure 7.1). The bottom projection of a bigraph B is a graph $H = (\bot, E_\bot)$ so that $(i, j) \in E_\bot$ if and only if $i \in \bot$ and $j \in \bot$ are connected at least once to the same top vertex. In addition to the "unweighted projection" (UP) considered in Gómez-Gardeñes et al. (2011), we also consider two weighted projections: the "unnormalized weighted projection" (UWP) and the "normalized weighted projection" (NWP). With the UWP method, the weight of the link between two players is proportional to the number of common games played by those players; with the NWP method, the sizes of such groups are taken into account when calculating the weights, so that interactions in smaller groups contribute more to the total weight of the link than interactions in larger groups (see section 7.4 for details).

The bigraph approach circumvents all of the limitations associated with the graph approach we mentioned above. Since the interaction bigraph is defined at the outset, it can have arbitrary numbers of games and players, different degree distributions for games and players and (if required) relatively low bipartite clustering coefficient. In addition, since the replacement graph is obtained as the bottom projection of the interaction graph, individuals playing together at least one game will be connected in the replacement graph. Hence, the neighborhood of player A in the replacement graph shown in Panel D of Figure 7.1 comprises all the individuals A interacts with, i.e. $\{B, C, D\}$. Finally, weighted projections take into account differences in the interaction patterns of players and reflect such differences in the resulting replacement graph. For instance, in the graph shown in Panel D of Figure 7.1 the weights of the links between players B and A and between players B and C are respectively given by 2 and 3, indicating the number of common games between each pair of players (in Panel D of Figure 7.1, weights are derived using the UWP method).

In this paper, we make use of the bigraph approach to explore the influence of different topological properties of network structures on the evolutionary dynamics of multiplayer games. We focus on the conventional and the distributed versions of the NPD, as these are among the most studied evolutionary multiplayer games on graphs. Specifically, we investigate the effects of different assumptions on the way of specifying replacement graphs, different top and bottom degree distributions, and different amounts of bipartite clustering. We build interaction bigraphs either from prescribed simple graphs using the graph approach, or from given degree distributions using the configuration model procedure (see section 7.4). We denote these interaction bigraphs respectively by the labels fromgraph-X and config-Y-Z, where X stands for the simple graph from which the bigraph is constructed, and Y and Z stand for the degree distributions of the

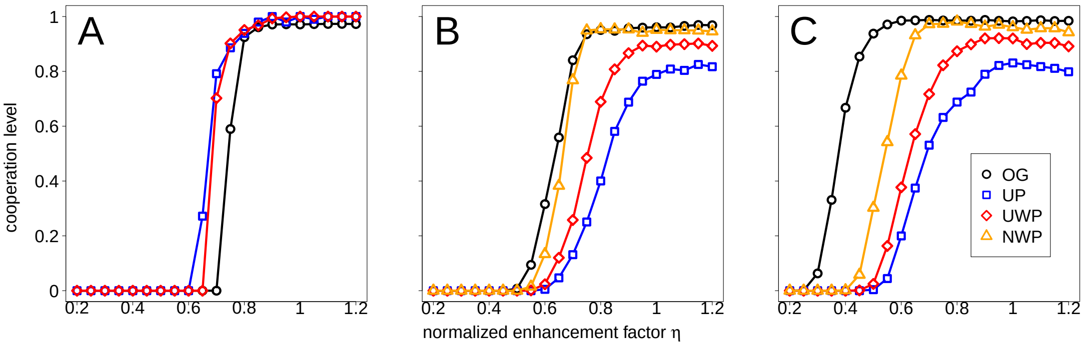

Figure 7.2: **Cooperation level for population structures with different replacement graphs.** Results are shown for the conventional NPD (Panels A and B) and the distributed NPD (Panel C). In each case, interaction graphs are constructed following the graph approach from rings (Panel A) or Barabási-Albert scale-free networks (Panels B and C) of order $Z = 512$ and mean degree $\langle z \rangle = 4$. The replacement graph is given by the original graph from which the interaction bigraph is constructed (OG) or the unweighted, unnormalized weighted or normalized weighted projection of the interaction graph (UP, UWP and NWP, respectively).

bottom and the top vertices, respectively. Replacement graphs are given either by the graph approach or by the bigraph approach.

7.2 Results

7.2.1 Replacement graphs

In the graph approach, the original graph from which the interaction bigraph is constructed automatically determines the replacement graph. As a result, the subset of players involved in imitation/competition with a given individual is generally smaller than the subset of players with whom such individual interacts. This implicit assumption is in stark contrast with most models of two-person games on graphs, where interaction and replacement neighborhoods perfectly overlap. In the following, we present the results of making interaction and replacement neighborhoods coincide in otherwise standard models of evolutionary multiplayer games on graphs.

Figure 7.2 depicts the results of the evolution of cooperation in the conventional and the distributed NPD for population structures with the same interaction bigraph but different replacement graphs. We plot the cooperation level (the average fraction of Cs for 2000 additional generations after an initial transient of 10^5 generations) as a function of the normalized enhancement factor $\eta = r/\nu$, where ν is the average degree of the top nodes of the interaction bigraphs, i.e. ν is the mean number of players per game in the population. In each case, the population structure is built (1) by defining a graph G of order Z (i.e. G has Z nodes) and mean degree $\langle z \rangle$, and (2) by constructing the interaction bigraph B from G using the graph approach. Hence, $\nu = \mu = \langle z \rangle + 1$, where μ is the average degree of the bottom nodes in the interaction bigraphs, i.e. the mean number of games per player in the population. The replacement graph H is given either by G itself (graph approach) or by the projection of B (bigraph approach). In this last case, weights are assigned to the edges of H according to one of three methods: UP, UWP and NWP. In any case, individuals engage in a given number of multiplayer games (according to their connectivity in the interaction bigraph) and accumulate payoffs. The accumulated payoff of each player is then associated with its fitness/success, and competition/imitation is implemented by using a finite population analogue of the replicator dynamics (Hauert & Doebeli, 2004; Santos et al., 2008): in social learning terms, each individual randomly chooses a neighbor in the replacement graph and, if the neighbor's success is greater than its own success, it imitates the neighbor's strategy with a probability proportional to the success difference (see section 7.4 for details).

Panel A of Figure 7.2 shows the results for the case where G is a ring of degree $z = 4$. We refer to the resulting bigraph B as fromgraph-ring. Referring to the original graph G, individuals interact with both their first-order neighbors and their second-order neighbors. If the replacement graph is given by the graph approach, only first-order neighbors in G are considered for competition/imitation. If the replacement graph is given by the bigraph approach, both first-order and second-order neighbors in G are considered for competition/imitation, possibly with a probability depending on the number of common games (UWP). Note that the larger replacement neighborhoods due to the bigraph approach favors cooperation slightly, but systematically. A detailed analysis of the origin of such promotion, considering the case of two contiguous clusters of Ds and Cs in a ring of degree $z = 4$, can be found in section 7.5.1 and Figure 7.3.

While the larger replacement neighborhoods brought about by the bigraph approach are beneficial to cooperation in bigraphs constructed from rings, they are detrimental to cooperation in bigraphs constructed from Barabási-Albert (BA) scale-free networks, which we call fromgraph-ba. Indeed, as evidenced in Panels B and C of Figure 7.2, in this case there is systematically less cooperation if replacement neighborhoods coincide with interaction neighborhoods (bigraph approach) than if the original graph is taken as the replacement graph (graph approach). Additionally, in the former case the assignment of weights to the edges of the replacement graph plays a key role in BA networks, as it is evident from

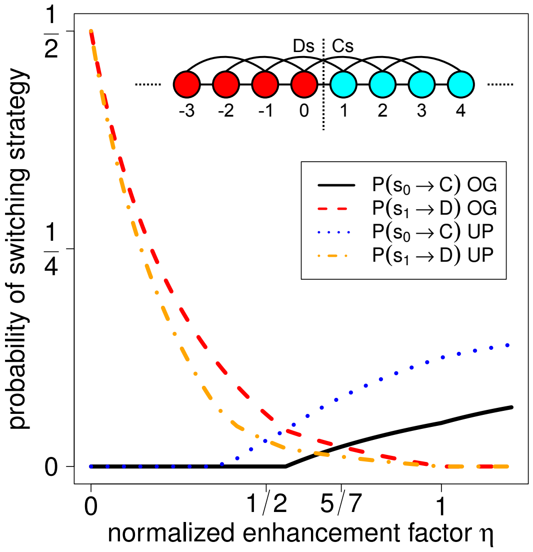

Figure 7.3: **Evolutionary dynamics on rings.** In the inset, we plot a ring of degree $z = 4$: the neighborhood of each node comprises the closest two nodes to the left and to the right. Following the graph approach, each node is the center of a game of size five so that each individual ends up interacting with the closest four neighbors to the left and the closest four neighbors to the right. We assume that the initial distribution of strategies is such that nodes $i > 0$ are Cs and nodes $i \leq 0$ are Ds. In the main panel, we plot the probabilities of switching strategies for the individuals at the boundary (nodes 0 and 1) when the replacement graph is given by the original graph (OG) and when it is given by the unweighted projection (UP) of the interaction bigraph. As shown, $P(s_0 \to C) > P(s_1 \to D) \Leftrightarrow r > 5/7$ for the graph approach, while $P(s_0 \to C) > P(s_1 \to D) \Leftrightarrow r > 1/2$ for the bigraph approach. See section 7.5.1 for the calculation of these probabilities.

the ordering of the curves, with NWP leading to more cooperation than UWP, and UWP to more cooperation than UP.

In order to explain these results, let us briefly recall the mechanism responsible for the promotion of cooperation in the distributed NPD when the interaction and replacement graphs are derived from scale-free networks using the graph approach (Santos et al., 2008). Scale-free networks are characterized by the co-existence of few hubs (very well connected individuals) with a vast majority of leaves (poorly connected individuals). Due to their large connectivity, hubs not only take part in many games, consequently accumulating high payoffs, but are also often targeted for competition/imitation by their neighbors. As a result of these two factors, C-hubs and D-hubs easily spread their strategies to their less connected neighbors. However, while C-hubs are favored by a positive feedback mechanism (the more they are imitated, the more Cs in their neighborhoods, and the more their own accumulated payoffs increase) D-hubs are penalized by a negative feedback mechanism (the more they are imitated, the more Ds in his neighborhood, and the more their own accumulated payoffs decrease) that eventually leads to their own demise. Hubs' inherent success along with the feedback mechanisms favoring Cs in inter-hub competition have been studied using star and double-star graphs as simple models of connectivity patterns in scale-free networks (Pacheco et al., 2009; Santos et al., 2008).

If the replacement graph H is no longer the original graph G (graph approach) but it is rather assumed to be the projection of the interaction bigraph B (bigraph approach), many additional links are present in H that were not in G. Indeed, since each top node of degree z induces a clique consisting of $z(z-1)/2$ edges, the projection of B is a relatively dense graph, particularly if the top degree distribution is highly heterogeneous Newman et al. (2001). This higher density of the replacement graph is at the origin of the hindering of the evolution of cooperation when moving from the graph approach (G taken as H) to the bigraph approach (the projection of B taken as H). Figures 7.4 and 7.5 show this effect for bigraphs built according to the graph approach from star and double-star graphs. In stars, and when the replacement graph is given by the projection of the interaction bigraph, leaves get connected to each other so that H is now a complete graph (see Panel D of Figure 7.4). This hinders the spreading of cooperative behavior from a C-center when defective leaves earn a higher payoff than cooperative leaves. In double-star graphs, leaves of the same star get interconnected and the center of one star gets connected to the leaves of the other star (see Panel D of Figure 7.5). This increased interconnection hinders cooperation by partially destroying both the positive feedback around C-centers and the negative feedback around D-centers on which inter-hub competition is based in the model of Santos et al. (2008). Note that, in all cases, the magnitude of these unfavorable effects depends on the weights attached to the links of the replacement graph.

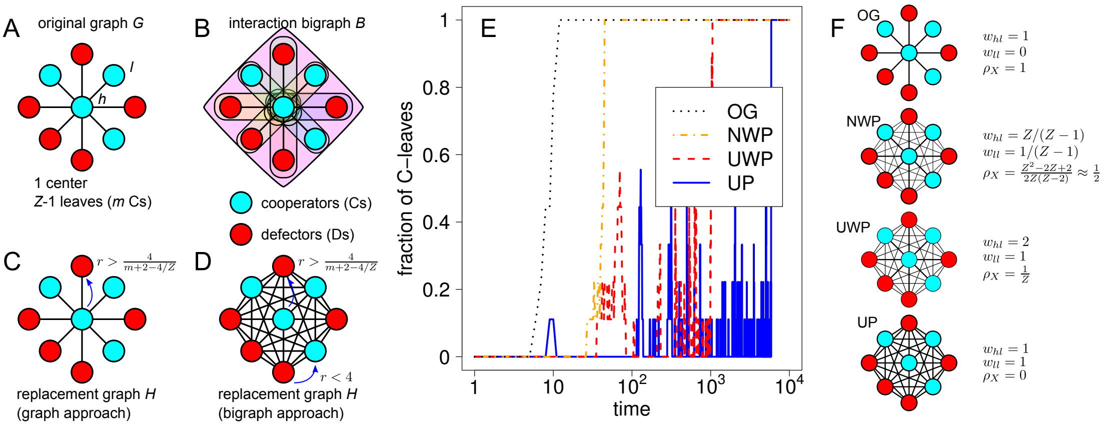

Figure 7.4: **Evolutionary dynamics on stars.** Consider a star graph G (Panel A) consisting of one C-center connected to $Z-1$ leaves (m of which are Cs) and the resulting interaction hypergraph B (Panel B) constructed from G using the graph approach. We assume that social interactions are modeled by the distributed NPD. In the graph approach, G is taken as the replacement graph (Panel C). In this case, competition/imitation occurs only between the center and the leaves. The C-center invades D-leaves for values of r above a critical value which reduces to $\alpha = 2/(1-2/Z)$ if $m = 0$ (the C-center is the only C). In the bigraph approach, the replacement graph is given by the projection of the interaction bigraph, so that leaves are now interconnected and the resulting topology is no longer a star but a complete graph (Panel D). The creation of these new links allows for inter-leaf competition/imitation, which is favorable to Ds if $r < 4$. As a result, for $\alpha < r < 4$, the time to fixation to the absorbing state where all individuals are Cs can become arbitrarily large depending on the weights attached to the links of the replacement graph, as it is shown in Panel E for $Z = 10$, $r = 2.8$ and for replacement graphs given by the OG, NWP, UWP and the UP methods. Panel F shows these replacement graphs together with the values of the weights of the links (w_{hl} for the weight of the link between the center and a leaf; w_{ll} for the weight of the link between two leaves) and their centralization indices (ρ_X). Note that more centralized graphs correspond to those more favorable to the spreading of cooperative behavior from the center. See section 7.6 for the derivation of the invasion conditions shown in Panels C and D, and sections 7.8 and 7.9 for the derivation of the centralization indices shown in Panel F.

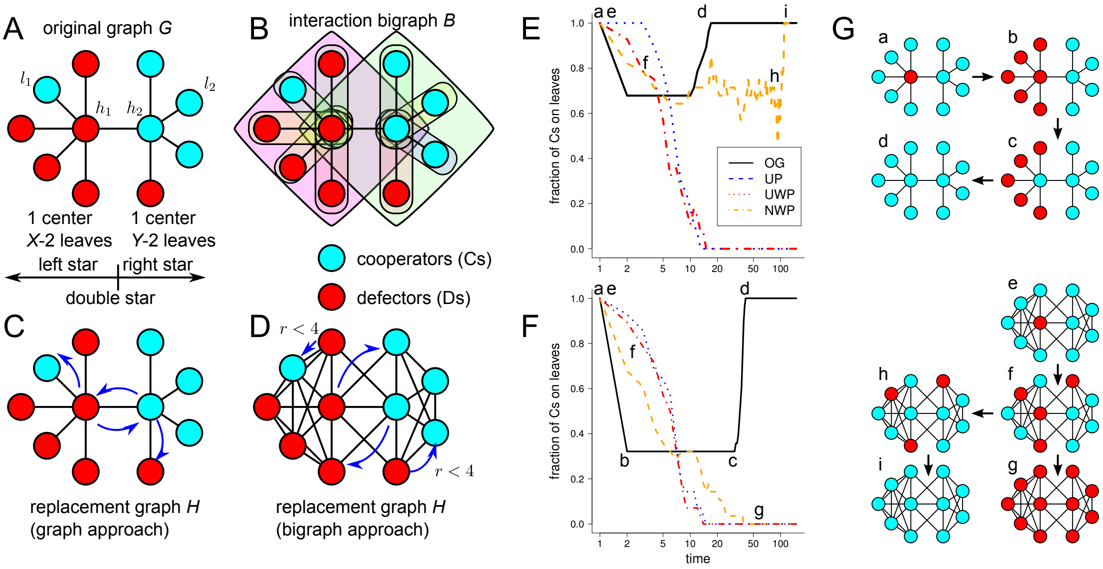

Figure 7.5: **Evolutionary dynamics on double stars.** Consider a double-star graph G (Panel A) consisting of a left and a right star connected by the centers, and the resulting interaction hypergraph B (Panel B) constructed following the graph approach. In the graph approach, G is taken as the replacement graph (Panel C). In this case, and for a wide range of values of r, spreading occurs preferentially from the centers (or hubs) to their respective leaves. Long-term evolution will ultimately depend on inter-hub competition, which is favorable to C-hubs due to the positive and negative feedback mechanisms brought about by the spreading from centers to (own) leaves. In the bigraph approach, the replacement graph is given by the projection of the interaction bigraph (Panel D), so that the center of one start gets connected to the leaves of the other star and leaves of the same star get connected with each other. This not only allows successful centers to breed copies of themselves in the leaves of the other star, but also makes inter-leaf competition possible, which is favorable to Ds if $r < 4$. As a result, the feedback mechanisms on which the evolution of cooperation on heterogeneous graphs is based are diminished and the evolutionary outcome is more favorable to Ds. This is illustrated in Panels E and F, which show typical scenarios for the time evolution of the fraction of Cs under the distributed NPD ($r = 1.3$) on the leaves of double-star graphs (Panel E: $X = 10$, $Y = 20$; Panel F: $X = 20$, $Y = 10$), for replacement graphs given by the OG, UP, UWP and NWP methods. In all cases we placed Cs on all nodes of the double-star, except for the left center, where we placed a D (see configurations **a** and **e** of Panel G). If the replacement graph is given by the original graph (OG), the dynamics are such that, typically, the D-center invades the leaves of his star (configuration **b**), then the C-center invades the D-center (**c**) and finally D-leaves on the left star are invaded by the C-center (**d**). When the replacement graph is given by the projection of the interaction graph, Ds can now easily spread from the initial center until they invade the whole population (**e**,**f**,**g**). Weights attached to the links of the projection play a key role in this case, with NWP still favoring Cs when the connectivity of the left star is small compared to that of the second star (**e**,**f**,**h**,**i**). See section 7.7 for the analytical derivation of the results shown in this figure.

Indeed, different projection methods lead to different weight distributions, which in turn affect the topological importance of different nodes in the evolutionary process. Such topological importance can be captured by what we call in this paper *replacement centrality*, which we define as the expected number of times a given node/individual is selected for competition/imitation by its neighbors (see section 7.8). Other things being equal, nodes with a higher replacement centrality play a more influential role in the evolutionary dynamics. We find that the level of centralization of the replacement graph (defined as the degree to which a single node is more central than others in the network; see section 7.8) correlates with the amount of cooperation exhibited in these topologies, as measured by the inverse fixation time of a single C-center in a star graph (see Panel E of Figure 7.4) or by the cooperation level in BA scale-free networks (Panels B and C of Figure 7.2). Figure 7.6 shows that the relationship between projection method and centralization of the network found in star graphs (OG > NWP > WP > UP) is maintained in BA scale-free networks. As evidenced by Figure 7.6 and Panels B and C of Figure 7.2, weight distributions leading to more centralized replacement graphs are also responsible for higher cooperation levels.

7.2.2 Degree distributions

In bigraphs constructed using the graph approach, *group diversity* (heterogeneity in the number of players per game) is inextricably intertwined with *individual diversity* (heterogeneity in the number of games per player). Indeed, the top degree distribution (determining group diversity) is exactly the same as the bottom degree distribution (determining individual diversity) in bigraphs built using the graph approach. In order to analyze group diversity and individual diversity independently of each other, we made use of random configuration model bigraphs (for which the degree sequences of top and bottom vertices can be specified independently of each other) as interaction bigraphs. We used two different degree sequences for top and bottom vertices: a constant sequence (all degrees are the same) and the degree sequence of a BA scale-free graph, which approximately follows a power-law. Combinations of these two degree sequences resulted in four bigraphs: config-reg-reg (with homogeneous top and bottom degree distributions), config-ba-reg (with heterogeneous bottom and homogeneous top degree distributions), config-reg-ba (with homogeneous bottom and heterogeneous top degree distributions), and config-ba-ba (with heterogeneous bottom and top degree distributions). The reason for using the degree sequence of a BA graph instead of determining the degree sequence by another method (for instance, by sampling the sequence from a random variable distributed according to a power-law distribution) is to be able to compare the results obtained for config-ba-ba with those obtained for fromgraph-ba in section 7.2.1. Indeed, config-ba-ba has

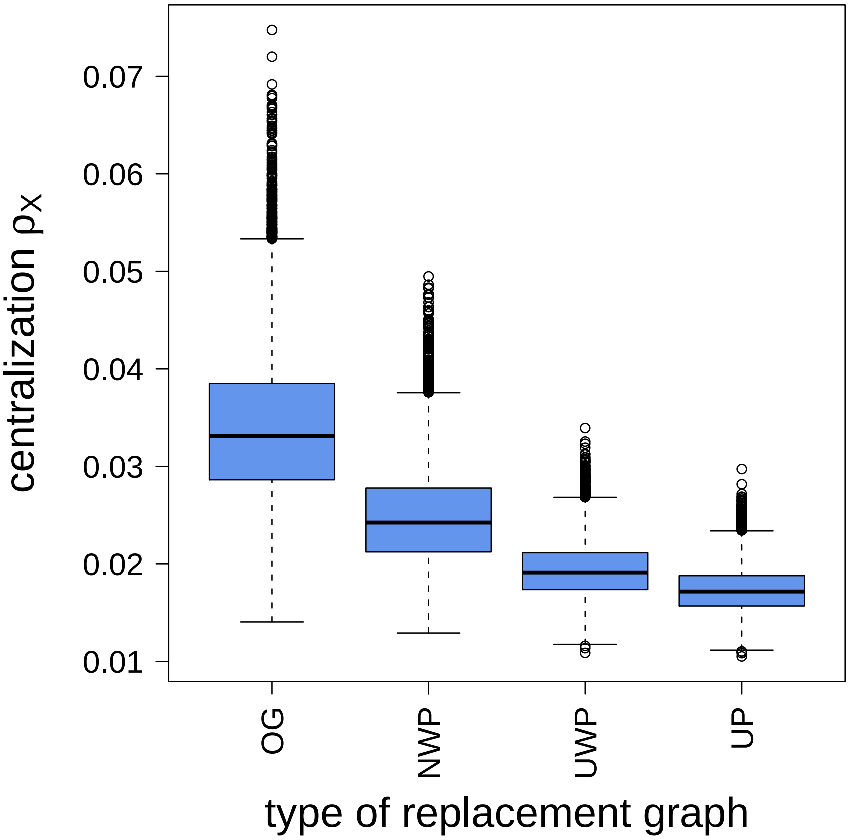

Figure 7.6: **Centralization of the replacement graphs for interaction bigraphs built from Barabási-Albert scale-free networks.** Each boxplot shows the distribution of the centralization for a random sample of 10^4 replacement graphs given by the original graph (OG), the normalized weighted projection (NWP), the unnormalized weighted projection (UWP) and the unweighted projection (UP). In all cases, the original graph is a Barabási-Albert scale-free network of order $Z = 512$ and mean degree $\langle z \rangle = 4$. The projections are taken from bipartite graphs constructed from the original graph using the graph approach. Notice that more centralized networks lead to higher cooperation levels in Panels B and C of Figure 2 in the main text. See section 7.8 for the definition of the centralization indices used in this figure.

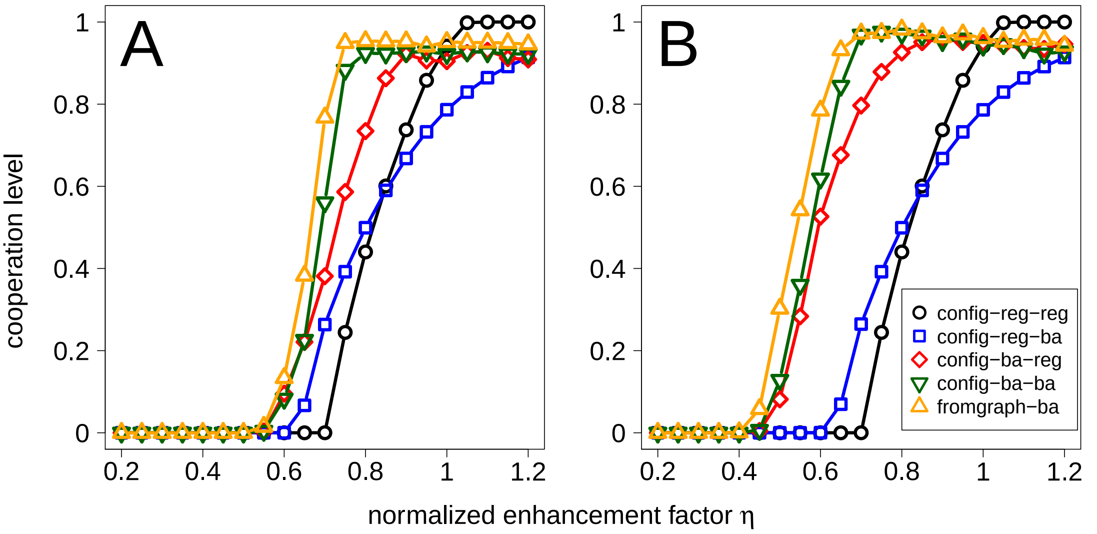

Figure 7.7: **Cooperation level for population structures with different degree distributions.** Panel A shows results for the conventional NPD; Panel B for the distributed NPD. config-X-Y stands for a configuration model bigraph with a degree sequence of type X for the bottom vertices (players) and of type Y for the top vertices (games). For the degree sequences themselves, reg is a regular sequence and ba is the degree sequence of a Barabási-Albert network. A bigraph constructed from a Barabási-Albert network following the graph approach (fromgraph-ba) is shown for comparison purposes. Parameters: $\mu = \nu = 5$, $Z = 512$, replacement graph given by the NWP method.

the same top and bottom degree sequences as fromgraph-ba, and can be effectively thought of as a randomization of such network.

Figure 7.7 shows the results for the evolution of cooperation in the conventional and the distributed NPD for the four configuration model bigraphs and for the fromgraph-ba. Let us consider first the results for config-reg-reg, i.e. the homogeneous population structure lacking social diversity of any kind. As shown in the figure, this network is able to sustain cooperation for values of η above $\eta_c \approx 0.7$. Furthermore, cooperation is fully established for $\eta > \eta_d$, with η_d close to its value for infinite well-mixed populations ($\eta_d = 1$). For $\eta_c < \eta < \eta_d$, Cs and Ds co-exist in dynamical equilibrium. If group diversity is introduced (config-reg-ba), the co-existence zone grows so that $\eta_c \approx 0.6$, and $\eta_d > 1.2$. This shows that group diversity has mixed effects in the evolutionary dynamics, promoting cooperation (with respect to config-reg-reg) up to a critical value $\eta^* \approx 0.85$, and hindering cooperation above this value. If diversity is instead introduced at the individual level (config-ba-reg), cooperation is evolutionarily viable for $\eta > 0.55$ in the conventional NPD and for $\eta > 0.45$ in the distributed NPD. Note, nonetheless, that defective behavior is not completely eradicated, not even for $\eta > 1$. From these results, it is evident that individual diversity leads to higher cooperation levels than group diversity (compare the curves for config-ba-reg with those for config-reg-ba) for all values of η. We also note that the levels of cooperation slightly improve when both kinds of social diversity are simultaneously present (compare config-ba-ba to config-ba-reg and config-reg-ba). Finally, the results obtained with config-ba-ba are almost the same as those obtained with fromgraph-ba, which suggests that the higher topological correlations present in fromgraph-ba and absent in config-ba-ba play a rather small role in the evolutionary dynamics.

The results for networks with homogeneous bottom degree distributions (config-reg-reg and config-reg-ba) and for networks with heterogeneous bottom degree distributions (config-ba-reg, config-ba-ba and fromgraph-ba-ba) differ not only quantitatively in their cooperation levels, but also qualitatively in their dynamics. Indeed, intermediate cooperation levels for bigraphs with homogeneous bottom degree distributions are mostly due to the co-existence of Cs and Ds. Contrastingly, in the case of bigraphs with heterogeneous bottom degree distributions intermediate cooperation levels are due to bi-stability, so that the vast majority of times the dynamics reaches the absorbing states of full defection or full cooperation. In this last case, intermediate cooperation levels are almost entirely determined by the proportion of times the dynamics ended up in the full cooperation absorbing state.

Figure 7.8 provides some insight on the different results obtained when diversity is introduced at the individual level (config-ba-reg) or at the group level (config-reg-ba). First, note that the degree distribution of the replacement graph for config-ba-reg is highly heterogeneous (see top panels of Figure 7.8). Indeed, it is well known that the degree distribution of the projection of a bigraph with a power law bottom degree distribution also follows a power law (Birmelé, 2009; Guillaume & Latapy, 2006; Nacher & Akutsu, 2011). Contrastingly, the degree distribution of the replacement graph for config-ba-reg is less heterogeneous. A second important difference between config-ba-reg and config-reg-ba is the way received benefits are distributed on these networks. When the population consists of 50% Cs randomly placed on the bottom vertices of the bigraph, the distribution of received benefits closely follows a power-law in the case of config-ba-reg, but it approximately follows a normal distribution in the case of config-reg-ba (see middle panels of Figure 7.8). The reason behind these different distributions is that on config-ba-reg both the per-capita per-game contribution and the number of games per individual are highly variable while on config-reg-ba they are constant. This leads to a highly heterogeneous distribution of received benefits on config-

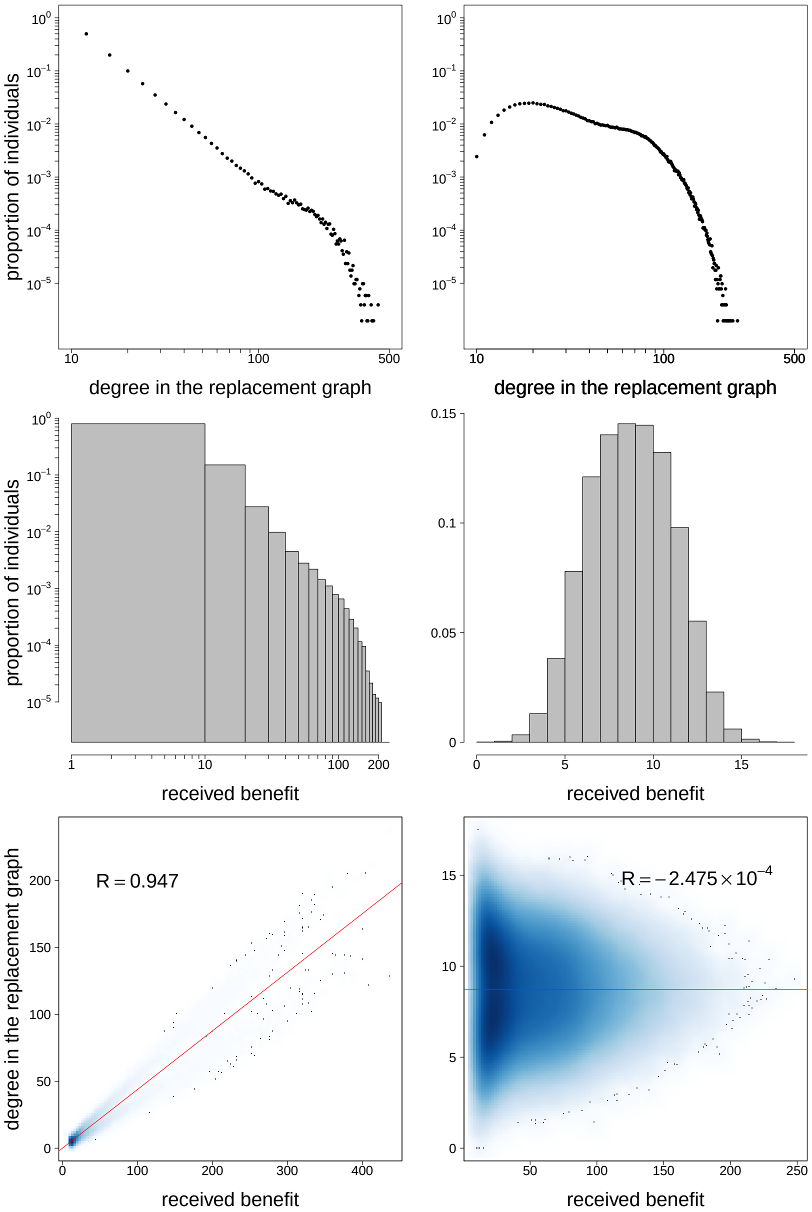

Figure 7.8: **Statistics for config-ba-reg and config-reg-ba.** The figure shows some statistics for config-ba-reg (left panels) and config-reg-ba (right panels). Top panels: degree distribution of the replacement graph. Middle panels: histograms for the received benefit. The received benefit is calculated as the payoff for Ds when approximately half of the population are Cs (randomly distributed) under the distributed NPD. Bottom panels: smooth scatter plots, regression lines and Pearson's correlation coefficients for the received benefit vs. degree in the replacement graph. Parameters: $Z = 512$, $\mu = \nu = 5$ and $\eta = 0.7$. The figures show statistics for 100 randomly generated networks of each type.

reg-ba and to a relatively homogeneous distribution on config-reg-ba. Finally, while there is a strong correlation between connectivity in the replacement graph and received benefit in config-ba-reg, such correlation is practically inexistent in config-reg-ba (see bottom panels of Figure 7.8). Indeed, for config-ba-reg hubs in the replacement graph are individuals participating in many games and hence accumulating large payoffs. Contrastingly, for config-reg-ba highly connected individuals in the replacement graphs are those participating in large groups, which have on average the same *proportion* of Cs and hence produce the same amount of public good than smaller groups. As a result, the evolutionary dynamics on config-ba-reg is dominated by a small number of very well connected and powerful individuals, while config-reg-ba is far more homogeneous, both concerning connectivity in the replacement graph and accumulated payoffs. These differences translate into two different modes of evolution. In config-ba-reg (see Figure 7.9) the influence of hubs is decisive to the evolutionary outcome, so that a majority of C-hubs leads the whole population to the all-Cs absorbing state, while a majority of D-hubs leads the population to the all-Ds absorbing state. Additionally, the proportion of Cs is also higher in high-degree classes (very well connected individuals) than in low-degree classes (poorly connected individuals). Contrastingly, in config-reg-ba (see Figure 7.10) the evolutionary dynamics is largely independent of what happens with well-connected individuals, and evolution unfolds as a process of dynamical self-organization in which Cs tend to cluster in small groups which are more favorable to cooperation while Ds tend to do so in large groups which are more favorable to defection.

7.2.3 Bipartite clustering coefficient

The bipartite clustering coefficient captures the degree to which bottom vertices' neighborhoods overlap (see section 7.10 for details). As pointed out in section 7.1, interaction bigraphs built using the graph approach lead, by construction, to relatively high bipartite clustering coefficients. In order to assess the real importance of clustering in the evolutionary dynamics, we considered four interaction bigraphs with the same top and bottom degree distributions (regular sequences in all cases) but different bipartite clustering coefficients: fromgraph-ring (constructed from a ring network of degree $z = 4$), fromgraph-reg (constructed from a random regular network of degree $z = 4$), fromgraph-vn (constructed from a square lattice with a von Neumann neighborhood), and config-reg-reg (random configuration model with regular top and bottom degree sequences).

Figure 7.11 shows the cooperation levels under the conventional NPD and Figure 7.12 the bipartite clustering coefficient and the mean degree of the replacement graph for these different bigraphs. Interestingly, bigraphs with more bipartite clustering (and consequently lower mean degree in the replacement graph)

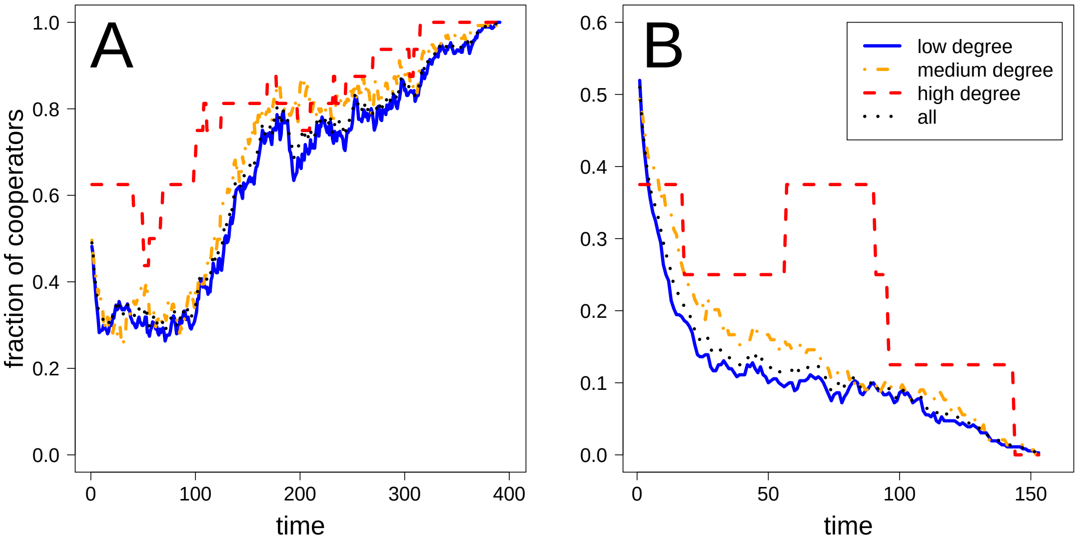

Figure 7.9: **Time-dependence of the fraction of cooperators for different connectivity classes in the config-ba-reg network.** The figure shows the fraction of Cs among low-degree ($z_i < \mu$), medium-degree ($\mu \leq z_i < z_{max}/3$) and high-degree ($z_{max}/3 \leq z_i \leq z_{max}$) individuals, for two different simulation runs. In Panel A, initially more than the 60% of the highly-connected individuals are Cs. C-hubs lead the evolutionary process and diffuse cooperative behavior among their less connected neighbors. In Panel B, initially less than 40% of the hubs are Cs. Less connected individuals quickly turn to defection, with medium-degree and high-degree individuals eventually following the trend. Parameters: $\eta = 0.7$, $\mu = \nu = 5$ and $Z = 512$.

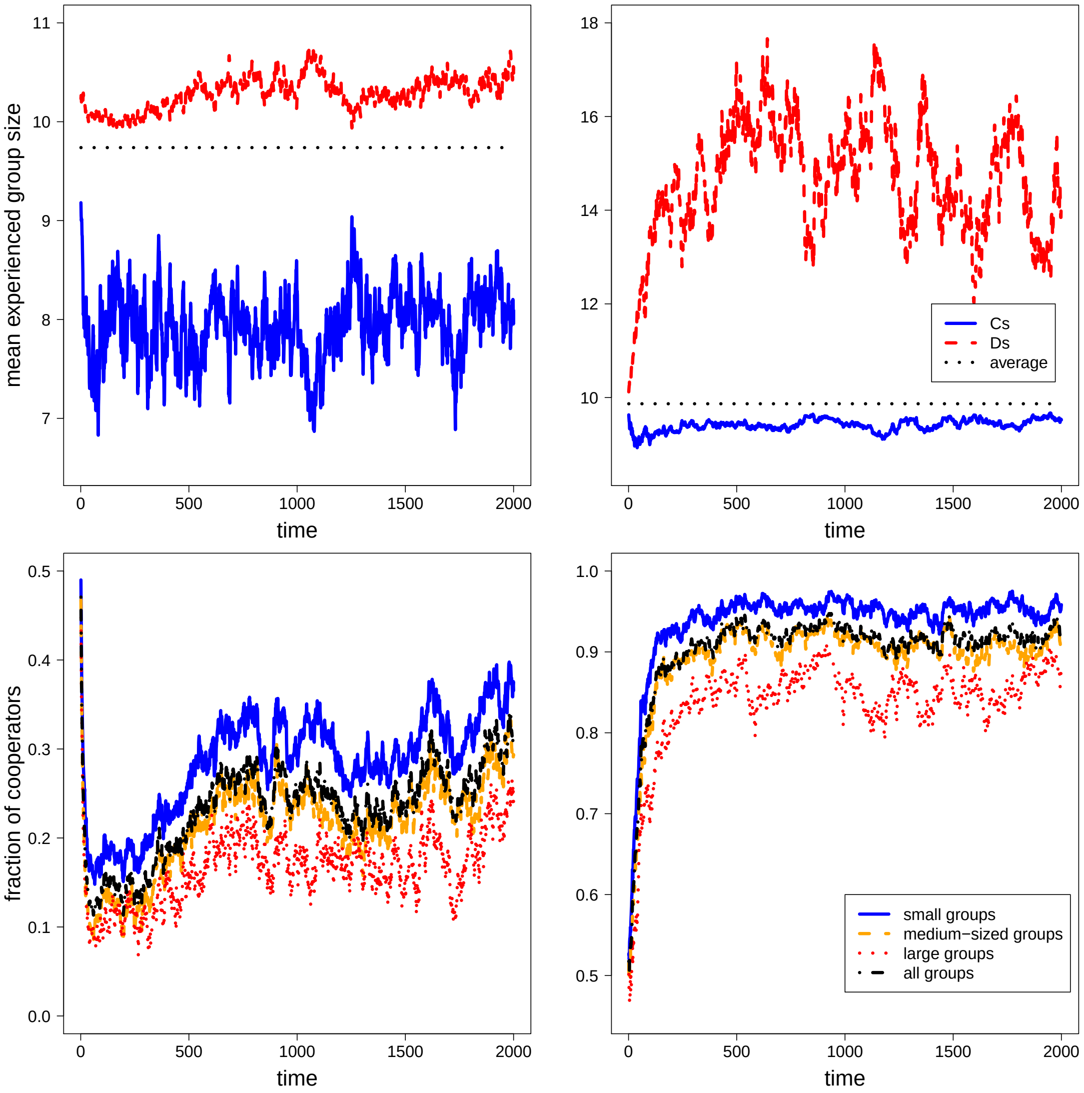

Figure 7.10: **Time-dependence of the average experienced group size and of the fraction of cooperators in groups of different size for config-reg-ba.** The figure shows the mean experienced group size for Cs and Ds (top panels) and the fraction of Cs in small ($N_i < \nu$), medium-sized ($\nu \leq N_i < N_{max}/3$) and large ($N_{max}/3 \leq N_i \leq N_{max}$) groups (bottom panels) for $\eta = 0.7$ (left panels) and $\eta = 1.2$ (right panels). The evolutionary dynamics on this population structure is such that Cs preferentially cluster together in small groups and Ds cluster together in large groups. Parameters: $\mu = \nu = 5$ and $Z = 512$.

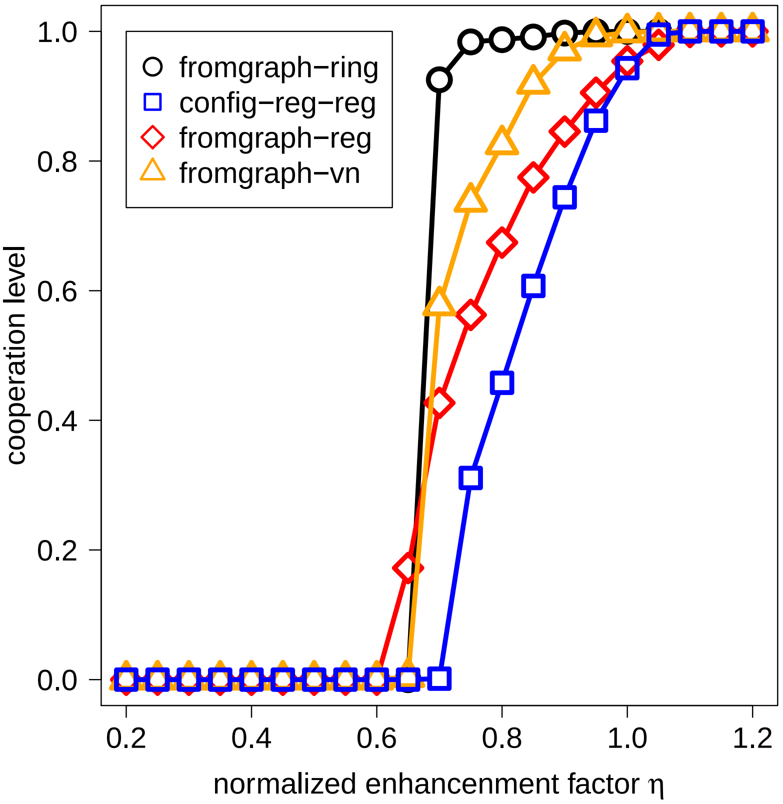

Figure 7.11: **Cooperation level for bigraphs with different bipartite clustering coefficients.** The interaction bigraphs are constructed following the graph approach with a ring (fromgraph-ring), a square lattice with von Neumann neighborhoods (fromgraph-vn), or a regular random network (fromgraph-reg) of degree $z = 4$ as original graphs, or given by a configuration model bigraph with regular degree sequences for both top and bottom vertices (config-reg-reg). In all four cases the degree distributions of top and bottom vertices is a regular sequence with $\mu = \nu = 5$, the replacement graph is given by the normalized weighted projection (NWP) of the interaction bigraph, and $Z = 1024$.

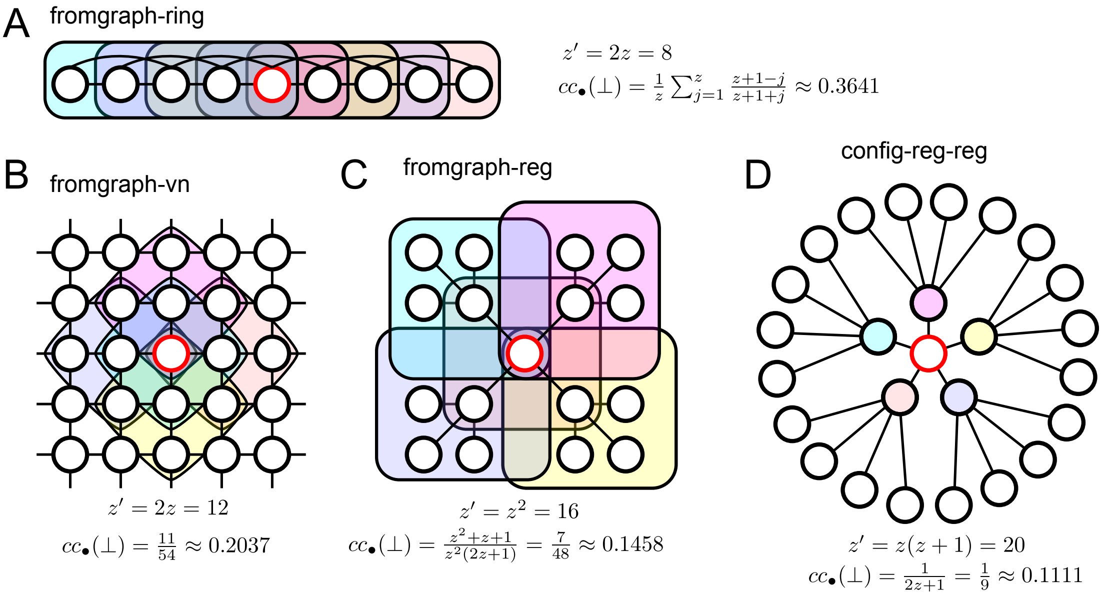

Figure 7.12: **Graphical representation and bipartite clustering coefficients of different interaction bigraphs.** The figure shows typical interaction neighborhoods for a focal individual (red node) as well as the degree of the replacement graph (z') and the bipartite clustering coefficient ($cc_\bullet(\perp)$) for fromgraph-ring (Panel A), fromgraph-vn (Panel B), fromgraph-reg (Panel C) and config-reg-reg (Panel D). For all networks, $\mu = \nu = 5$. Values of z' and $cc_\bullet(\perp)$ are exact for fromgraph-ring and fromgraph-vn and analytical approximations (assuming networks are Bethe lattices) for fromgraph-reg and config-reg-reg.

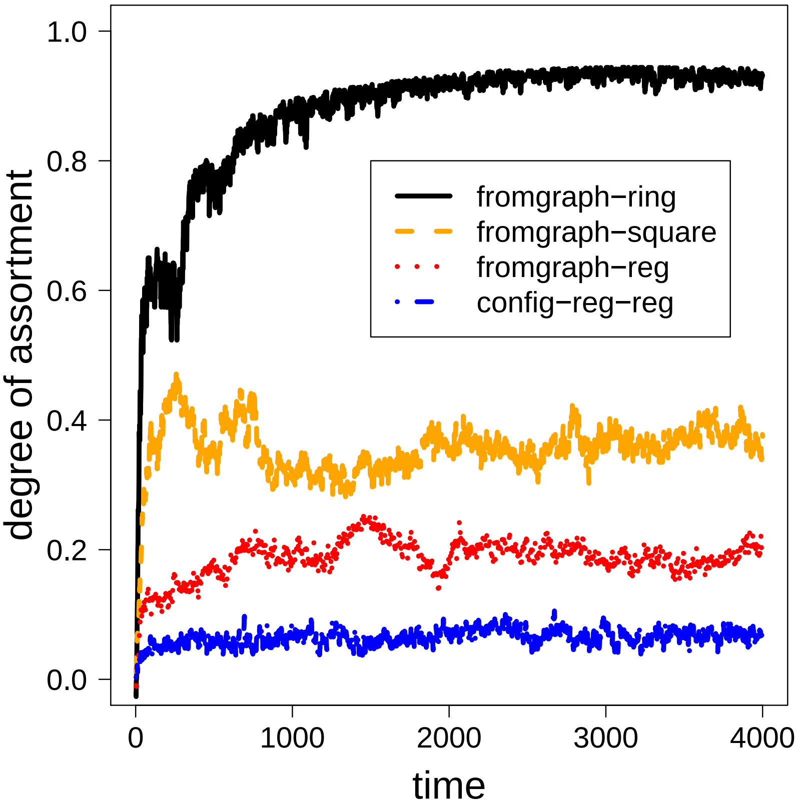

Figure 7.13: **Time evolution of the degree of assortment in the replacement graphs of interaction bigraphs with different bipartite clustering coefficients.** The figure shows the time evolution of the degree of assortment in the replacement graph. See section 7.11 for the definition of degree of assortment we used in this figure.

lead in general to equal or higher cooperation levels for all the considered values of the normalized enhancement parameter η. These results make sense in the light of well established results on the effects of local interactions on the evolutionary dynamics of the pairwise and multiplayer versions of the NPD. It is well known that spatial structure enables Cs to form clusters within which they preferentially interact with other Cs, thus reducing the exploitation by surrounding Ds. Cluster formation is brought about by a feedback mechanism resulting from imitation/competition with direct neighbors that amplifies initial inhomogeneities in the distribution of strategies. As it is shown in Figure 7.13, large values of bipartite clustering coefficient favor cluster formation by allowing Cs to find each other more easily and to reduce the number of connections with surrounding Ds.

7.3 Discussion

Since the seminal works by Axelrod (1984) and Nowak & May (1992) on the evolution of cooperation on lattices, games on graphs have traditionally made use of unipartite graphs in order to model population structures. Despite its usefulness for exploring the effects of local interactions on the evolutionary dynamics of two-player games, the use of unipartite graphs as population structures entails a certain number of construction limitations when applied to general multiplayer games, leading not only to a lack of flexibility but also to unrealistic assumptions about the topological properties of networked populations. In this paper, we have shown how the use of bipartite graphs and of constructing procedures that fully take into account the bipartite nature of social and biological populations can circumvent the limitations of the standard graph approach, opening up new opportunities for studying the role of different properties of network topologies on the evolution of strategic interactions. In particular, it is important to emphasize the need of explicitly defining two graphs: the interaction bigraph, determining who plays with whom, and the replacement graph, determining who competes with whom. As demonstrated in this paper, different ways of constructing any of these two graphs or of deriving one from the other can have important consequences in the evolutionary dynamics of multiplayer games.

First, the implicit assumption that the replacement graph coincides with the original graph in the graph approach is crucial for the success of BA scale-free networks as cooperation-promoting topologies reported in Santos et al. (2008). When the replacement graph is derived in a more natural way, so that interaction and replacement neighborhoods perfectly overlap (the usual assumption in evolutionary two-person games on networks) cooperation is hindered in BA scale-free networks to a point that any advantage of social heterogeneity is effectively canceled by the resulting larger replacement neighborhoods (see Figure 7.2). The introduction of weights in the replacement graph somewhat alleviates this problem, as weighted links partly restore the high centralization characteristic of BA scale-free networks.

Second, while individual diversity (heterogeneous bottom degree distributions) systematically fosters cooperation, group diversity (heterogeneous top degree distributions) promotes cooperation up to a critical value of the enhancement factor, but hinders cooperation above such value (see Figure 7.7). We also showed that networks with both kinds of social diversity foster more cooperation than networks with only one kind of diversity, but that the difference between the cooperation levels of networks with both individual and group diversity and the cooperation levels of networks with only individual diversity are relatively small. Finally, intermediate cooperation levels in networks without individual diversity are mostly due to co-existence of Ds and Cs, while intermediate cooperation levels in networks with individual diversity are characterized by bi-stable evolutionary dynamics. In other words, the results for config-reg-reg and config-reg-ba shown in Figure 7.7 can be better understood as representing the final proportion of Cs in a population where both Cs and Ds are present. Contrastingly, the results for config-ba-ba, config-ba-reg and fromgraph-ba can be better interpreted as a probability of ending up in a fully cooperative state when starting from a condition where 50% Cs are randomly placed on the network.

Third, bipartite clustering, i.e. group overlap, plays an important role in the evolution of cooperation under the conventional NPD. We provided clear evidence of the beneficial role of bipartite clustering on cluster formation and, consequently, on the evolution of cooperation on regular structures. In this respect, our results mirror similar conclusions on the beneficial effects of unipartite clustering on the evolution of cooperation under the standard evolutionary two-player PD (Assenza et al., 2008; Pusch et al., 2008; Roca et al., 2009a).

Apart from the present paper and to the best of our knowledge, only two studies have made use of the bigraph approach for studying evolutionary multiplayer games: Gómez-Gardeñes et al. (2011), where the use of bigraphs as population structures for evolutionary games on networks was first introduced, and Gómez-Gardeñes et al. (2011), a subsequent study on the effects of social diversity on the evolution of cooperation under the NPD. In the first of these studies, the evolution of cooperation under the NPD on a real bipartite collaboration network is compared to the dynamics on its bottom projection. Higher cooperation levels are found for the bipartite network than for its projection. These results have been interpreted as hinting that "the intrinsic group structure (described by means of the bipartite graph) promotes cooperation in PGGs, this being a new mechanism for this phenomenon beyond the scale-free character and other features of the one-mode (projected) complex network" (Gómez-Gardeñes et al., 2011). We would like to point out that a simpler explanation is that, by construction, the mean group size in the bigraph built from a projected network is always larger than the mean group size in the original bipartite network, and that larger group sizes hinder the evolution of cooperation under the NPD. In order to assess the influence of group structure and other mesoscopic properties on the evolutionary dynamics, a comparison of real bipartite networks with their "randomized" versions should be carried out, as it has been done for real unipartite networks and two-person games (Lozano et al., 2008).

In the second study (Gómez-Gardeñes et al., 2011) the evolutionary dynamics of the conventional and distributed versions of the NPD were investigated on interaction bigraphs with tunable individual diversity but no group diversity at all. The main finding of this study is that bigraphs with low individual diversity (Poisson-like bottom degree distributions) can actually allow for more cooperation than bigraphs with high individual diversity (bottom degree distributions following a power law) in the case of the conventional NPD. This result contrasts sharply with our own results, which suggest that individual diversity generally promotes cooperation. Note, however, that we used both a different network model (configuration random networks) and different degree distributions (with zero instead of moderate individual diversity). These different setups could account for the divergent results. We also note that Gómez-Gardeñes et al. (2011) suggest that the ability of BA scale-free networks to outperform homogeneous networks reported in Santos et al. (2008) is "intrinsically due to the entanglement of social and group heterogeneities". Although our own results partially support this view, given the (moderate) synergy between individual and group diversity, we have provided evidence that the promotion of cooperation reported in Santos et al. (2008) is mainly due to the implicit assumption that the replacement graph is equal to the original graph from which the interaction topology is constructed.

The choice of the NPD as case of study in this paper was based on the fact that most of the theoretical work on evolutionary multiplayer games has focused on this particular game. However, recent empirical Gore et al. (2009) and theoretical Archetti & Scheuring (2011a) work testifies a growing discomfort with the NPD as model of realistic social dilemmas, in particular because of its linearity and because of the fact that cooperation is a strictly dominated strategy in this game. Several of the conclusions drawn in the present study will necessarily change if strategic interactions are modeled after PGGs different from the NPD. For instance, it has been recently shown that, even in the absence of a fixed topology, group diversity can importantly affect the evolutionary dynamics of non-linear PGGs (Peña, 2012). In the light of these results, we would expect group diversity to play a more prominent role in the evolutionary dynamics of non-linear games played on bigraphs with highly heterogeneous top degree distributions. Also, bipartite clustering could be partially detrimental, instead of largely beneficial, for the evolution of cooperation if the social dilemma is modeled after a multiplayer game with a structure similar to the snowdrift game, as it is already the case for two-person games (Hauert & Doebeli, 2004).

7.4 Methods

7.4.1 Population structures

Population structures are modeled by means of two graphs: the interaction bigraph $B = (\top, \bot, E_B)$ and the replacement graph $H = (\bot, E_H)$. The two sets of vertices of the interaction bigraph ($\top$ and $\bot$) represent, respectively, the set of groups/games and the set of individuals/players.

7.4.1.1 Graph approach

In what we call the graph approach (Hauert et al., 2002; Santos et al., 2008), first the replacement graph $H = (\bot, E_H)$ is defined, then the interaction bigraph $B = (\top, \bot, E_B)$ is constructed from the replacement graph as follows. Denote by $v_1, v_2, \ldots, v_Z$ the vertices of the graph H and by $N_H[v_i]$ the closed neighborhood of vertex v_i, defined as the set of vertices adjacent to v_i plus v_i itself. Further, denote by $b_1, b_2, \ldots, b_Z$ the bottom ($\bot$) vertices of B and by $t_1, t_2, \ldots, t_Z$ the top ($\top$) vertices of B. Then, E_B is defined as the set of all pairs $(b_i, t_j) \in \bot \times \top$ such that $v_i \in N_H[v_j]$.

7.4.1.2 Bigraph approach

In what we call the bigraph approach (Gómez-Gardeñes et al., 2011), first the interaction bigraph $B = (\top, \bot, E_B)$ is defined, then the replacement graph $H = (V, E_H)$ is constructed by projecting the interaction bigraph into its set of bottom vertices. In addition, weights can be attached or not to the edges of H according to one of the following three methods:

1. **Unweighted projection (UP).** As done in Gómez-Gardeñes et al. (2011), no weights are attached to the edges or, equivalently, the weights of all edges have a value of one.

2. **Unnormalized weighted projection (UWP).** The weight w_{ij} of the link $(i, j) \in E_H$ is given by the number of games i and j are connected to in the interaction bigraph (Wasserman & Faust, 1994). From a social learning perspective, the reason behind this heuristic is that the more often i interacts with j, the better i is supposed to be acquainted with j and therefore the more often i should consider j as target for imitation.

3. **Normalized weighted projection (NWP).** The weight w_{ij} is given by (Newman, 2001)

$$w_{ij} = \sum_k \frac{\delta_i^k \delta_j^k}{n_k - 1},$$

   where $\delta_i^k = 1$ if i participates in game k, $\delta_i^k = 0$ otherwise, and n_k is the number of players of game k. From a social learning perspective, the reason behind this heuristic is the assumption that individuals get acquainted with others more easily in smaller than in larger groups.

7.4.1.3 Bigraphs built from simple graphs using the graph approach

For fromgraph-X interaction bigraphs, we considered four different kinds of graphs: rings, scale-free networks, square lattices with von Neumann neighborhoods and regular random networks. Rings are one-dimensional lattices with degree z. Regular random networks (maximally random graphs where each node has the same degree z) were constructed using the igraph (Csárdi & Nepusz, 2006) implementation of the algorithm by Viger & Latapy (2005). Scale-free networks were obtained by means of the Barabási-Albert (BA) model (Barabási & Albert, 1999), i.e. growing networks using a preferential attachment rule. In order to get graphs with average degrees exactly equal to $\langle z \rangle$, we started the growing procedure from a fully connected graph of $m_0 = \langle z \rangle + 1$ nodes, and added $m = \langle z \rangle / 2$ new edges per new node.

7.4.1.4 Configuration model bigraphs

Config-X-Y bigraphs were constructed using the configuration model (Guillaume & Latapy, 2006; Molloy & Reed, 1995; Newman et al., 2001) with a top degree distribution of type X and a bottom degree distribution of type Y. For the degree distributions, we used regular sequences (reg) and degree sequences from BA scale-free networks (ba), constructed following the procedure mentioned before.

7.4.2 Multiplayer games

Each individual i participates in all games k such that $(i, k) \in E_B$. The social success of an individual is given by the sum of the payoffs obtained in all games it takes part in. We considered two versions of the NPD: the conventional NPD and the distributed NPD (Pacheco et al., 2009; Santos et al., 2008). In the conventional NPD, the payoffs of a D and a C in a group k of size N_k are respectively given by $\Pi_D = r m_k c / N_k$ and $\Pi_C = \Pi_D - c$, where m_k is the number of Cs in group k, c is the cost of cooperation and r is the enhancement factor. In the distributed NPD, each C of degree z_i (i.e. taking part in z_i games) contributes c/z_i to each game, so that the overall contribution of any C is equal to c. In this case, the payoff of individual i with strategy s_i (1 if C, 0 if D) is given by (Santos et al., 2008)

$$\Pi_i = \sum_{k \in N_B(i)} \left(\frac{r}{z_k} \sum_{j \in N_B(k)} \frac{c}{z_j} s_j \right) - c s_i,$$

where $N_B(i)$ is the open neighborhood of player i in B (i.e. the set of games played by i), $N_B(j)$ is the open neighborhood of game k in B (i.e. the set of players participating in game j), and s_j and z_j stand respectively for the strategy and the degree of the j-th player in the k-th group.

7.4.3 Evolutionary dynamics

The success/fitness of each individual was calculated as the sum of the payoffs obtained in all the games it participates in. Strategies are updated synchronously using a finite population analogue of the replicator dynamics commonly used in the literature of games on networks (Hauert & Doebeli, 2004; Santos et al., 2008). When updating the strategy of individual i, a neighbor j of i in the replacement graph is randomly chosen with a probability p_{ij} given by

$$p_{ij} = \frac{w_{ij}}{\sum_{k \in N_H(i)} w_{ik}},$$

where w_{ij} is the weight of the link $(i, j) \in E_H$. Denote by Π_i the accumulated payoff of individual i. Then, if $\Pi_i \geq \Pi_j$, i stays with its current strategy; otherwise it changes its strategy to j's with a probability given by $(\Pi_j - \Pi_i)/M$, where M is a normalization factor given by the highest possible difference between the accumulated payoffs of i and j.

7.4.4 Simulations

Simulations were started with 50% of Cs randomly placed on the graph. We measured the average fraction of Cs for 2000 additional generations after an initial transient of 10^5 generations, and called this value the cooperation level. Data points in Figures 7.2 and 7.7 correspond to the mean cooperation level over 1000 simulations; data points in Figure 7.11 correspond to the mean cooperation level over 100 simulations. A new realization of the graph is done for each simulation.

7.5 Supporting Information

7.5.1 Promotion of cooperation in the ring due to extended replacement neighborhoods

In order to understand the origin of the promotion of cooperation in rings shown in Panel A of Figure 7.2, consider the case of two contiguous clusters of Ds and Cs in a ring of degree $z = 4$. As shown in Figure 7.3, the probability that the D-player at the C-D boundary (player 0) becomes C is always higher with the larger replacement neighborhood due to the bigraph approach than with the smaller replacement neighborhood due to the graph approach. This is because in the network given by the graph approach player 0 compares its success with C-players close to the boundary (players 1 and 2), but in the network given by the bigraph approach player 0 can also compare its success with C-players away from the boundary (players 3 and 4), who interact with more Cs than players 1 and 2 and thus obtain larger payoffs. Likewise, the probability that the C-player at the boundary (player 1) changes its strategy to D is always smaller with the larger replacement neighborhood. Defining η_c as the critical value above which the probability that player 0 becomes C is higher than the probability that player 1 becomes D, it is clear that η_c is lower for the bigraph approach ($\eta_c = 1/2$) than for the graph approach ($\eta_c = 5/7 \approx 0.71$). Notice also that, at least for latter case, η_c is a good approximation of the critical value of η for which the cooperation level becomes larger than zero in Panel A of Figure 2.

The calculations of the probabilities of strategy switching leading to Figure 7.3 are detailed in the following.

Let us denote by $s_i = \{0, 1\}$ the strategy of individual i, with $s_i = 0$ if i is a D and $s_i = 1$ if i is a C. Consider the distribution of strategies in the population shown in the inset of Figure 7.3. We are interested in the probabilities of strategy switching after one time step for players 0 and 1, i.e. $\Pr(s_i \to 1 - s_i)$ for $i = 0$ and $i = 1$. From the definition of the evolutionary dynamics used in this study, it can be easily shown that, in the case of unweighted replacement graphs, such probability is given by

$$\Pr(s_i \to 1 - s_i) = \frac{1}{|N_H(i)|M} \sum_{j \in N_H(i)} |s_j - s_i| \, (P_j - P_i)\theta(P_j - P_i), \tag{7.1}$$

where $N_H(i)$ is the open neighborhood of i in the replacement graph H, $|x|$ is the cardinality of x if x is a set or the absolute value of x if x is a number, $\theta(x)$ is the Heaviside step function, such that $\theta(x < 0) = 0$ and $\theta(x \geq 0) = 1$, and $M = P_{max} - P_{min}$, with P_{max} and P_{min} the maximum and minimum possible payoffs. For a ring of degree $z = 4$, and whenever $r < 5$, the maximum possible payoff for a player is that of a D surrounded by Cs and the minimum possible payoff that of a C surrounded by Ds. When $r > 5$ the maximum possible payoff is that of a C surrounded by Cs and the minimum possible payoff that of a D surrounded by Ds. This leads to

$$M = \begin{cases} c(3r + 5) & \text{if } r < 5 \\ 5c(r - 1) & \text{if } r \geq 5 \end{cases} . \tag{7.2}$$

By calculating the payoffs P_i for $i \in \{-3, -2, \ldots, 3, 4\}$ and using Eq. 7.1 and Eq. 7.2 we obtain, in the case the replacement graph is given by the graph approach ($|N_H(i)| = 4 \; \forall i$),

$$\Pr(s_0 \to C) = \begin{cases} 0 & \text{if } r < 25/9 \\ \frac{9r-25}{20(3r+5)} & \text{if } 25/9 \leq r < 5 \\ \frac{7r-25}{50(r-1)} & \text{if } r \geq 5 \end{cases} , \tag{7.3}$$

and

$$\Pr(s_1 \to D) = \begin{cases} \frac{25-7r}{10(3r+5)} & \text{if } r < 25/9 \\ \frac{5-r}{4(3r+5)} & \text{if } 25/9 \leq r < 5 \\ 0 & \text{if } r \geq 5 \end{cases} . \tag{7.4}$$

Likewise, in the case the replacement graph is the unweighted projection of the interaction bigraph ($|N_H(i)| = 8 \ \forall i$):

$$\Pr(s_0 \to C) = \begin{cases} 0 & \text{if } r < 25/14 \\ \frac{14r-25}{40(3r+5)} & \text{if } 25/14 \leq r < 25/12 \\ \frac{13r-25}{20(3r+5)} & \text{if } 25/12 \leq r < 25/9 \\ \frac{7r-15}{8(3r+5)} & \text{if } 25/9 \leq r < 5 \\ \frac{2r-5}{10(r-1)} & \text{if } r \geq 5 \end{cases} , \tag{7.5}$$

and

$$\Pr(s_1 \to D) = \begin{cases} \frac{5-2r}{2(3r+5)} & \text{if } r < 25/14 \\ \frac{75-26r}{40(3r+5)} & \text{if } 25/14 \leq r < 25/12 \\ \frac{25-7r}{20(3r+5)} & \text{if } 25/12 \leq r < 25/9 \\ \frac{5-r}{8(3r+5)} & \text{if } 25/9 \leq r < 5 \\ 0 & \text{if } r \geq 5 \end{cases} . \tag{7.6}$$

Equations 7.3, 7.4, 7.5 and 7.6 are graphically summarized in Figure 7.3.

7.6 Evolutionary dynamics on the star graph

Consider a star graph G of order Z comprising one center (h) and $Z-1$ leaves (l) as that shown in Panel A of Figure 3 in the main text. Suppose that the center and m out of the $Z-1$ leaves are Cs. From this graph G, the interaction bigraph B is constructed using the graph approach. The accumulated payoff of the C-center, of D-leaves and of C-leaves under the distributed NPD are respectively given by

$$\begin{aligned} \Pi(h) &= \frac{rc\left[(m+2)Z^2 + 2(m-1)Z + 4\right]}{4Z^2} - c, \\ \Pi(l^D) &= \frac{rc\left[(m+1)Z + 2\right]}{2Z^2}, \\ \Pi(l^C) &= \frac{rc\left[Z^2 + 2Z(m+1) + 4\right]}{4Z^2} - c. \end{aligned}$$

The accumulated payoff of the C-center will be higher than that of a D-leaf if

$$\Pi(h) > \Pi(l^D) \Leftrightarrow r > \frac{4}{(m+2) - 4/Z},$$

which, for $m = 0$ (the center is the only C) reduces to (Santos et al., 2008)

$$r > \frac{2}{1 - 2/Z} \equiv \alpha(Z).$$

Note that α is a monotone decreasing function of Z and that $\alpha = 2$ in the limit of large Z. Consider first the standard case where G (the star graph itself) is taken as the replacement graph H. In this case, and starting with $m = 0$ Cs in the leaves, the C-center invades the whole population for $r > \alpha$, while a D-leaf takes over the C-center if $r < \alpha$ (see Panel C of Figure 3 in the main text). Consider now the case where the replacement graph H is built from the projection of B: H is no longer a star, but a complete graph with different weights attached to the links according to the type of projection used (see Panel D of Figure 3 in the main text). In this case, it can be shown that a D-leaf can invade a C-leaf if $r < 4$. From this, the fate of a single C located on the center depends on r as follows:

1. $r < \alpha$: the C-center is invaded by a defective leaf.
2. $\alpha \leq r < 4$: the C-center invades D-leaves, but C-leaves can be invaded by D-leaves. In any case the system will eventually evolve to a state where all individuals are Cs (this is the only absorbing state), but the time of convergence will depend on the weights of the replacement graph.
3. $r \geq 4$: the C-center and the C-leaves invade D-leaves. The system quickly converges to the all-C state.

7.7 Evolutionary dynamics on the double-star graph

Following previous related work (Pacheco et al., 2009; Santos et al., 2008), we consider the evolutionary dynamics on the double-star graph, as it gives hints about the evolutionary dynamics on networks largely dominated by the presence of few hubs, such as scale-free networks. We have two centers, each with $X - 2$ and $Y - 2$ leaves respectively, plus one edge connecting the two centers. We denote by h_1 and h_2 the two centers and by l_i a leaf connected to center h_i, with $i = 1, 2$ (see Panel A of Figure 4 in the main text). Let us assume that h_1 is a D, h_2 a C, m out of the $X - 2$ leaves l_1 are Cs and n out of the $Y - 2$ leaves l_2 are Cs. We denote by l_i^C (l_i^D) a leaf l_i with strategy C (D). Their accumulated payoffs under the distributed NPD can be shown to be given by

$$\begin{aligned}
P(h_1) &= \frac{rc(mY+2)}{2XY} + \frac{rc(nY+2)}{2Y^2} + \frac{mrc}{4}, \\
P(l_1^C) &= \frac{rc(mY+2)}{2XY} + \frac{rc}{4} - c, \\
P(l_1^D) &= \frac{rc(mY+2)}{2XY}, \\
P(h_2) &= \frac{rc(mY+2)}{2XY} + \frac{rc(nY+2)}{2Y^2} + \frac{nrc(Y+2)}{4Y} + \frac{rc(Y-2-n)}{2Y} - c, \\
P(l_2^C) &= \frac{rc(nY+2)}{2Y^2} + \frac{rc(Y+2)}{4Y} - c, \\
P(l_2^D) &= \frac{rc(nY+2)}{2Y^2} + \frac{rc}{2Y}.
\end{aligned}$$

Let us consider the case where $m = X - 2$ and $n = Y - 2$, so that all the individuals in the population are Cs except for the center h_2. If the replacement graph is given by the double star itself (graph approach) leaves compete only with their respective centers, and each center with its leaves and the other center. In this case, it has been shown (Santos et al., 2008) that the time evolution of the system is such that, typically, the D-strategy spreads preferentially to the leaves of the second star, thus contributing to reducing the fitness of the D-center and to facilitating an invasion from the C-center, after which cooperation easily spreads to the remaining leaves. When the replacement graph is given by the bottom projection of the interaction bigraph (bigraph approach), leaves compete also with other leaves of the same star and with the center of the other star. In this case, the D-center easily invades not only its own leaves but also the leaves of the second star. If $r < 4$, inter-leave competition or social learning eventually leads to the majority of leaves to be Ds and to the D-center to invade the C-center.

7.8 Replacement centrality

Centrality is a key concept that has been studied in social network analysis since its origins (Bavelas, 1950), and has since been adopted in other network-related disciplines (Newman, 2010). Measures of centrality, such as degree, closeness, betweenness and eigenvector centrality, describe individuals' positions in a network relative to others and provide an efficient way of identifying influential actors (Bonacich, 1987; Freeman, 1978; Wasserman & Faust, 1994). Likewise, measures of the *centralization* of a network index the tendency of a single node to be more central than other nodes in the network (Freeman, 1978).

Here, we generalize the definition of the power index recently proposed by Neal & Neal (2011) to weighted networks and define the replacement centrality of node i as

$$\rho_i = \sum_{j \in N_H(i)} \frac{w_{ij}}{\sum_{k \in N_H(j)} w_{jk}}, \tag{7.7}$$

where $N_H(i)$ is the open neighborhood of node i in the replacement graph and w_{ij} denotes the weight of the link between i and j. According to the evolutionary dynamics considered in this study, ρ_i is equal to the expected number of times individual i is chosen for competition/imitation by other individuals per generation. Other things being equal, replacement centrality measures the importance of an individual in the evolutionary process.

In order to measure the degree of centralization of the network, we make use of the measure used in Freeman (1978):

$$\rho_X = \frac{\sum_{i=1}^{Z} [\rho^* - \rho_i]}{\max \sum_{i=1}^{Z} [\rho^* - \rho_i]},$$

where ρ^* is the largest value of ρ for any node in the network and the maximum operator in the denominator is taken over all possible realizations of a network with Z nodes, so that ρ_X is normalized between 0 and 1. In our case, such maximum is obtained for an unweighted star graph of size Z so that we can write

$$\rho_X = \frac{\sum_{i=1}^{Z} [\rho^* - \rho_i]}{Z(Z-2)}. \tag{7.8}$$

This is the measure of centralization used for deriving the results shown in Panel F of Figure 7.4 and in Figure 7.6.

7.9 Replacement centrality on the star graph

Consider a star graph G of order Z with 1 center and $Z-1$ leaves, and the bigraph B built from G via the graph approach. Let the replacement graph H be equal to G (graph approach) or to the projection of the bigraph B (bigraph approach). Then, using Eq. 7.7 the replacement centrality ρ_h of the center node and the replacement centrality ρ_l of a leaf are respectively given by

$$\rho_h = \frac{(Z-1)w_{hl}}{w_{hl} + (Z-2)w_{ll}}, \tag{7.9}$$

and

$$\rho_l = \frac{1}{Z-1} + \frac{(Z-2)w_{ll}}{w_{hl} + (Z-2)w_{ll}}, \tag{7.10}$$

where w_{hl} is the weight of the edge between the center and a leaf and w_{ll} is the weight of the edge between any two leaves. Using Eq. 7.9, 7.10 and the values of w_{hl} and w_{ll} given in Panel F of Figure 7.4, we derive the centralization indices shown in Panel F of Figure 7.4.

7.10 Bipartite clustering coefficient

The bipartite clustering coefficient captures correlations between neighborhoods in a bigraph. In this study, we make use of the definition of bipartite clustering coefficient proposed in Latapy et al. (2008). In order to calculate the bipartite clustering coefficient of the bottom vertices of a bipartite graph, the bipartite clustering coefficient $cc_\bullet(u,v)$ for a pair (u,v) of bottom nodes is defined as their Jaccard similarity coefficient (Jaccard, 1901)

$$cc_\bullet(u,v) = \frac{|N(u) \cap N(v)|}{|N(u) \cup N(v)|},$$

where $N(u)$ denotes the neighborhood of node u. The bipartite clustering coefficient of a single node is then defined as the sum of Jaccard indices implying this node, divided by the number of nodes at distance 2

$$cc_\bullet(u) = \frac{\sum_{v \in N(N(u))} cc_\bullet(u,v)}{|N(N(u)|}.$$

Finally, the bipartite clustering coefficient of the set of bottom nodes is the average of the bottom vertices' bipartite clustering coefficient,

$$cc_\bullet(\perp) = \frac{\sum_{u \in \perp} cc_\bullet(u)}{|\perp|}.$$

7.11 Degree of assortment

The degree of assortment r can be defined as the difference between the probability that a random neighbor is a C, given that the focal individual is a C, and the probability that the neighbor is a C, given that the focal individual is a D (**?**)

$$r = \Pr(C|C) - \Pr(C|D),$$

which can be calculated each time step as

$$r = \frac{2n_{CC}}{2n_{CC} + n_{CD}} - \frac{n_{CD}}{2n_{DD} + n_{CD}},$$

where n_{xy} denotes the number of edges whose extreme points' strategies are x and y.

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Chapter 8

Via inequality to cooperation and vice versa: the asymmetric donation game on networks[†]

Abstract

The evolution of cooperation on complex networks has been the focus of much research in recent years, where most of the available results have been derived describing interactions in terms of simple two-person symmetric games such as the well-known Prisoner's Dilemma. It can be argued, however, that interactions in the real world can be better described by asymmetric games in which different individuals assume some roles more often than others. Here I study the effects of taking into account such asymmetries in the evolution of cooperation under the Donation game. Instead of considering the conventional setup whereby an individual interacts with all of its neighbors both as donor and as recipient, I propose to repeatedly sample pairs of interaction partners according to one of three different interaction rules: 'link' (L), 'donor-recipient' (DR) and 'recipient-donor' (RD). While the L rule recovers (in the mean sense) the case of standard symmetric interactions, the DR (RD) rule gives rise to a situation in which well-connected individuals interact predominantly as recipients (donors), inducing a promotion (hindering) of the evolution of cooperation. In particular, DR interactions lead to a very unequal wealth distribution favoring well connected individuals, who become pivotal for the establishment of a state in which everybody cooperates. Such fully cooperative state is however not the Pareto optimal outcome associated with the solution of a social dilemma, since a considerable proportion of the population ends up earning less than what they would have gained in a fully defective

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[†] J. Peña. *Working paper.*

state. This work provides a simple example of how asymmetrical interactions on heterogeneous social networks can lead to high levels of both cooperation and inequality, characteristic of many human socioeconomic systems. Moreover, it shows how cooperation can often lead to inequality and vice versa.

8.1 Introduction

Understanding the evolution of cooperative behavior has fascinated theoretical biologists, social scientists and mathematicians ever since Darwin (Axelrod & Hamilton, 1981; Darwin, 1859; Hamilton, 1964; Kropotkin, 1908; Skyrms, 2004; Trivers, 1971; Wilson, 1975). At first sight, it would seem that cooperation should be favored by natural selection since it increases the fitness of groups of individuals. However, in a population of cooperators (Cs), defectors (Ds) who do not invest in helping and rather opt to free-ride on the cooperative acts of others will receive the benefits of cooperation while avoiding to pay the associated costs. Consequently, the relative fitness of Ds will be larger than that of Cs and defective behavior will spread and go to fixation in the population.

The tension between collective and individual interests lying at the core of the problem of the evolution of cooperation can be captured in a simple way by the well-known Prisoner's Dilemma (PD). This is a symmetric two-person game described by the generic payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array}, \tag{8.1}$$

where $T > R > P > S$. Each player has two possible moves: to cooperate (C) or to defect (D). The ordering of the payoff entries guarantees that the two players gain more if they opt for mutual cooperation than if they opt for mutual defection ($R > P$) but also that a D will earn more than a C if the two players choose to play opposite moves ($T > S$). Hence, C is the optimal strategy at the collective level while D is optimal individually. Moreover, if both players agree to play C there is always a temptation to unilaterally switch to D ($T > R$), but if both players agree to play D there is no parallel incentive to unilaterally switch to C ($S < P$). In technical terms, (D, D) is not only the unique Nash Equilibrium of the PD, but also a Pareto inefficient outcome: mutual cooperation would be collectively preferable ($R > P$) but the fact that C is strongly dominated by D ($T > R$ and $P > S$) makes it irrational to play (C, C). Such dilemma is still present if we consider large evolving populations rather than pairs of individuals making rational decisions. Indeed, D is the only Evolutionarily Stable Strategy in the PD, so that standard ways of modeling the action of natural selection or social learning will ultimately lead the population to the Pareto inefficient state in which everybody defects.

The grim prediction that cooperation can not evolve under the PD is however the result of one standard assumption made by classical models of evolutionary game theory (Hofbauer & Sigmund, 1998; Maynard Smith, 1982; Weibull, 1995): that players meet randomly. Contrastingly, cooperation can be shown to be evolutionarily viable if the patterns of interaction are non-random, so that phenotypically similar individuals interact with each other more often than they interact with individuals drawn uniformly at random from the entire population (Eshel & Cavalli-Sforza, 1982; Fletcher & Doebeli, 2009; Lehmann & Keller, 2006; Skyrms, 2004). The problem of how such correlated interactions are created in different situations is at the heart of many of the models aiming to explain the evolution of cooperation, including those based on kin selection (Frank, 1998; Grafen, 1985, 2009; Hamilton, 1964), direct reciprocity (Axelrod & Hamilton, 1981; Trivers, 1971), indirect reciprocity (Alexander, 1987; Boyd & Richerson, 1989; Nowak & Sigmund, 2005), group or multilevel selection (Traulsen & Nowak, 2006; Wilson, 1975) and network reciprocity (Nowak & May, 1992; Ohtsuki et al., 2006).

Models of network reciprocity are based on local interactions and local competition (see Grafen (2007); Grafen & Archetti (2008); Lehmann et al. (2007); Taylor et al. (2007) for the close connections between network reciprocity and kin selection via limited dispersal, and between games on networks and inclusive fitness theory). The population of players is no longer infinite and well-mixed, as in standard evolutionary game theory, but finite and placed on the nodes of a graph representing geographical isolation or social ties. Both interaction and competition or imitation are limited to nearest neighbors in the graph. Since the seminal works of Axelrod (1984) and Nowak & May (1992), several studies have addressed the effect of networked population structures on the evolutionary dynamics of the PD [see Szabó & Fáth (2007) for a comprehensive review]. It has been well established that several network topologies can support unconditional cooperation, making it evolutionarily viable (Nowak & May, 1992; Ohtsuki et al., 2006). Most notably, topologies with highly heterogeneous degree distributions such as scale-free networks (Barabási & Albert, 1999) can significantly promote the evolution of cooperation under the PD (Santos & Pacheco, 2005), although it has also been shown that the extent of this effect strongly depends on several additional assumptions [see e.g. Fu et al. (2009); Masuda (2007); Peña et al. (2009); Roca et al. (2009b); Rong et al. (2007); Szolnoki et al. (2008); Tomassini et al. (2007)].

The vast majority of studies dealing with such games on networks has focused on the evolutionary dynamics of the PD and other related symmetric two-person games, such as the Snowdrift game (Hauert & Doebeli, 2004) and the Stag Hunt (Skyrms, 2004), on static networks. However, symmetrical pairwise interactions on rigid network topologies are obviously only first-order approximations to real-life interactions, which often involve individuals assuming different roles, taking part in many-person games, and interacting in coevolving or self-organizing social networks. Recently, several works have introduced some of these more realistic assumptions in models dealing with two-person games on adaptive networks [see Perc & Szolnoki (2010) and chapter 5 of Gross & Blasius (2008) for reviews] and with many-person games on static networks [e.g. Gómez-Gardeñes et al. (2011); Hauert et al. (2002); Santos & Pacheco (2011); Santos et al. (2008); see also chapter 7]. Asymmetric games in which players have different roles have been considered less often, or studied only in their symmetrized versions, so that individuals are assumed to enact one of the two roles half of the time. An example of the use of such *symmetrized* asymmetric games is the standard treatment of the Ultimatum game (UG) on complex networks. The UG is a simple bargaining game often considered to investigate egalitarian motives and punitive behavior (Güth et al., 1982; Henrich et al., 2006). In this game, two players, one assuming the role of the proposer and the other the role of the responder, have to decide how to distribute a reward. The proposer makes an offer and the responder decides whether to accept it or not. If the responder accepts, the reward is split accordingly to the proposer's offer, otherwise both the proposer and the responder receive nothing. When the UG is studied on complex networks [e.g. Eguíluz & Tessone (2009); Iranzo et al. (2011); Kuperman & Risau-Gusman (2008); Sinatra et al. (2009)] it is usually assumed that individuals play twice with each neighbor, once as proposer and once as responder, hence transforming the originally asymmetric game into a symmetric one.

Perhaps a better known example of an asymmetric game often used in its symmetrized form is the so-called Donation game (DG) (Sigmund, 2010). In this game, player I (the *donor*) has to decide whether to give help to player II (the *recipient*) or not. To give help (i.e. to cooperate) means for the donor to pay a cost c in order for the recipient to get a benefit b, with $b > c > 0$. To defect means refusing to help and leaving the payoffs of both players unchanged. The DG has been often used as a metaphor of social interactions in studies of the evolution of cooperation by indirect reciprocity [see Nowak & Sigmund (2005) for a review]. In these models, reciprocators acting as donors decide to give help if they have experienced cooperation from third parties in the past ['upstream' indirect reciprocity (Boyd & Richerson, 1989; Nowak & Sigmund, 2005), also called generalized reciprocity (Pfeiffer et al., 2005)] or if the recipient has a good reputation, for instance because it is known that she has previously helped others when acting as a donor ['downstream' indirect reciprocity (Nowak & Sigmund, 1998b, 2005)]. Either in the well-mixed populations assumed on most of the studies or on the networks used as population structures in some recent models of upstream indirect reciprocity (Iwagami & Masuda, 2010; Nowak

& Roch, 2007; Peña et al., 2011; van Doorn & Taborsky, 2011), each individual interacts on average half of the time as donor and half of the time as recipient. As a consequence, the existence of different roles in the DG (donor and recipient) is somewhat blurred, and the final game can be thought of as being effectively symmetric.

The DG has also been occasionally used for investigating the evolution of unconditional cooperation on graphs. In this case, as with the UG on networks, individuals play twice with each neighbor, once as donor and once as recipient. Hence, the interaction with each neighbor can be represented by a symmetric two-person game with payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix}, \end{array} \tag{8.2}$$

so that the resulting accumulated payoff of player i over all the interactions with its neighbors is then given by

$$\Pi_i = \sum_{j \in N_i} (s_j b - s_i c) = k_i b - s_i z_i c, \tag{8.3}$$

where N_i is the open neighborhood of i, i.e. the subset of nodes connected to i, $z_i = |N_i|$ is i's degree, s_i is i's strategy ($s_i = 1$ if C, 0 if D) and $k_i = \sum_{j \in N_i} s_j$ is the number of Cs in N_i. Note that the payoff matrix given by Eq. 8.2 is a special case of the PD, since the ordering of the payoff entries always satisfies $b > b - c > 0 > -c$. However, aside from special cases such as the mathematical analyses of the evolution of unconditional cooperation on homogeneous graphs [e.g. Ohtsuki & Nowak (2006a,b)], the bulk of simulation studies of games on heterogeneous networks has been carried out using different parameterizations of the PD, in particular the setting

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} 1 & 0 \\ b & 0 \end{pmatrix} \end{array} \tag{8.4}$$

with $b > 1$, introduced in Nowak & May (1992) [see Szabó & Fáth (2007) for a review]. Due to the fact that the accumulated payoff is not invariant with respect to linear transformations of payoff values when applied locally in heterogeneous networks (Luthi et al., 2009; Masuda, 2007), results using one parameterization (e.g. Eq 8.4) may not hold when using a different one (e.g. Eq. 8.2).

Here I study the evolution of unconditional cooperation under the DG on graphs using a novel approach. Instead of considering the conventional setup of

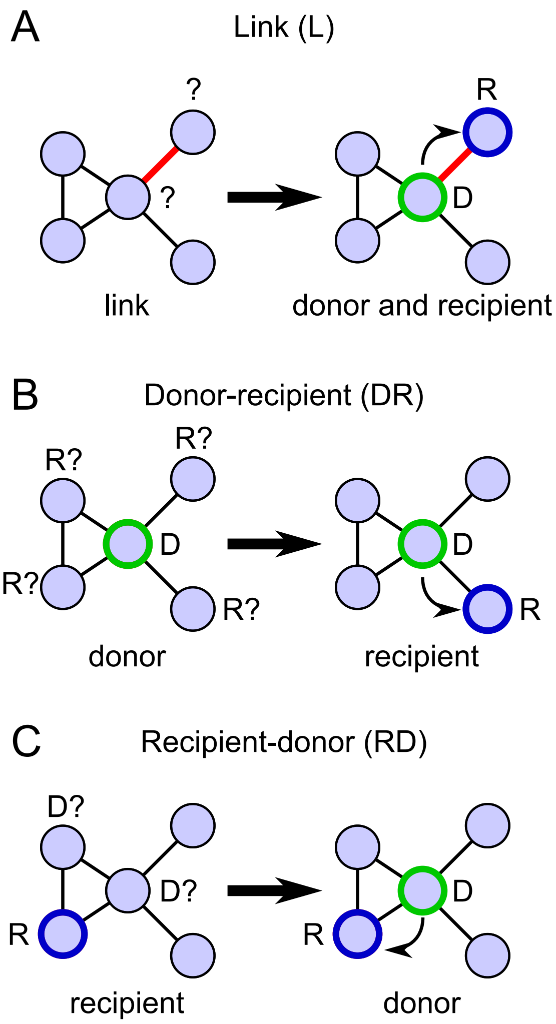

Figure 8.1: Interaction rules. **A.** Link (L). One link is drawn uniformly at random from the set of links. One of its endpoints is randomly chosen as donor, the other as recipient. **B.** Donor-recipient (DR). One donor is drawn uniformly at random from the set of nodes; one of its neighbors is chosen as recipient, again randomly. **C.** Recipient-donor (RD). One recipient is drawn uniformly at random from the entire population; one of its neighbors is chosen as donor.

games on networks, in which an individual plays with all of its neighbors once as donor and once as recipient, I propose to repeatedly sample pairs of interaction partners according to one of three different *interaction* rules, which I call ‘link’ (L), ‘donor-recipient’ (DR) and ‘recipient-donor’ (RD) (see Figure 8.1). For L interactions, first a link is drawn uniformly at random from the set of links, then one of its endpoints is randomly chosen as donor, the other as recipient. For DR (RD) interactions, first a random individual from the entire population is chosen as donor (recipient), then one of its neighbors is chosen as recipient (donor). On homogeneous graphs, these three interaction rules define equivalent stochastic processes in which each individual in the population interacts the same number of times as donor and as recipient. On heterogeneous graphs, however, DR and RD interactions are characterized by some individuals playing more often as donors or as recipients, depending on their connectivity and on the connectivity of their neighbors. Such asymmetry in the assumption of different roles changes the evolutionary dynamics of the DG, resulting either in a promotion or a hindering of the evolution of unconditional cooperation with respect to what is obtained in the standard symmetric case. In particular, DR interactions lead to very unequal wealth distributions favoring well connected individuals, who thus become pivotal for the establishment of a state in which everybody cooperates. Such state is, however, not the Pareto superior outcome usually associated with full cooperation, since a non-negligible proportion of the individuals ends up gaining even less than what they would gain in a population entirely comprised of defectors. In this sense, inequality is shown to lead to cooperation and vice versa.

8.2 Results

Figure 8.2 shows the final fraction of Cs for different network topologies and different interaction rules. The three network topologies investigated (see section 8.4.1 for details) are a (homogeneous) regular network (REG), a (moderately heterogeneous) Erdős-Rényi random network (ER), and a (highly heterogeneous) Barabási-Albert scale-free network (SF). Each generation, T pairs of individuals (one donor and one recipient) are drawn at random from the population of players according to one of the proposed interaction rules to engage in a one-shot DG. The accumulated payoff resulting from the T interactions is equated with reproductive fitness or social success, which determine the composition of the population in the next generation. To model the action of natural selection or social learning, I made use of the pairwise comparison rule (Szabó & Tőke, 1998; Traulsen et al., 2006) in the limit of strong selection, so that individuals copy the strategy of a randomly chosen neighbor if and only if the neighbor’s payoff is greater than the self’s (see section 8.4.2 for details).

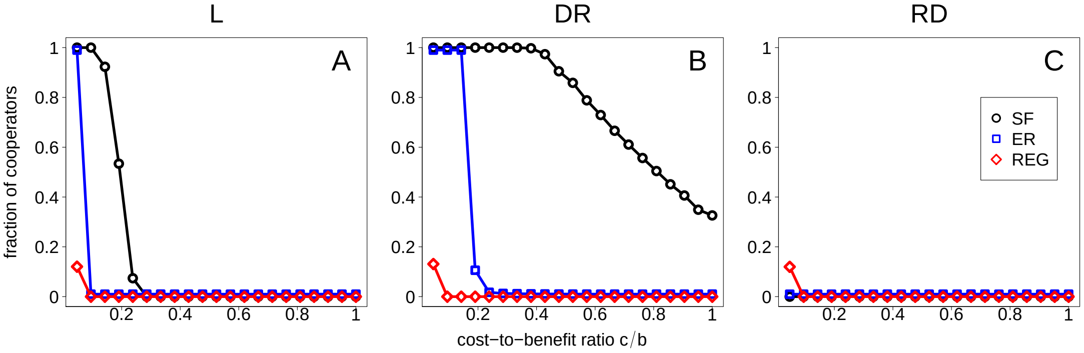

Figure 8.2: Fraction of cooperators as a function of the cost-to-benefit ratio c/b. On regular structures (REG), cooperation can only be sustained at extremely low cost-to-benefit ratios and at very low frequencies. For L interactions (**A**), cooperation can be established on random networks (ER) up to $c/b \approx 0.05$ and on scale-free networks (SF) up to $c/b \approx 0.23$. For DR interactions (**B**) the advantage of Cs is greatly enhanced in heterogeneous structures, particularly in SF networks. For RD interactions (**C**) heterogeneous networks fail to make cooperation evolve, and the results for SF networks become practically indistinguishable from those of REG networks. Parameters: $n = 1024$, $\langle z \rangle = 4$, $T = 16n$.

Figure 8.2A shows the evolutionary outcome of the DG when interaction partners are sampled according to the L rule. While cooperation is practically impossible on regular structures, Cs stand a chance on heterogeneous networks, albeit for low cost-to-benefit ratios. For L interactions, it is clear that an individual takes part in a game with a probability that is proportional to its degree in the network, so that well connected individuals play on average more often than poorly connected individuals. All individuals interact, however, on average half of the time as donors and half of the time as recipients. Hence, the standard symmetric DG characterized by Eq. 8.2 is recovered in the mean sense for L interactions. Indeed, although the accumulated payoff is now a random variable, its expected value can be shown to be equal (up to a multiplicative factor) to the expression given by Eq. 8.3 (see section 8.4.4 for the derivation of this result). The mechanism underlying the promotion of cooperation introduced by heterogeneous population structures in Figure 8.2A is thus similar to the one identified in previous studies of the symmetric PD (Santos & Pacheco, 2005, 2006). Highly connected individuals (for which $z_i \gg 1$, i.e. *hubs*) play a crucial role in promoting cooperative behavior, as they are able to influence a large part of the population, both because of their intrinsic large connectivity and because of the high accumulated payoffs they obtain. As long as hubs are preferentially occu-

Table 8.1: Statistics for the different interaction rules.

interaction rule	$\bar{n}_i$	$\bar{q}_i$	$\bar{\Pi}_i$
L	$\frac{2Tz_i}{n\langle z\rangle}$	1/2	$k_i b - z_i s_i c$
DR	$\frac{T(1+\rho_i)}{n}$	$\frac{\rho_i}{1+\rho_i}$	$\langle z\rangle \left(\sum_{j\in V_i} \frac{s_j}{z_j}\right) b - \langle z\rangle s_i c$
RD	$\frac{T(1+\rho_i)}{n}$	$\frac{1}{1+\rho_i}$	$\langle z\rangle \frac{k_i}{z_i} b - \langle z\rangle \rho_i s_i c$

The table shows the expected total number of interactions ($\bar{n}_i$), the expected proportion of times interacting as recipient ($\bar{q}_i$) and the expected accumulated payoff ($\bar{\Pi}_i$) for an individual i after T interaction steps. The expected accumulated payoffs have been normalized by the factor $T/(2m)$. See the main text for the meanings of the different symbols.

pied by Cs, cooperative behavior can easily spread and get to fixation in the population. Obviously, such mechanism is more important on SF networks than on ER networks, given the higher heterogeneity of the former (power-law degree distributions) with respect to the latter (Poisson-like degree distributions).

The results shown in Figure 8.2A are obtained for L interactions, which lead to a symmetrized DG equivalent on average to standard formulations of the DG on networks. Figures 8.2B and 8.2C show the results for DR and RD interactions, respectively. The fact that the three interaction rules reduce to the same stochastic process on homogeneous networks makes the final fraction of Cs to be the same for L, DR and RD interactions on these topologies. Results are however strikingly different for heterogeneous networks. Indeed, in this case DR interactions impressively promote the evolution of cooperation, particularly on SF networks, while RD interactions completely suppress the advantage of cooperation, with the fraction of Cs at equilibrium dwindling to zero over the whole range of the cost-to-benefit ratio c/b.

In order to understand the reason behind these results, let us examine, for a given individual i, the expected number of times it takes part on a game ($\bar{n}_i$), the expected proportion of times it interacts as recipient ($\bar{q}_i$), and the resulting expected accumulated payoff ($\bar{\Pi}_i$). These different expected values are shown in Table 8.1 for the three different interaction rules considered in this paper. Obviously, the expected proportion of times individual i interacts as donor is simply given by $\bar{p}_i = 1 - \bar{q}_i$. Note that for DR or RD interactions, $\bar{n}_i$ and $\bar{q}_i$ depend on

$$\rho_i \equiv \sum_{j\in V_i} \frac{1}{z_j}, \tag{8.5}$$

i.e. the sum of i's neighbors' inverse degrees. The quantity ρ_i has been recently

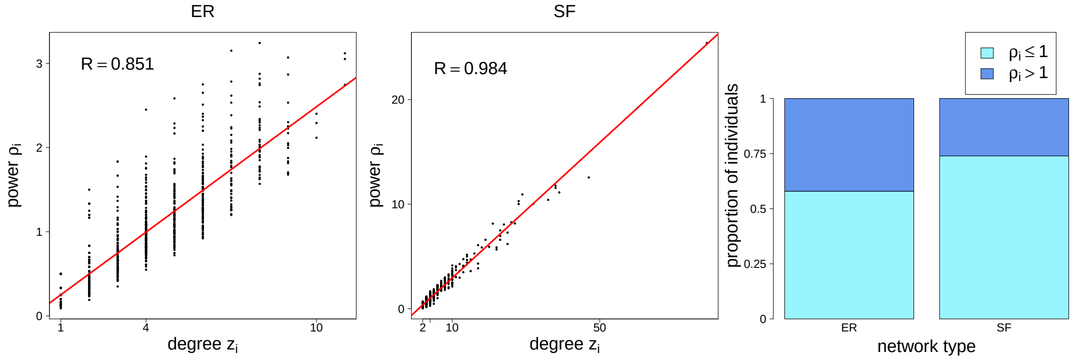

Figure 8.3: Power in ER and SF networks. Left and middle panels show the correlation between the power ρ_i and the degree z_i of a node i in ER and SF networks, respectively. R is Pearson's correlation coefficient for power vs. degree. The right panel shows the proportion of 'powerful' individuals, for which $\rho_i > 1$, and 'powerless' individuals, for which $\rho_i \leq 1$. Statistics are calculated for one typical realization of each graph, with $n = 1024$ and $\langle z \rangle = 4$.

proposed as a measure of 'power' in social network analysis (Neal & Neal, 2011; Neal, 2011), powerful individuals being those with significant bargaining and negotiating influence over its neighbors, and of 'replacement centrality' in games on networks (see chapter 7). In this paper, ρ_i is referred to as i's power. Two properties of this measure are worth mentioning at this point. First, as it is already evident from Eq. 8.5, power is positively correlated with degree so that, in general, the larger the connectivity of a node the larger its power. This correlation, almost perfect in the case of SF networks, is shown in the left and middle panels of Figure 8.3 for both ER and SF networks. Second, it is easy to show that the average power over all nodes of a connected graph is always equal to one, i.e. $\langle \rho \rangle = 1$. This allows us to define nodes with $\rho_i > 1$ as 'powerful' and nodes with $\rho_i \leq 1$ as 'powerless'. The right panel of Figure 8.3 shows the proportion of powerful and powerless individuals on ER and SF networks. Note that the more heterogeneous SF networks lead to a smaller proportion of powerful individuals than the less heterogeneous ER networks.

For DR and RD interactions, $\bar{n}_i = T(1 + \rho_i)/n$, so that the more powerful an individual, the more often it will interact in a game. Also, since the average number of interactions over the population of players is equal to $\langle \bar{n} \rangle = 2T/n$, we have that $\rho_i \gtrless 1 \Rightarrow \bar{n}_i \gtrless \langle \bar{n} \rangle$, i.e. on average, powerful (powerless) individuals take part in more (less) games than the average individual. Moreover, ρ_i determines not only how often i takes part in a game, but also how often it does so in the role of the recipient. For DR interactions $\rho_i \gtrless 1 \Rightarrow \bar{q}_i \gtrless 1/2$, so that powerful

Table 8.2: Statistics and invasion conditions on the star graph.

interaction rule	$\bar{q}_h$ / $\bar{p}_l$	$\bar{\Pi}_h^C > \bar{\Pi}_l^D$
L	1/2	$c/b < \frac{k-1}{z}$
DR	$\frac{z}{z+1}$	$c/b < k - \frac{1}{z}$
RD	$\frac{1}{z+1}$	$c/b < \frac{1}{z}\left(\frac{k}{z} - 1\right)$

The table shows the expected proportion of times the hub plays as recipient ($\bar{q}_h$) or a leaf plays as donor ($\bar{p}_l$) as well as the condition for the expected payoff of a C-hub ($\bar{\Pi}_h^C$) to be greater than the expected payoff of a D-leaf ($\bar{\Pi}_l^D$) for L, DR and RD interactions. In all cases $\bar{n}_h = T$ and $\bar{n}_l = T/z$. See the main text for the meanings of the different symbols.

individuals interact more often as recipients and powerless individuals more often as donors. For RD interactions the converse happens, so that $\rho_i \gtrless 1 \Rightarrow \bar{q}_i \lessgtr 1/2$: powerful individuals interact more often as donors and powerless individuals more often as recipients. All in all, the DG played on heterogeneous networks is no longer symmetric for DR and RD interactions, not even in the mean sense as for L interactions. Instead, individuals assume more often one role than another, depending on the interaction rule and on their social context. Thus, hubs play more often as recipients for DR interactions and more often as donors for RD interactions. Such asymmetry in the proportion of time different roles are assumed is reflected in the hubs' payoff advantage, which is amplified for DR interactions and suppressed for RD interactions with respect to the payoffs resulting from the L rule (see section 8.4.4). In turn, such favoring/disfavoring of well connected individuals plays an important role on the evolutionary dynamics of the whole population, and is the reason behind the different results obtained for each of the interaction rules investigated here.

In order to better illustrate this idea, and similarly to what has been done in previous studies of the PD on networks (Pacheco et al., 2009; Santos et al., 2008) (see also chapter 7), let us consider star and generalized double-star graphs as stylized examples of the prototypical connectivity patterns found in heterogeneous networks, and study locally the process of evolutionary competition on these topologies. More specifically, let us investigate the mathematical conditions under which the accumulated payoff of a cooperative hub becomes higher than that of any of the surrounding players, so that it is able to resist invasion from neighboring Ds and to spread cooperative behavior in its neighborhood. For the star graph depicted in Figure 8.4A, these conditions are given in Table 8.2 together with the values of $\bar{q}_i$ for the hub and $\bar{p}_i$ for the leaves. Note that, for a fixed number k of Cs on the leaves, the critical cost-to-benefit ratio below which the C-hub invades

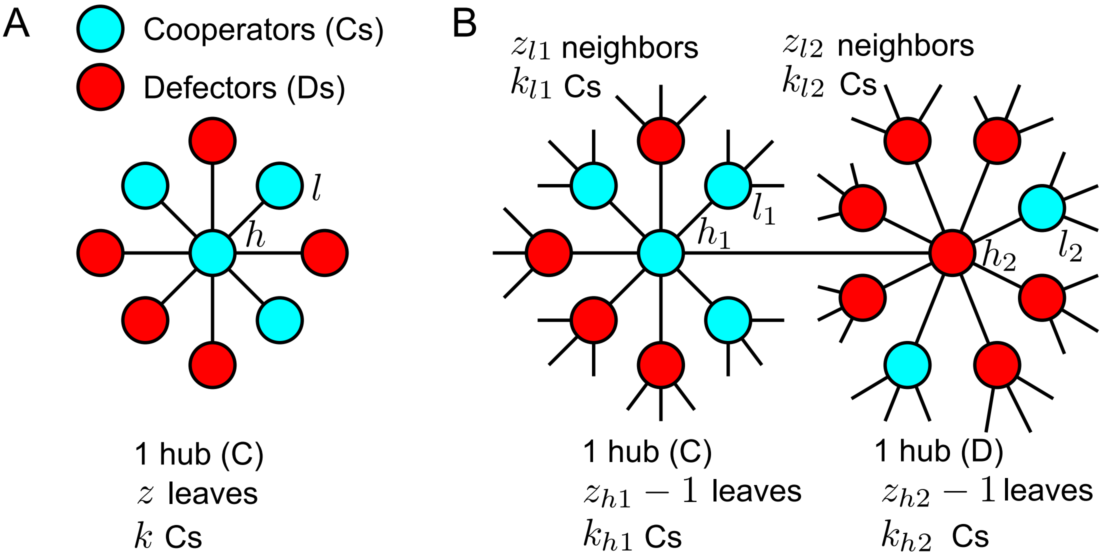

Figure 8.4: Star and generalized double-star graphs. **A.** The star graph consists of one hub, connected to z leaves. In addition the the hub, k leaves are assumed to play C. **B.** The generalized double-star graph consists of two stars with a link connecting the left hub (h_1) and the right hub (h_2). The left hub (assumed to be a C) is connected to $z_{h1}-1$ leaves, k_{h1} out of which are Cs. The right hub (a D) is connected to z_{h2} leaves, $k_{h2}-1$ out of which are Cs, so that it is connected to k_{h2} Cs in total. Left leaves (l_1) have each z_{l1} neighbors (k_{l1} of which are Cs, including the C-hub) and right leaves (l_2) have each z_{l2} neighbors (k_{l2} of which are Cs). The rest of the nodes (not shown here) are supposed to have a degree z_0.

Table 8.3: Invasion conditions on the generalized double-star graph.

interaction rule	$\bar{\Pi}^C_{h1} > \bar{\Pi}^D_{l1}$	$\bar{\Pi}^C_{h1} > \bar{\Pi}^D_{h2}$	$\bar{\Pi}^C_{l2} > \bar{\Pi}^D_{h2}$
L	$c/b < \frac{k_{h1}-k_{l1}}{z_{h1}}$	$c/b < \frac{k_{h1}-k_{h2}}{z_{h1}}$	$c/b < \frac{k_{l2}-k_{h2}}{z_{l2}}$
DR	$c/b < \frac{k_{h1}}{z_{l1}} - \frac{1}{z_{h1}} - \frac{k_{l1}-1}{z_0}$	$c/b < \frac{k_{h1}}{z_{l1}} - \frac{1}{z_{h1}} - \frac{k_{h2}-1}{z_{l2}}$	$c/b < \frac{k_{l2}}{z_0} - \frac{1}{z_{h1}} - \frac{k_{h2}-1}{z_{l2}}$
RD	$c/b < \frac{\frac{k_{h1}}{z_{h1}} - \frac{k_{l1}}{z_{l1}}}{\frac{z_{h1}-1}{z_{l1}} + \frac{1}{z_{h2}}}$	$c/b < \frac{\frac{k_{h1}}{z_{h1}} - \frac{k_{h2}}{z_{h2}}}{\frac{z_{h1}-1}{z_{l1}} + \frac{1}{z_{h2}}}$	$c/b < \frac{\frac{k_{l2}}{z_{l2}} - \frac{k_{h2}}{z_{h2}}}{\frac{z_{l2}-1}{z_0} + \frac{1}{z_{h2}}}$

The superscript refers to the individual's strategy, the subscript to the individual's position in the generalized double-star graph. See Figure 8.4B and the main text for the meanings of the different symbols.

D-leaves is *inversely* proportional to the hub's connectivity z under the L rule but *directly* proportional to z under the DR rule. Indeed, while for L interactions the critical cost-to-benefit ratio is approximately equal to the *proportion* of Cs on the leaves, for DR interactions the C-hub is always advantageous if $k > 2$ for any c/b and any z. In the limit of large z, even a single C-leaf is enough for the C-hub to invade the rest of the D-leaves and turn them to cooperation. Contrastingly, for RD interactions the C-hub is *never* advantageous under any condition. D-leaves are always able to invade the hub and, from there, the rest of the population. Such striking difference between the invasion pattern for DR and RD interactions is brought about by the roles preferentially assumed by the hub and the leaves under each of the interaction rules. In the star, $\rho_h = z \gg 1$ leads to the C-hub to act preferentially as recipient for DR interactions and preferentially as donor for RD interactions. In the limit of large z the C-hub interacts *exclusively* as recipient under DR and *exclusively* as donor under RD.

While the conditions of invasion on star graphs help understand the process by which hubs in heterogeneous networks are able to disseminate their strategies, the conditions of invasion on generalized double-star graphs shed light on the process of inter-hub competition. Consider now the generalized double-star graph depicted in Figure 8.4B and the invasion conditions given in Table 8.3. For L and DR interactions, the conditions for one hub taking over the other hub are in general more stringent than the conditions for hubs invading neighboring leaves. As a result, hubs invade many of their own leaves before entering in competition with each other, effectively turning many of their neighbors to their own strategies. However, while the C-hub benefits from such invasion by having more willing donors in its neighborhood and hence increasing its own fitness, the D-hub suffers from spreading its own behavior by having less neighboring Cs, which leads to a decrease in its own fitness. Other things being equal, once the number of Cs surrounding the C-hub is greater than the number of Cs surrounding the D-hub, the C-hub can invade the D-hub. Once both hubs have turned to cooperation, invasion of the remaining nodes is easily accomplished.

The previous scenario holds both for L and DR interactions. However, for DR interactions, and similarly to what happens on simple star graphs, invasion conditions become less stringent the *larger* the connectivity of the C-hub. This is in contrast to what happens under the L rule, for which the C-hub is less advantageous the higher its connectivity. Furthermore, the DR rule leads to less stringent conditions for the spreading of cooperative behavior from the C-hub to both neighboring D-leaves and to the D-hub, as it roughly depends inversely on the connectivity of the leaves (and leaves' neighbors) rather than inversely on its own connectivity, as it is the case for L interactions. Concerning RD interactions, the resulting invasion pattern is again in stark contrast to the invasion patterns for L and DR interactions. In this case, the critical cost-to-benefit ratio below which a C wins over a D is proportional to the difference in *proportions* of Cs around each node and inversely proportional to the C's power. This makes the C-hub disadvantageous to a point that it becomes easier to invade the D-hub from a C-leaf than from the C-hub itself. As it was already the case for the simpler star graph, the evolutionary dynamics on the generalized double-star graph under RD interactions are such that leaves more easily invade hubs than the converse, with Ds almost invariably winning the evolutionary race.

The analysis of invasion conditions on star and double-generalized star graphs summarized in Tables 8.2 and 8.3, together with the dependence of $\bar{n}_i$ and $\bar{q}_i$ on the individual power ρ_i summarized in Table 8.1, provides a clear explanation for the different evolutionary dynamics resulting from the application of the different interaction rules on heterogenous networks. Cooperation is more easily established when the interplay between interaction rule and population structure ends up favoring hubs by allowing them to increase their fitness. This is particularly the case for DR interactions on SF networks, which results in the introduction of an asymmetry in the way the DG is played at the population level, with hubs preferentially acting as recipients and leaves as donors. When the asymmetry is introduced in the opposite direction, so that it is hubs which act more often as donors and leaves as recipients, cooperation plummets and defection prevails.

The final fraction of Cs for different networks and interaction rules shown in Figure 8.2 were obtained for $T = 16n$, which is a relatively large value of T. Figure 8.5 shows what happens for L and DR interactions on SF and ER networks with smaller values of T (results on REG networks and for RD interactions are not shown as they always lead to negligible levels of cooperation for all the tested values of the cost-to-benefit ratio). Figure 8.5 also shows the results for a deterministic approximation in which the stochastic payoff resulting from the T interactions is replaced by its normalized expected value. Note that the qualitative results of the model do not change with different values of T. Moreover, the differences between L and DR interactions and between SF and ER networks

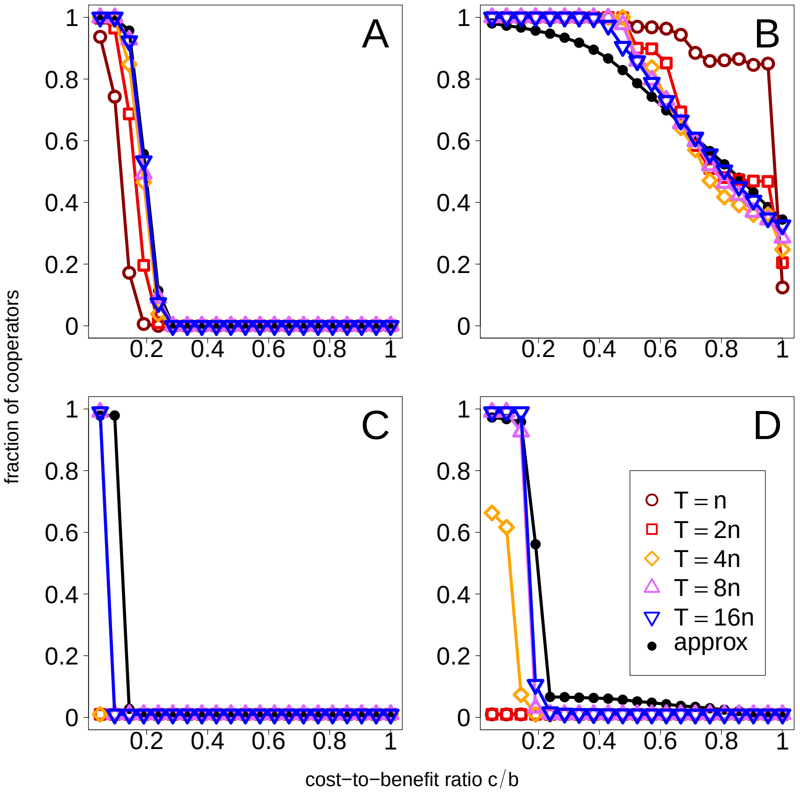

Figure 8.5: Dependence on the number T of interactions per generation. The figure shows the fraction of cooperators as a function of the cost-to-benefit ratio c/b for different values of T. Results are shown for SF (panels **A** and **B**) and ER (panels **C** and **D**) networks and for L (panels **A** and **C**) and DR (panels **B** and **D**) interactions. Filled black dots stand for a deterministic approximation, in which the stochastic payoff is replaced by its expected value. Parameters: $n = 1024$, $\langle z \rangle = 4$.

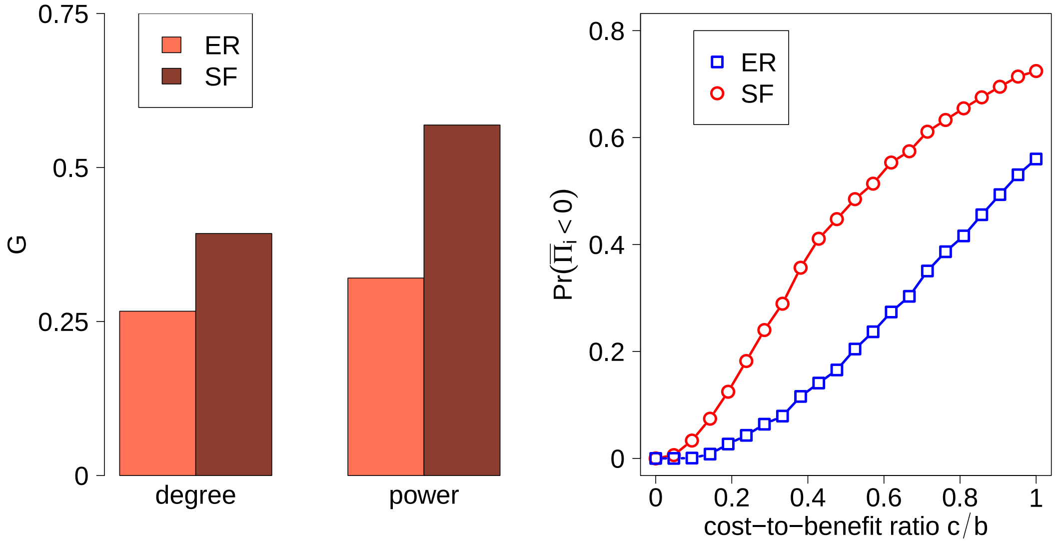

Figure 8.6: Emergence of inequality in cooperative populations. The left panel shows the Gini coefficient (G) of degree and power on ER and SF networks. In populations comprised entirely of cooperators, the received benefit per individual is proportional to the degree for L interactions and to the power for DR interactions. Inequality in the received benefit is thus greater for DR than for L interactions and more important on SF than on ER networks. Statistics are calculated for one typical realization of each graph, with $n = 1024$ and $\langle z \rangle = 4$. The right panel shows the proportion of individuals with negative accumulated payoff in full cooperative populations interacting according to the DR model. These extremely poor individuals would be faring better in full defective societies. Statistics are calculated by averaging 100 different realizations of each kind of graph, with $n = 1024$ and $\langle z \rangle = 4$.

are often accentuated for smaller values of T. The difference between different values of T obviously stem from the increasing noiseness of accumulated payoffs with decreasing values of T.

Let us now shift the focus of the analysis from an evolutionary to an economical perspective and investigate the accumulation of wealth (accumulated payoff) in populations of 100% Cs playing the DG under the L and the DR interaction rules. Similar analyses have been done in other studies of games on graphs (see e.g. Du et al. (2009); Santos et al. (2008); Vukov et al. (2011)). In fully cooperative populations, the expected payoff for individual i is given by

$$\bar{\Pi}_i^L = \underbrace{z_i b}_{\text{received benefit}} - \underbrace{c z_i}_{\text{payed cost}} \tag{8.6}$$

for L interactions, and by

$$\bar{\Pi}_i^{DR} = \underbrace{\langle z\rangle\rho_i b}_{\text{received benefit}} - \underbrace{\langle z\rangle c}_{\text{payed cost}} \tag{8.7}$$

for DR interactions. Note that for L interactions an individual's received benefit is proportional to its degree in the social network, while for DR interactions it is proportional to its power. Hence, unequal degree and power distributions automatically lead to unequal received benefits. The left panel of Figure 8.6 shows the Gini coefficient G for the degree and power distributions of a typical realization of ER and SF networks. G is a measure of statistical dispersion, often used to quantify the amount of inequality within a population (Cowell, 2011; Gini, 1912). For a non-negative characteristic x distributed according to a given probability distribution, G varies from a minimum value of zero, when the distribution is uniform, to a maximum of one in an infinite population in which every individual but one has $x = 0$. In the model studied in this paper, more heterogeneous networks lead to more unequal distributions of both degree and power. Moreover, power and hence received benefit for DR interactions is distributed in a more unequal way than degree and hence received benefit for L interactions (note that G is invariant with respect to multiplication by a constant). For instance, the value of G for the distribution of received benefits under L interactions on ER networks is comparable to the value of G for the distribution of family income of relatively egalitarian European countries such as Finland ($G = 0.268$) or Germany ($G = 0.27$), respectively the 11th and 12th most egalitarian countries in the world. Contrastingly, the value of G for the distribution of benefits for DR interactions on SF networks is similar to that of the most inegalitarian Latin American countries, such as Haití ($G = 0.592$) and Colombia ($G = 0.585$), ranking respectively 8th and 9th in the list of most inegalitarian countries in the world[1].

Considering the total expected accumulated payoff (both received benefits and payed costs) a more striking difference between L and DR interactions emerges. For L interactions the expected accumulated payoff of a given individual $\bar{\Pi}_i^L$ is always positive, since $b - c > 0$ always hold. Thus, even if well connected individuals end up earning more and poorly connected individuals less, in a population with 100% Cs *everybody* is better off than in the state where all play D, where $\bar{\Pi}_i^L = 0$ $\forall i$. Contrastingly, for DR interactions the wealth of an individual i in a fully cooperative population can become negative if $\rho_i < c/b$. In this case, even if the average wealth of the society is given by $\langle\bar{\Pi}^{DR}\rangle = \langle z\rangle(b - c)$, hence positive and better than the average wealth in a fully defective population where $\langle\bar{\Pi}^{DR}\rangle = 0$,

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[1] Data from the CIA's The World Factbook. *https://www.cia.gov/library/publications/the-world-factbook/rankorder/2172rank.html.* February 2, 2012.

individuals for which $\rho_i < c/b$ are *individually worse off* than in a state where nobody cooperates. As it is shown in the right panel of Figure 8.6, the proportion of such extremely poor individuals can be considerably important, and growing with the heterogeneity of the network and with the cost-to-benefit ratio. For instance, on SF networks and for a cost-to-benefit ratio of 0.4 (for which the evolutionary dynamics leads to a fully cooperative state, see Figure 8.2) approximately the 40% of the population has a negative accumulated payoff. This situation is even more dramatic on simple star graphs consisting of one center and z leaves such as the one shown in Figure 8.4A. In this case, for fully cooperative populations under DR interactions and whenever $c/b > 1/z$, all individuals in the population but the center earn a negative payoff and are thus worse off than in if they were 'living' in a fully defective state.

8.3 Discussion

The present study demonstrates the effects of taking into account the asymmetric nature of social interactions in the evolutionary dynamics of cooperation on networks. As it is evident from Figure 8.2, the evolution of unconditional cooperation under the DG on heterogeneous networks can be greatly enhanced or dramatically suppressed depending on whether or not asymmetric interactions favor hubs. If the sampling of interaction pairs is made in such a way that hubs play prominently as donors, cooperation plummets and its evolution becomes impossible. Contrastingly, if hubs play more often as recipients and hence accumulate large payoffs, cooperation can flourish even if the act of cooperation is relatively costly. However, in this last case the global nature of the game is radically different from its local counterpart, not only for the good (cooperation is more easily established) but also for the bad: the wealth distribution becomes so unequal that a considerable proportion of individuals fare worse in a fully cooperative population than in a state where everybody defects (see Figure 8.6). Indeed, although the transition from a full defective state to a full cooperative state can be said to solve the social dilemma *in the mean sense* as the average wealth of the population shifts from $\langle \Pi^{DR} \rangle = 0$ to $\langle \Pi^{DR} \rangle = \langle z \rangle (b - c)$, the state where everybody willingly helps each other is not Pareto superior with respect to the state where nobody helps, since not everybody is better off. Overall, the model studied in this work provides a simple example of how asymmetrical interactions on heterogeneous networks can lead to both the high levels of cooperation and the highly inegalitarian wealth distributions characteristic of many human socioeconomic systems.

In this paper, asymmetric interactions on heterogeneous networks were introduced by defining three *interaction* rules specifying the way players are sampled from the population: L, DR and RD. The reader may be familiar with somewhat related *updating* rules describing stochastic processes on networks, such as the 'link-update' and 'node-update' rules used in voter models on complex networks (Suchecki et al., 2005) or the 'birth-death' (BD) and 'death-birth' (DB) rules used in some studies of games on graphs [see e.g. Ohtsuki et al. (2006)]. The rationales behind the interaction rules proposed in this paper and those behind the above-mentioned updating rules are similar. Both updating and interaction rules are about sampling pairs of individuals in a population and assigning roles to them either with regard to social interaction (donor or recipient) or to evolutionary competition (reproducing/model individual or dying/copying individual). Often, the choice of one rule over another can lead to impressive differences in the resulting evolutionary dynamics. An example of this is the already classical result according to which, in the limit of weak selection, evolution never favors unconditional cooperation under the symmetric DG on homogeneous networks for BD updating, while Cs are favored over Ds for DB updating if $c/b < 1/\langle z \rangle$ (Ohtsuki et al., 2006; Taylor et al., 2007). The present study shows that similarly contrasting results can be the consequence of a change in the interaction rather than in the updating rule when the population structure is heterogeneous. Although abstract in nature, the different interaction rules used in this paper can be thought of as simple models of different situations that can be encountered in real life. DR interactions, for which all inviduals have the same and independent probability of assuming the role of donor, may be more typical of times of economic prosperity, where everybody is able to give help to anybody else at approximately the same rate. Contrastingly, RD interactions in which individuals play as recipients at the same rate, may be more characteristic of times of economic regression, where everybody is in need of help to the same extent. Finally, L interactions recover in the mean sense the traditional assumption of the DG on networks, in which everybody plays as donor or recipient the same number of times. Somewhat paradoxically, cooperation in the asymmetric DG flourishes during bonanza times but plummets during periods of crisis.

The present study is not the first one having explored the consequences of asymmetric interactions in the evolution of unconditional cooperation on networks. In a recent paper, Pacheco et al. (2009) explored the consequences of making cooperative investments variable and dependent on the focal player's connectivity. More specifically, they studied a two-person public goods game in which each of two players has to decide whether to contribute a cost to a common pool (to cooperate) or not (to defect). The total contribution is multiplied by an enhancement factor F and then equally shared between the two players. For $1 < F < 2$ the game is a particular instance of the PD. Each player plays once with each neighbor in the network, accumulating a payoff

$$\Pi_i = \sum_{j \in N_i} \left[\frac{F\left(\gamma_i s_i + \gamma_j s_j\right)}{2} - s_i \gamma_i \right],$$

where γ_x is the contribution of player x. Pacheco and co-workers studied two variants of this game. In the first, dubbed *conventional prisoner's dilemma* (CPD), all individual contributions per game are the same, irrespective of the node's connectivity, i.e. $\gamma_i = \gamma$ for all i. In the second variant or *distributed prisoner's dilemma* (DPD), the overall contribution of each player is equal to γ, so that the contribution per game is given by $\gamma_i = \gamma / z_i$, where z_i denotes as before the degree of individual i. Although motivated from different microscopic mechanisms, the CPD and the DPD of Pacheco et al. are closely related to, respectively, the DG under L and DR interaction rules explored in this paper. Indeed, it is straightforward to show that the replacements $F\gamma/2 \to b$ and $(F/2-1)\gamma \to -c$ make the CPD equivalent to the DG with L interactions, in the sense that the expected accumulated payoff due to the latter is equal to the deterministic accumulated payoff of the former up to a scaling factor. Likewise, the DPD can be shown to be equivalent (again in the mean sense and up to a scaling factor) to the DG with DR interactions. Hence, it is not coincidental that the final fraction of Cs for the DG under L and DR interactions shown in Figure 8.2 of this paper are similar to those shown in Figure 1 of Pacheco et al. (2009) for the CPD and the DPD, after the transformation $c/b \leftrightarrow 2/F - 1$.

A more important consequence of the equivalence between the DG with DR interactions and Pacheco et al. (2009)'s DPD is that the results derived here concerning the emergence of extreme social inequality summarized in Figure 8.6 also hold true for the DPD. This fact calls for some caution when drawing conclusions about the effects of social diversity in the evolution of cooperation. Pacheco et al. (2009) write, for instance, that 'changing the contributive scheme from CPD to DPD in SF population structures acts to change a prisoner's dilemma effectively into a Harmony game where Cs become advantageous irrespectively of the fraction of Cs'. In its two-player incarnation, the Harmony game is a two-person symmetric game with payoff matrix given by Eq. 8.1 and payoffs ordered so that $R > T > S > P$. The ordering of the payoff entries guarantees that cooperation is both dominant ($R > T$, $S > P$) and Pareto superior ($R > P$) with respect to defection. Note that the last condition is necessary to characterize a given social interaction as a Harmony game. However, in the case of the DPD it is in general not true that the state where everybody cooperates is Pareto superior with respect to the state where everybody defects, because at least some individuals will get a negative payoff, whereas they would have obtained a payoff of zero if nobody had cooperated. The evolutionary dynamics can lead to a state where everybody cooperates but this state not necessarily means a solution of the social dilemma, at least strictly in terms of Pareto superiority. The results regarding the DG with RD interactions presented in this paper also warn against the generality of supposedly beneficial effects of social diversity on the evolution of cooperation (Pacheco et al., 2009; Santos et al., 2011, 2008). Note that social diversity is large for RD interactions, not necessarily in received benefits but in payed costs, which are proportional to individuals' power. The contrasting results between the final fraction of Cs for DR interactions and for RD interactions underlines the fact that diversity *per se* does not promote cooperation. Rather, social diversity can promote cooperation if it benefits already powerful individuals in the social network. In this case, however, and because of the above-mentioned considerations, 'cooperation' is a label which is at best optimistic and at worst hypocritical, since not everybody ends up winning more than in a state of full defection.

In addition to Pacheco et al. (2009), other papers have studied the evolutionary dynamics of asymmetric or distributed two-person and N-person games on networks (see e.g. Du et al. (2009); Gómez-Gardeñes et al. (2011); Santos & Pacheco (2011); Santos et al. (2008); see also chapter 7). In these and other related models, asymmetric interactions are usually introduced by making cooperative investments dependent on the connectivity of the focal player in an originally symmetric game, such as the two-person or the N-person PD. Contrastingly, in the present paper asymmetries are introduced by sampling players according to different interaction rules and letting them play asymmetric games, such as the DG. Note that the same methodology can be used with other asymmetric games, such as the already introduced UG, the Dictator game (Eckel & Grossman, 1996), and the Asynchronous Snowdrift game (Kun et al., 2006), to mention only a few. It will be of particular interest to explore the consequences of a diverse distribution of player roles in these and other asymmetric games on networks.

In summary, inequality can lead to cooperation and vice versa. More specifically, the interplay between heterogeneity in the number of social ties and asymmetric interactions in the DG can lead to highly unequal wealth distributions which, when favoring those already powerful and rich, further promote the establishment of cooperation. Likewise, heterogeneity and asymmetry make the full cooperative state one in which a significant proportion of the population is worse off than if everybody defected. It is interesting to note that similar causal links going from cooperation to inequality and from inequality back again to cooperation can be traced back to early texts of political philosophy, particularly Rousseau's *A Discourse on Inequality.* In this book, famous among game theorists for providing the story after which the Stag Hunt game is named (Skyrms, 2004), Rousseau suggests that social inequality among men is the direct consequence of division of labor and cooperation amplifying existing natural differences. In Rousseau's words, 'from the instant one man needed the help of another, and it was found to be useful for one man to have provisions enough for two, equality disappeared' (Rousseau, 1984). Moreover, Rousseau also advances that the resulting emergence of social classes is at the origin of the social contract, which he portrays as almost nothing more than a swindle used by the rich to control the poor and maintain the status quo. Much like Rousseau's rich men, who say to the poor '[l]et us unite, [...] let us institute rules of justice and peace to which all shall be obliged to conform, without exception, rules which compensate in a way for the caprice of fortune by subjecting equally the powerful and the weak to reciprocal duties' (Rousseau, 1984) cooperative hubs in the DG with DR interactions presented here preach cooperation to their poor neighbors, while keeping most of the benefits for themselves.

8.4 Methods

8.4.1 Networks

Three different network topologies were considered in this study: REG, ER and SF networks, all with a mean degree $\langle z \rangle = 4$. REG networks are rings (one-dimensional lattices with periodic boundary conditions). ER networks are Erdős-Rényi random networks of the $G(n, p)$ type (Erdős & Rényi, 1959, 1960), i.e. a graph with n nodes where the probability that each possible edge is present is equal to $p = \langle z \rangle / n$. SF networks are Barabási-Albert scale-free networks based on growth and preferential attachment (Barabási & Albert, 1999). The growing procedure was started from a ring of $m_0 = \langle z \rangle / 2$ nodes, adding $m = \langle z \rangle / 2$ new edges per new node.

8.4.2 Evolutionary dynamics

At the end of each generation, most successful individuals tend to reproduce more or to be imitated more often by their neighbors. Among the different updating rules that have been proposed in the literature to emulate such behavioral evolution, I made use of the pairwise comparison rule. According to this rule, each individual i adopts the strategy of a randomly chosen neighbor j with a probability given by $p = 1/\left(1 + e^{-\beta(\Pi_j - \Pi_i)}\right)$, where Π_x is the accumulated payoff of individual x and β is a parameter associated with decision-making noise (cultural evolution) or controlling the relative forces of natural selection and random drift (biological evolution). When $\beta = 0$ strategy adoption is completely random and natural selection is not at work. When $\beta = \infty$, strategy adoption is completely deterministic and the pairwise comparison rule becomes identical to the heuristic 'imitate if better'. Results were obtained in all cases in the limit case of strong selection ($\beta = \infty$).

8.4.3 Simulations

Simulations were carried out in populations of $n = 1024$ individuals with an initial proportion of 50% Cs randomly placed in the network. A value of $c = 1$ for the cost of cooperation was used for all simulations. The reported equilibrium fractions of Cs was calculated by averaging over 2000 generations after an initial transient period of 10^5 generations. Each point in Figure 8.2 corresponds to an average over 1000 runs and 100 different realizations of the same type of network.

8.4.4 Expected payoffs for L, DR and RD interactions

Here, I derive the expressions for the expected payoff of an individual i with strategy s_i ($s_i = 1$ if C, $s_i = 0$ if D) and degree z_i which has k_i C-neighbors. I denote by n the number of nodes (individuals) and by m the number of edges of the graph describing the population structure.

8.4.4.1 Link (L) interactions

For L interactions, a link is randomly chosen from the population graph and their endpoints are randomly assigned the roles of donor and recipient. The probability that player i is chosen as donor or recipient is thus given by

$$\Pr(i \to \mathit{donor}|L) = \Pr(i \to \mathit{recipient}|L) = \frac{z_i}{2m},$$

so that its expected payoff can be written as

$$\bar{\Pi}_i^L = T\left(\frac{z_i}{2m}\frac{k_i}{z_i}b - \frac{z_i}{2m}s_i c\right),$$

where k_i/z_i gives the probability that a neighbor of i plays C. Normalizing by the factor $T/(2m)$ and simplifying, the previous equation reads

$$\bar{\Pi}_i^L = k_i b - s_i z_i c. \tag{8.8}$$

Note that this expression is equal to the accumulated payoff for an individual due to the standard way of playing the DG on networks, given by Eq. 8.3.

8.4.4.2 Donor-recipient (DR) interactions.

For DR interactions, a node is first randomly chosen as the donor and then one of its neighbors is chosen as recipient. Hence, the probability that player i is chosen as donor is given by

$$\Pr(i \to \mathit{donor}|DR) = \frac{1}{n},$$

and as recipient by

$$\Pr(i \to \mathit{recipient}|RD) = \frac{n-1}{n} \sum_{j \in V_i} \frac{1}{n-1} \frac{1}{z_j} = \frac{1}{n} \sum_{j \in V_i} \frac{1}{z_j} = \frac{\rho_i}{n}.$$

The conditional probability that i plays as recipient given that it has been chosen to interact (either as donor or recipient) is thus given by

$$\bar{q}_i = \frac{\rho_i/n}{1/n + \rho_i/n} = \frac{\rho_i}{1+\rho_i},$$

and its expected payoff by

$$\bar{\Pi}_i^{DR} = T \left(\frac{1}{n} \sum_{j \in V_i} \frac{s_j}{z_j} b - \frac{1}{n} s_i c \right).$$

Normalizing again by $T/(2m)$ and simplifying we obtain

$$\bar{\Pi}_i^{DR} = \langle z \rangle \left(\sum_{j \in V_i} \frac{s_j}{z_j} \right) b - \langle z \rangle s_i c, \tag{8.9}$$

where $\langle z \rangle = 2m/n$ is the mean degree of the graph. Comparing Eq. 8.9 and Eq. 8.8 it can be easily shown that $\bar{\Pi}_i^{DR} > \bar{\Pi}_i^{L}$ whenever

$$b \left[\sum_{j \in V_i} \left(\frac{\langle z \rangle}{z_j} - 1 \right) s_j \right] > \left(\langle z \rangle - z_i \right) s_i c.$$

Note that if i is a hub the previous condition often holds, as in this case it is generally true that $z_j < \langle z \rangle < z_i$. DR interactions amplify the payoff advantage of hubs in heterogeneous networks with respect to what is obtained for L interactions.

8.4.4.3 Recipient-donor (RD) interactions.

For the RD rule, first a node is randomly chosen as the recipient and then one of its neighbors is chosen as donor. The probability that player i is chosen as recipient is thus given by

$$\Pr(i \to \mathit{recipient}|RD) = \frac{1}{n},$$

and as donor by

$$\Pr(i \to \mathit{donor}|RD) = \frac{n-1}{n} \sum_{j \in V_i} \frac{1}{n-1} \frac{1}{z_j} = \frac{1}{n} \sum_{j \in V_i} \frac{1}{z_j} = \frac{\rho_i}{n}.$$

Hence, the conditional probability that i plays as recipient given that it has been chosen to interact (either as donor or recipient) is given by

$$\bar{q}_i = \frac{1/n}{1/n + \rho_i/n} = \frac{1}{1+\rho_i},$$

and its expected payoff by

$$\bar{\Pi}_i^{RD} = T \left(\frac{1}{n} \frac{k_i}{z_i} b - \frac{1}{n} \rho_i s_i c \right).$$

Normalizing again by $T/(2m)$ we obtain

$$\bar{\Pi}_i^{RD} = \langle z \rangle \frac{k_i}{z_i} b - \langle z \rangle \rho_i s_i c. \tag{8.10}$$

Comparing Eq. 8.10 and Eq. 8.8 it can be easily shown that $\bar{\Pi}_i^{RD} > \bar{\Pi}_i^{L}$ whenever

$$k_i \left(1 - \frac{\langle z \rangle}{z_i} \right) b > \left[\sum_{j \in V_i} \left(1 - \frac{\langle z \rangle}{z_j} \right) \right] s_i c.$$

In this case a hub i (for which in general $z_j < \langle z \rangle < z_i$) will systematically obtain a smaller payoff under the RD rule than under the L rule.

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Chapter 9

Conclusions

9.1 Discussion

> Human behaviour reveals uniformities which constitute natural laws. If these uniformities did not exist, then there would be neither social science nor political economy, and even the study of history would largely be useless. In effect, if the future actions of men having nothing in common with their past actions, our knowledge of them, although possibly satisfying our curiosity by way of an interesting story, would be entirely useless to us as a guide in life.
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>
> Vilfredo Pareto, *Cours d'économie politique professé à l'Université de Lausanne*

Vilfredo Pareto was an Italian engineer-turned-economist of the Lausanne school of economics, who made important contributions to the social sciences and economics. He is most famous for two concepts named after him. The first one is *Pareto efficiency*, which is key for the definition of a social dilemma in game theory terms: a game with at least one Pareto inefficient Nash equilibrium (Archetti & Scheuring, 2011b; Kollock, 1998). The second concept is that of a *Pareto distribution*, a power-law probability distribution as the one resulting from the degree distribution of the scale-free networks used as population structures in chapters 3, 4, 7 and 8, and similar to the discrete Waring distribution used in chapter 6 for modeling variable group sizes. Pareto invented the Pareto distribution when studying income distribution, after finding that data on economic wealth of different countries over different centuries followed highly skewed distributions. For instance, he found that the 80% of the land in Italy belonged to only 20% of the population (which led to the so-called 80-20 rule or the *Pareto principle*). The results presented in the Part III of this thesis make interesting connections between the concepts of Pareto efficiency and Pareto distribution.

They show that heterogeneity in the social contexts of the individuals, i.e. social diversity, can greatly influence the evolutionary dynamics of social dilemmas. In particular, chapter 8 makes some interesting connections between cooperation, heterogeneity and economic inequality.

Recently, a review paper by Santos et al. (2011) advanced the view of social diversity as 'a fundamental mechanism in promoting the emergence and maintenance of cooperation'. This conclusion is supported by the results obtained by Santos and co-workers showing how heterogeneous networks can promote the evolution of cooperation in (i) models of different two-person symmetric social dilemmas (Santos & Pacheco, 2005, 2006; Santos et al., 2006), and (ii) models of N-person and two-person publics goods games with context-dependent investment (Pacheco et al., 2009; Santos et al., 2008). Social diversity has been portrayed as providing 'a unifying framework for the emergence of cooperation' (Santos & Pacheco, 2005), 'a new route to the evolution of cooperation' (Santos & Pacheco, 2006) and as '[promoting] the evolution of cooperation in public goods games' (Santos et al., 2008). The results presented in this thesis show that, although social diversity can be an important factor on the evolutionary dynamics of different social dilemmas, the beneficial effects and the robustness of such mechanism have to be taken with a grain of salt. First, social diversity can both promote and hinder the evolution of cooperation. This is particularly clear in the model presented in chapter 8, regarding the asymmetric donation game on heterogeneous networks under different interaction rules. The obtained results make clear that social diversity can promote the evolution of cooperation as long as such diversity translates into a fitness advantage of well connected individuals. Contrastingly, when social diversity makes such well connected individuals to be worse off than less connected ones, the evolution of cooperation plummets. Second, as evidenced also in this model, social diversity, even when promoting cooperation, can generate such a high wealth inequality that the full cooperative state is not the Pareto efficient outcome usually associated to the solution of a social dilemma. This conclusion is also applicable to the model by Pacheco et al. (2009), due to the similarities between this model and one of the models presented in chapter 8. Third, the results of models of games on heterogeneous networks seem to be highly dependent on particular assumptions of the evolutionary dynamics. For instance, results presented in chapter 7 reveal that the beneficial effects of social diversity reported by Santos et al. (2008) are highly dependent on how replacement graphs (determining who imitates whom in cultural evolution or who competes with whom in biological evolution) are defined. An increase in the size of replacement neighborhoods systematically lead to a *decrease* in the cooperation levels obtained on heterogeneous networks, while they lead to an *increase* in the cooperation levels obtained on regular networks, so that the results on one kind of topology or the other become comparable. As it is shown in chapter 3, a similar effect is obtained if individuals partially imitate according to a conformist bias: conformity promotes cooperation on regular structures and hinder it on heterogeneous networks to a point that, again, results with and without social diversity become comparable.

In addition to social diversity at the individual level, concerning heterogeneity in the number of interactions per individual, this thesis has also explored the consequences of social diversity at the group level, or group-size diversity, on the evolutionary dynamics of multiplayer social dilemmas. The results presented in chapter 7, using a methodology allowing for disentangling group diversity from individual diversity, show that group-size diversity in the N-person linear public goods game does not importantly affect the evolutionary dynamics. Group-size diversity was studied in more detail in chapter 6, for the case of infinite well-mixed populations. In this chapter it is formally shown that the evolutionary dynamics of linear multiplayer games are not affected by group-size diversity. Contrastingly, the outcome of *nonlinear* public goods games depend on the level of heterogeneity of the group-size distribution. Depending on the game and the game parameters, this can lead to more cooperation (e.g. a higher fraction of cooperators at a polymorphic equilibrium or a higher basin of attraction for the cooperative equilibrium) or to less cooperation. This shows again that although social diversity can be sometimes important in affecting social evolution, its final effects can be either positive or negative, depending on further assumptions of the model.

Part II of this thesis has provided some new insights into models of upstream reciprocity as a secondary mechanism for the evolution of cooperation. Results presented in chapters 4 and 5 suggest that the view of upstream reciprocity acting in synergy with population structure for promoting cooperation in the prisoner's dilemma advanced by Nowak & Roch (2007) can be an artifact of specific modeling choices. Indeed, chapter 4 shows that the assumption that donor-recipient pairs are sampled along random walks in the population of individuals leads to interaction rates which are both non-uniform and strategy-dependent. When controlling for such heterogeneity by introducing participation costs, upstream reciprocity can fail to evolve in structured populations. Moreover, the use of random walks makes that only altruistic acts (and not defective acts) can be passed and reciprocated, making unclear the distinction between reciprocators and unconditional cooperators. All of these assumptions are removed from the model presented in chapter 5, which explores the evolution of upstream reciprocity when the population structure is given by a cycle. Interestingly, some mathematical conditions of the original model by Nowak & Roch (2007) are recovered, although the general conclusion is strikingly different: upstream reciprocity is found to be *never* evolutionarily stable against both unconditional defection and unconditional cooperation. These results are in line with less optimistic models of upstream reciprocity, such as the one by Rankin & Taborsky (2009).

Finally, Part I of this thesis has explored the consequences of allowing for partially conformist cultural transmission in models of two-person social dilemmas in network-structured populations. As evidenced by the results shown in chapters 2 and 3, conformity reinforces positive assortment in regular structures, leading to an easier formation of clusters of individuals of the same strategy. Within such clusters, cooperators not only benefit from the cooperation of other cooperators, but they are also protected from the exploitation of surrounding defectors. On heterogeneous networks, however, conformity can hinder the evolution of cooperation under both the prisoner's dilemma and the snowdrift game. The reason of such a striking difference in the results is that the evolutionary dynamics on heterogenous networks are not governed by a mechanism of cluster formation, but by a biased flow of information making lesss connected individuals preferentially adopt the strategies of their well connected neighbors. Conformity partially reverses such flow of information, making imitation of a defective neighbor by a cooperative hub more likely. This phenomenon accounts for the relatively negative results obtained for the partially conformist evolution of cooperation on heterogeneous networks.

In addition to the exploration of specific models of the effects of conformity, upstream reciprocity and social diversity on the evolution of cooperation, this thesis has made three particular methodological contributions to the multidisciplinary field of games on graphs. First, chapter 7 has made a case for the use of bigraphs for modeling population structures in multiplayer games, showing how it overcomes a series of difficulties endemic of the standard approach based on unipartite graphs. In particular, the importance of properly defining a replacement graph as a possibly weighted projection of the interaction bigraph has been underlined. Second, chapters 7 and 8 have shown the relevance of centrality measures in gauging the role of influential players in heterogeneous netowrks. Finally, chapter 8 has introduced the notion of 'interaction rules' in order to model asymmetric interactions on heterogenous networks. Although the model presented in chapter 8 explored only the simple Donation game, the methodology can be readily applied to study the effects of global asymmetric interactions in other asymmetric games, such as the Ultimatum and the Dictator games, to name a few.

9.2 Future research

> The end is the beginning is the end.
>
> Smashing Pumpkins

Understanding the mechanisms leading to or promoting the evolution of cooperation is an old problem, first dealt with by Darwin in *The Descent of Man*, yet of contemporary interest. Indeed, the question 'how did cooperative behavior evolve?' has been recently suggested as one of the top 25 scientific questions in the 125th anniversary issue of *Science* magazine (Pennisi, 2005).

Most theoretical answers to this question make use of one of two methodologies: inclusive fitness theory and evolutionary game theory, which have developed for decades adopting different approaches, almost without influencing each other. On the one hand, inclusive fitness, first advanced by Hamilton (1964), usually makes simplifying assumptions such as weak selection and additivity of various effects, but pays particular attention to the evolutionary consequences of population structures (Frank, 1998; Rousset, 2004). On the other hand, evolutionary game theory, invented by Maynard Smith & Price (1973) explores the properties of nonlinear dynamical systems arising from populations of players interacting in games without paying much attention to the population structure Hofbauer & Sigmund (1998). Evolutionary graph theory (Lieberman et al., 2005; Nowak & May, 1992; Szabó & Fáth, 2007) is a recent attempt to remedy this problem, but the resulting spatially or network explicit models add substantial complexity, making mathematical analysis virtually impossible, except for extremely simple cases [e.g. regular isothermal graphs (Ohtsuki et al., 2006; Ohtsuki & Nowak, 2006a)].

In my view, a closer connection between the two approaches is required in order to obtain a general and unifying understanding of the conditions promoting or inhibiting the evolution of helping behaviors. Recent papers testify to growing interest in making connections between game theoretic and inclusive fitness models and showing how different models relate to each other (Hauert & Imhof, 2011; Lehmann & Keller, 2006; Lehmann et al., 2007; Ohtsuki, 2010; Rousset, 2004). I think that it is necessary to devote more attention to developing hybrid models that incorporate both the precise description of interactions characteristic of evolutionary game theory and the rigorous descriptions of population structure championed by population genetics in general and inclusive fitness in particular. The effective use of both approaches will be key to continuing the investigation not only of conformity, upstream reciprocity and social diversity, but also of other factors affecting the evolution of cooperative behavior.

List of Publications

Working papers arising from this thesis

1. **Peña, J.** Evolutionary dynamics of upstream reciprocity on cycles.
2. **Peña, J.** Via inequality to cooperation and vice versa: the asymmetric donation game on networks.

Publications arising from this thesis

1. **Peña, J.** & Rochat, Y. (2012). Bipartite graphs as models of population structures in evolutionary multiplayer games. *PLoS ONE*, *7*(9), e44514.
2. **Peña, J.** (2011). Group-size diversity in public goods games. (2012) *Evolution*, *66*(3), 623–636.
3. **Peña, J.**, Pestelacci, E., Berchtold, A., & Tomassini, M. (2011). Participation costs can suppress the evolution of upstream reciprocity. *Journal of Theoretical Biology*, *273*(1), 197–206.
4. **Peña, J.**, Volken, H., Pestelacci, E., & Tomassini, M. (2009). Conformity hinders the evolution of cooperation on scale-free networks. *Phys. Rev. E*, *80*(1), 016110.
5. **Peña, J.** (2008). Conformist transmission and the evolution of cooperation. In S. Bullock, J. Noble, R. Watson, & M. A. Bedau (Eds.), *Artificial Life XI: Proceedings of the Eleventh International Conference on the Simulation and Synthesis of Living Systems* (pp. 458–465). Cambridge, MA: MIT Press.

Other publications (not included in this thesis)

1. Buesser, P., **Peña, J.**, Pestelacci, E., & Tomassini, M. (2011). The influence of tie strength on evolutionary games on networks: An empirical inves-

tigation. *Physica A: Statistical Mechanics and its Applications*, *390*(23-24), 4502–4513.

2. **Peña, J.**, Pestelacci, E., Tomassini, M., & Volken, H. (2009). Conformity and network effects in the prisoner's dilemma. In *Proceedings of the IEEE Congress on Evolutionary Computation, 2009. CEC '09*, (pp. 506 – 513).

3. Montes de Oca, M. A., **Peña, J.**, Stützle, T., Pinciroli, C., & Dorigo, M. (2009). Heterogeneous particle swarm optimizers. In *Proceedings of the IEEE Congress on Evolutionary Computation, 2009. CEC '09.*, (pp. 698 – 705).

4. Peña, J. C., **Peña, J.**, & Upegui, A. (2008). Evolutionary graph models with dynamic topologies on the ubichip. In G. Hornby, L. Sekanina, & P. Haddow (Eds.), *Evolvable Systems: From Biology to Hardware. Lecture Notes in Computer Science*, volume 5216 (pp. 59–70). Springer Berlin / Heidelberg.

5. **Peña, J.** (2008). Simple dynamic particle swarms without velocity. In M. Dorigo, M. Birattari, C. Blum, M. Clerc, T. Sttzle, & A. Winfield (Eds.), *Ant Colony Optimization and Swarm Intelligence. Lecture Notes in Computer Science*, volume 5217 (pp. 144–154). Springer Berlin / Heidelberg.

6. **Peña, J.** (2008). Theoretical and empirical study of particle swarms with additive stochasticity and different recombination operators. In *Proceedings of the 10th annual conference on Genetic and evolutionary computation*, GECCO '08, (pp. 95–102)., New York, NY, USA. ACM.

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