Ph.D. Thesis in Physics of

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On the influence of resources use and destruction on the evolution of cooperation

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Barcelona, Junio de 2012

- Pez que nada contra la corriente muere electrocutado - parafraseó Sancho Panza.
- A no ser que sea una anguila - contestó un soñador.
- La excepción que confirma la regla - agregó Sancho Panza.
- O quizás un producto evolutivo - respondió el soñador.

A todos aquellos que,
cual modernos Quijotes,
sueñan con un mundo mejor.

A mi familia y amigos, en especial a
mi querida hermana Henar,
mis padres, Jesús y Yolanda,
mis abuelos, Eduardo y Sagrario,
y mi maravillosa novia Daniela.

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Contents

Preface: The importance of the problem of cooperation and the finiteness of resources

0.1 Summary

The explosive introduction of network theory and stochastic methods for the study of finite populations has recently led to a new step in the use of evolutionary game theoretical methods. The complexity of the represented systems has grown exponentially, and has attracted the interest of scientists from many different branches, as biology, physics, economy, sociology or linguistics. And on the core of most studies still lies the same original problem, that of the emergence and evolution of cooperation, not only in biological contexts, but also in a human one, where the complexity of the relationships and contact networks is increasing in a society shaped by the appearance of new information and communication technologies.

However, the development of a new theoretical framework, evolutionary game theory, which is able to represent some of the intricacies of our society and nature, did not carry attached a deep analyses of one of the most important factors in evolution: the finiteness of resources in ecosystems as in the Earth. This factor, together with cooperation, is of fundamental importance in the formation of societies and multicellular life (among other higher-order structures). In this work, I aim to make a first approach to the introduction of such resource constraints into evolutionary models by studying the interplay between the emergence and stability of cooperative behaviours and finiteness of resources.

In addition, I provide in this study a definition of cooperative behaviours, and remark that pacifist, pacific, and conflict avoiding behaviours, are cooperative behaviours,

even if they lead to no appreciable direct benefit. To finish, I also study the effect of destructive behaviours on the evolution of cooperation, finding the first example –to my knowledge– of a simple behaviour that allows for robust evolutionary cycles.

0.2 Cooperation and finiteness of resources

We, humans, have developed all along history the most complex social organisation of the natural world, and the foundations of such development rely on two main components: Joint efforts –cooperation, mutual aid– between humans, and the use of natural resources.

Cooperation and use of resources may be observed not only in humans, but all along nature and at every stage of evolution. In this way, bacteria cooperate in order to synthesise nutrients, eusocial insects as ants and bees cooperate to create nests, sentinel meerkats cooperate watching for predators while others eat, and vampire bats share their bloody food with conspecifics; in an even more dramatic way, cooperation plays a fundamental role in the appearance and maintenance of higher-order entities (as societies, animal groups, insect colonies, multicellular life and eukaryotes) from their lower level components (humans, animals, insects, eukaryotic cells, prokaryotes). However, even if examples of cooperation can be easily found, it is not so easy to understand how and why cooperative behaviours may emerge and be maintained.

The question on the evolution of cooperation represents a conundrum, originated by the possibility of exploitation of cooperative individuals. A cooperative individual provides some kind of benefit to others at some personal cost. Any non-cooperative individual who enjoys the benefits of the cooperative acts, but avoids to spend any necessary cost for cooperating, will have higher benefits (earn more money, have more free time, reproduce more, ...) than cooperative individuals. It is thus easier for such kind of selfish behaviours to spread, leading cooperative behaviours to extinction, and ultimately reducing any cooperative social welfare of the population.

The problem of selfishness and cooperation was initially investigated within a human context by philosophers and economists, such as Hobbes, Voltaire, Rousseau and Adam Smith, and then formulated within an evolutionary context by Darwin and Wallace, attracting the attention of scientists as Kropotkin and Hamilton. The latter developed the theory of kin selection, finding that altruism (a form of cooperation) may evolve between genetically related individuals.

However, cooperative behaviours do not need to happen between genetically related organisms, but refer to much more general situations, including interspecies mutualisms as that of sharks and remoras. Evolutionary game theory was conceived in order to explain such situations. It models behaviours and interactions using game theoretical methods, and evolution through Darwinian selection dynamics. The use of such framework has led to the discovery of some mechanisms that allow for the evolution of cooperation, as reciprocity or the effect of interaction networks.

However, the development of the theory has relegated to oblivion the fact that the use of resources also plays a fundamental role, both in the origin of any higher-level unit, as societies or multicellular life, and in their stability once formed. Most models assume such a limitation of resources to be either nonexistent (assuming infinitely large populations) or just to impose a constant population size. I develop here several models which introduce the limitation of resources explicitly, assuming that a constant flux of resources leads the system out of equilibrium, and studying how this affects the evolution of cooperation.

To achieve the goal of understanding how the limitation of resources influences cooperation, I tried to keep the models as simple as possible, on the one side, to capture the essence of the problem on its most stylised form, on the other, to make the results applicable –with some modifications– in a very wide range of scenarios, which are outlined in the next section.

0.3 The importance of simple models

The development of simple models to explain the evolution of cooperation is important from three different perspectives: natural-sociological, socio-technological, and healthcare related.

The natural-sociological point of view relates to the understanding of the formation and evolution of cooperative groups of animals (including humans), the stability of ecosystems, the maintenance and increase of common goods, and the occurrence of the major transitions of evolution, which include the appearance of eukaryotes, multicellular organisms, and human societies.

The social-technological perspective focuses on the understanding of the formation of collaboration networks, both in a classical way or in an internet-based framework, the management of common goods, as healthcare and educative systems, and the implications of technological development and resources consumption in the increase or decrease of common welfare.

The healthcare related point of view does not try to increase altruism or cooperation anymore, but regards the different structural components of diseases such as cancer (healthy and sick cells) as interacting individuals, and applies the evolutionary game theoretical knowledge to try to cure or minimise the virulence and harmful effects of the malign agents.

In the three cases, the development of simple models allows for the understanding of the processes involved and the subjacent micro-dynamics, useful for the design of experiments, and for a gradual increase in the complexity of the models grounded on a solid basis.

0.4 Objectives and structure of the present study

The objectives of the present study are:

1. To provide a general definition of cooperation including parasitic behaviours and analyse the dynamics of a population of parasites, altruists and neutral individuals, called free-riders.

2. To study the influence of the limitation of resources in the evolution of cooperation.

3. to study the influence of destructive behaviours in the evolution of cooperation.

   Each objective is developed in one of the three parts in which this thesis is divided, as explained next.

Part I of the present study (Chapters 1 and 2) is devoted to introduce the problem and the most important concepts related to the evolution of cooperation. I begin in Chapter 1 with a historical introduction of the most important works which inspired this study, and explain how two different branches of science, evolutionary biology and game theory, gave rise to the evolutionary game theoretical framework. I also introduce here some of the most important concepts used along the study, as the replicator equation, the prisoner's dilemma or the public goods game. In Chapter 2, I provide a full classification of the concepts, and remark the necessity to include conflict-avoiding behaviours as cooperative behaviours –something never done explicitly in evolutionary game theoretical models– when compared to parasitism. This kind of behaviours will be studied in deep in Part II by means of a prisoners dilemma. I also provide here a mathematical proof of situations in which the prisoners dilemma is the appropriate model to represent nature. To finish, I show that the introduction of parasites, free-riding non-aggressive individuals, and altruists in a model allows for the survival of the latter two in unexpected high levels, which remarks the necessity to include conflict-avoiding, pacific and pacifist behaviours as cooperative.

In Part II (Chapters 3, 4 and 5) I return to the problem which, after Malthus ideas, inspired Wallace and Darwin to conceive the natural selection process: that of the finiteness of resources. I show that the limitation of resources is able to constrain the parasitic ability of the individuals in some situations, allowing for cooperative pacific individuals to thrive and dominate parasites, or for stable coexistence between parasites and pacific individuals in others. Chapter 5 provides simplified analytical versions for the models presented in chapters 3 and 4, showing phase transitions from defective states to states where cooperative individuals survive, and even dominate.

Part III (Chapters 6 and 7) is devoted to present a model for the evolution of altruism based on evolutionary game theory and stochastic processes in which the inclusion of destructive individuals, called Jokers, allows for the appearance of robust evolutionary cycles in which the system spends relevant times in cooperative states. I will also discuss how this relates to cooperation promoted by common enemies or risks.

To finish, in Part IV I summarise the main results obtained and list the publications derived from the present work.

Part I

The evolution of cooperation. History and concepts

Chapter 1

Introduction: How evolution met game theory

1.1 Evolution, natural selection and the problem of cooperation

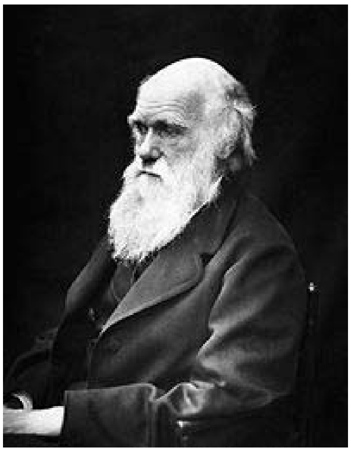


Figure 1.1: *Charles Robert Darwin.*

The publication in 1859 of the book *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* by Charles Darwin marked the end of an old era dominated by religious beliefs in which the human being –specially the occidental human being– was in the middle of the universe of creation. The idea of evolution, independently found by Wallace and Darwin himself at a time in which scientific circles questioned creationist theories, laid the foundations for scientific proof of the revolutionary ideas: man, as well as any other living organism, is the product of a long evolutionary process involving small changes and selection.

The first ideas related to evolutionary processes root on the late 1700's and early 1800's lively debate on the formation and shaping of the earth, where some geologists, as James Hutton and Charles Lyell [2–5], proposed that very slow long term processes of microscopic change driven by natural forces, as wind and water flow frictions or temperature changes, where the actual cause for the observed earth structure (Hutton [3] and Lyell [5], specially the first, already suggested the applicability of such ideas to the study of biological processes). Johann W. Goethe [6] also noticed that, given the morphological similarities between all plants, they might have developed by metamorphosis from an equal original form or ur-plant. In this context, Jean-Baptiste Lamarck made the first proposal of a biological evolutionary process giving rise to new species [7].

Figure 1.2: *Alfred Russel Wallace.*

At the same time as the evolutionary geology debate was held, economist T. Malthus ideas on population growth, overuse and competition for resources spread, reaching Wallace and Darwin. Malthus argued that any increase in available resources in society would lead to a subsequent increase in the population, until the same original subsistence per-capita amount of resources was reached [8]. Darwin and Wallace thought that, if this was to happen in human societies in which individuals may restrain their own reproductive and consumption rates, it would happen still more intensely in nature, where animals were thought not to do so, neither to have the ability to increase their resource supply.

Figure 1.3: *Thomas Robert Malthus.*

The application of geological and economic born ideas, together with the competition triggered by the finiteness of resources, led Darwin and Wallace to the conception of the evolutionary process in which individuals reproduce and give birth to similar –but not equal– offspring, and natural selection allows for the survival and spread of the best adapted traits, those associated to the fittest individuals, understood as the most successful from a reproductive and survival perspective.

However, Darwin himself realised the paradox implicit in natural selection acting at the individual level: any living being exploiting others would have a net evolutionary advantage over those individuals which assume some reproductive cost in order to produce a benefit on the rest; thus, the evolution of cooperative and altruistic behaviours seems to be doomed, which led to the imposition of the most dramatic view of the struggle for life in some scientific circles [9] in the late 1800's and early 1900's, and to the denial of the existence of cooperative benefits from an evolutionary perspective.

The evolution of cooperative behaviours was analysed from an opposed point of view in 1902 by Piotr Kropotkin in his book *Mutual Aid: A Factor in Evolution*, where he gathered a collection of articles in which he showed that cooperation, present both in animals and humans, is an important factor to take into account from an evolutionary perspective. He did not neglect natural selection, but argued that the struggle against an inclement nature favoured the evolution of mutual aid instead of fight between conspecifics.

Figure 1.4: *Pyotr Alexeyevich Kropotkin.*

Despite some experimental results showing the benefits of group formation against under-crowding in unfavourable environments [10], the debate continued, with supporters on both sides. It would still take another seventy years for theoreticians to develop a theory consistent with the observed results, and able to account for the evolution of cooperation.

1.2 Genes, populations, relatedness and assortment

At the time Wallace and Darwin proposed the theory of natural selection it was still unknown how heredity of traits between parents and offspring was realised. The works on heredity of Mendel, published in 1866, remained unknown until the beginning of the 1900's, when three European scientists –Hugo de Vries, Carl Correns, and Erich von Tschermak– found similar results and rediscovered it. They found experimental results proving the transmission of discrete traits between parents and offspring, and a few years later the term gene was coined.

Even when the discovery of the DNA as carrier of the genetic information should still wait until the 1940's, the knowledge of the existence of such inherited information as discrete traits allowed theoreticians –S.Wright, R. A. Fisher and J.B.S. Haldane– during the 1920's and 1930's to develop a mathematical framework for the evolution of gene frequencies and their associated traits within populations, in what is now called population genetics.

In this context, the importance of relatedness as a measurement of genetic similarity came into attention as a possible factor allowing for the evolution of altruistic sacrifice, as illustrated by J.B.S. Haldane statement that he would not risk his life for saving a drowning brother, but he would do it for two brothers or eight cousins. This intuitive statement was formalised mathematically in 1964, when W.D.Hamilton published his seminal works on kin selection [11, 12], anticipating the ideas of inclusive fitness theory.

Figure 1.5: *Gregor Johann Mendel.*

Inclusive fitness theory is based on the assumption that, although selection is carried out at an individual level, it is the genes which are actually selected, and equal genes are indistinguishable from an evolutionary perspective. Thus, the fitness of a behavioural trait, which is a measurement of its reproductive value and directly related to the number of offspring it will produce, is not only that of the trait in the individual, but also the addition of the effects of its behaviour on the fitness of all other individuals carrying such trait. Furthermore, it is usually assumed that evolution acts so as to maximise the inclusive fitness of the individuals.

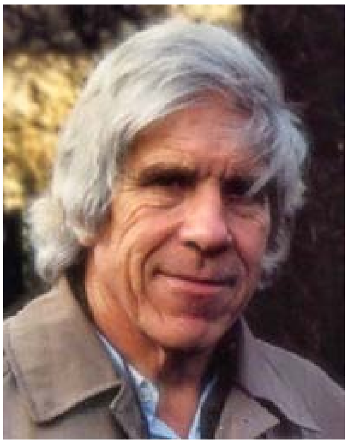


Figure 1.6: *William Donald Hamilton.*

With the previous assumptions applied to identical genes by descent, i.e. genes which are a perfect replica of those of a common ancestor, Hamilton proved that altruistic traits which imply a cost $-c < 0$ to the actor might evolve whenever the benefit $b > 0$ of the altruistic behaviour is directed towards individuals whose relatedness r –a measurement of genetic similarity– fulfils the so called Hamilton rule

$$r > \frac{c}{b}, \tag{1.1}$$

situation in which the inclusive fitness effects of the costly action to the altruistic donor trait are outweighed by the benefits accrued on enough similar individuals (see [13] for a detailed explanation of the meaning of r).

Figure 1.7: *George Robert Price.*

This results were expanded in 1971 by G.R. Price. He proved that, if the fitness of the individuals carrying a trait i of value z_i at time t is given by $w_i = \bar{w}q'_i/q_i$, where q_i, q'_i are the frequencies of individuals carrying such trait at times t and $t' = t + 1$, and $\bar{w}$ is the mean population fitness, then the variation of the mean value of such trait $\Delta z = z' - z$ fulfils

$$w\Delta z = Cov(w_i, z_i) + E(w_i \Delta z_i), \tag{1.2}$$

where w is the mean population fitness, $Cov(w_i, z_i) = E(w_i z_i) - E(w_i)E(z_i)$ is the covariance between fitness and trait value, and $E(X)$ is the expected value of X.

The Price equation applied to the evolution of altruistic behaviours results in the Hamilton's rule, but its interpretation changes. The fundamental feature which allows for the evolution of altruism is no longer genetic relatedness, but the assortment between altruistic behaviours [14], i.e. the fact that enough benefits given by altruists are enjoyed by other altruists.

1.3 The mathematics of games, or how to model behaviours

The origin of game theory dates back to the 1920's, when John von Neumann published a series of articles on the issue, and the latter book *The Theory of Games and Economic behaviour* in collaboration with Oskar Morgenstern. Its development continued during the rest of the century, attracting initially the attention of economists and politicians.

Game theory focuses on the study of cooperation and conflict between rational decision makers interacting together, i.e. individuals who possess information about the possible outcomes of the interactions (the game) and decide how to act according to it. The specification of a behaviour of an individual in any situation is called strategy, and the outcome of every interaction depends on the strategies chosen by all interacting individuals (players). The main goal of game theory is to predict which strategies will be played by each player and the associated distribution of benefits, for which reason John Forbes Nash introduced in 1951 the concept later called Nash equilibrium. A Nash equilibrium happens whenever none of the players increases its benefits by changing its actual strategy. In this way, if one assumes that individuals are rational, the Nash equilibrium represents the outcome of the interaction.

Full rationality was initially assumed in game theoretical models. This means that individuals are rational, and take into account that their interacting partners are rational as well. This assumption is often unrealistic, on the one side because information might not be fully available or costly to acquire, and on the other side because it leads to an infinite iteration of the form I know that you know that I know that you know..., for which reason the concept of bounded rationality was introduced into economic game theory.

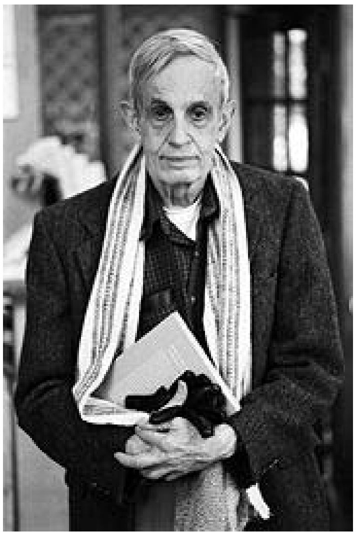


Figure 1.9: *John Forbes Nash.*

Bounded rational individuals do not possess any longer all the information of the system, or cannot process it, and their behaviour is influenced only by a few variables related to the situation. This point of view seems more appropriate to describe the real world, in which animals (including humans) neither have infinite perception of the reality surrounding them, nor –often– the time to process all important information before having to interact. And this is specially important in a situation in which life, reproduction and death come into play.

All previous concerns illustrate the necessity of a dynamic framework in which to embed the game theoretical analysis (this was already suggested by Nash), which led to the birth of evolutionary game theory.

1.4 Evolutionary game theory to model behavioural evolution

In 1973 J. Maynard-Smith and G.R. Price published a paper in which they reinterpreted the payoffs of the game as fitness changes of the individuals, and thus in their reproductive capacity. The static view of game theory was transformed into a dynamic framework, and the Nash equilibrium concept was changed for that of evolutionary stability, to refer to those populations which, once established, cannot be invaded by just a few mutant individuals [15,16]. In this way, the branch of biology called evolutionary game theory was born.

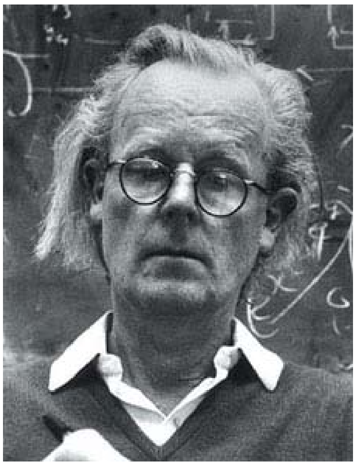


Figure 1.10: *John Maynard Smith.*

In the following years the replicator equation (see appendixes 1.B and 1.5.1),

$$\frac{dx_i}{dt} = x_i(f_i - \bar{f}), \tag{1.3}$$

became the main tool for analysing the dynamics resulting from the evolutionary processes [17,18]. In this equation x_i is the fraction of individuals following strategy i, f_i is their fitness and $\bar{f}$ the mean population fitness. This equation, which reduces to the Price equation under some assumption [19,20], describes the frequency-dependent dynamics of infinite –or very big– populations of replicating individuals, i.e. the dynamics in a fitness landscape which depends on the population composition. On its mutation regarding version, the so called replicator-mutator equation has been proposed as a dynamical equation describing the entire evolutionary process of reproduction, mutation and selection.

In the last two decades the evolutionary game theoretical framework has expanded to cover a much broader range of situations. In addition to the study of evolution in nature, culture and society have been regarded from an evolutionary perspective. In cultural evolution and social learning contexts, strategies are no longer linked to genes, and the reproduction and death process are reinterpreted as a change of strategy during the lifetime of the individual. Furthermore, new microscopic update rules have been introduced to represent specific learning methods and reproduction-death processes, broadening the range of applications to include sociological and psychological research.

1.4.1 Evolutionary game theory vs. inclusive fitness theory

The debate on the most fundamental approach to formulate mathematical models of evolution has been a hot topic during the last two years [21–37]. In the beginning, inclusive fitness theory was mostly supported by biologists, while evolutionary game theory was supported by mathematicians and scientists coming from other disciplines. However, in the last years both theories have gained adepts from any discipline.

Although recent studies show that both disciplines provide the same results [38] in many cases, it has been recently suggested [20,37] that they are fundamentally different. One of the main differences is that the Price equation is not dynamically sufficient in some situations, i.e. cannot be used to predict all variables in future temporal steps knowing their previous values, which suggests that the evolutionary game theoretical framework might be more appropriate whenever we want to describe the dynamics of the system and calculate associated quantities, as fixation probabilities or invasion times. For this reason, an evolutionary game theoretical framework will be assumed in the present work.

1.5 The evolution of altruism, an evolutionary game theoretical viewpoint

The study of the evolution of cooperation has focused almost exclusively in the problem of altruism (cooperation, C) versus free-riding –I present another example in chapter 2 and study it in successive chapters–. Altruists (cooperators, C) are individuals who pay a cost c to give a benefit b to other individuals, cost and benefit measured as fitness (i.e. growth rates). Free-riders (defectors, D) are those who enjoy the benefits but do not pay any cost, thus getting higher net benefits and spreading their behavioural trait in the population, eventually leading altruists to extinction.

If interactions between altruists and free riders are dyadic, i.e. happen in pairs, their result might be summarised in the following payoff matrix

$$\begin{array}{l|cc} \text{(a)} & \text{C} & \text{D} \\ \hline \text{C (altruist)} & R = b - c & S = -c \\ \text{D (free-rider)} & T = b & P = 0 \end{array} \tag{1.4}$$

which determines a prisoner's dilemma (defined below, see also appendix 1.A for its original setting) whenever the benefit provided by altruists is bigger than the cost of the altruistic act, $b > c$. In a prisoner's dilemma it is always better to defect (D) than to cooperate (C) from a fitness self-maximising point of view. This happens because, if the co-player is a cooperator, by defecting one gets $T = b$, higher than $R = b - c$ by cooperating; if the co-player is a defector, then cooperating yields $S = -c$, while defecting yields $P = 0$. Thus, regardless of the co-player being a cooperator or a defector, defecting (free-riding) increases fitness in a quantity c (equal to the cost paid) over cooperating (behaving altruistically).

In general, a prisoner's dilemma (PD) is defined by the payoff structure $T > R > P > S$, which ensures that defecting results in a higher benefit than cooperating if the interaction partner is a cooperator ($T > R$) or a defector ($P > S$), although both individuals fare better if they cooperate than if none does ($R > P$). This situation, in an evolutionary context, represents an example of the tragedy of the commons [39], where selfish individuals maximising their instantaneous fitness spread in the population, leading ultimately to populations of minimum fitness ($P = 0$ in the altruist vs. free-rider case), while the spread of altruism would lead to populations with a higher fitness ($R = b - c$) where everyone enjoyed the benefits of the altruistic acts.

The public goods (PG) game is introduced to model situations in which interactions happen in groups. In this case, altruistic individuals are assumed to pay a cost c in order to yield a benefit $b = rc$, which is redistributed within the entire group. Whenever the interaction group size n is bigger than the amplification factor, $n > r > 1$, this situation represents again a tragedy of the commons, as individuals avoiding to pay costs receive higher benefits than those paying it, and evolution leads to none cooperating, and to mean interaction benefits equal to zero.

1.5.1 Dynamical outcomes of the replicator dynamics for two-strategy symmetric games

The prisoner's dilemma (PD) is one of the four possible two-player, two-strategy symmetric games. In the PD the payoff ordering is $T > R > P > S$ (see equation (1.4)). As it has been discussed, this makes defection more beneficial from a self-maximising point of view in any interaction. The other three games are the snowdrift (SD) game, corresponding to $T > R > S > P$, the stag-hunt (SH) game, corresponding to $R > T > P > S$, and the harmony game (HG), where $R > T > S > P$. In the following, I make use of the replicator equation (1.3) to show the dynamical outcomes of the four games, and how the PD represents the most difficult case for the evolution of altruism in large, well-mixed populations (mean field limit in which every individual interacts with any other with equal probability).

The replicator equation (1.3) depends on the difference between the mean payoff of the strategy and the mean population payoff. Therefore, as shown in appendix 1.B, the addition of a constant to any column of the payoff matrix leaves the dynamics invariant. The payoff matrix for two strategies may thus be written (subtracting the diagonal term in each column) as

$$\begin{array}{c|cc} & \mathrm{A} & \mathrm{B} \\ \hline \mathrm{A} & 0 & a \\ \mathrm{B} & b & 0 \end{array} \tag{1.5}$$

where $a = S - P$ and $b = T - R$ in the terminology of equation (1.4).

Since the fractions of strategies add up to one, $x_a + x_b = 1$, the entire dynamics may be expressed with just one differential equation, let us say that for $x \equiv x_a$:

$$\frac{dx}{dt} = \dot{x} = x(1-x)[a-(a+b)x] \tag{1.6}$$

In this case factor a corresponds to the per-capita growth rate of strategy A when rare, i.e.

$$a = \lim_{x \to 0} \frac{\dot{x}}{x} = \left.\frac{d\dot{x}}{dx}\right|_{x=0} \tag{1.7}$$

It can be proven in a similar way that b is the per-capita growth of strategy B when rare in the population.

Generally, there will be three solutions for equation (1.6) with parameters $a, b \neq 0$. Two of them represent always valid solutions, i.e. $x = 0$ and $x = 1$. The third one

$$x^* = \frac{a}{a+b} \tag{1.8}$$

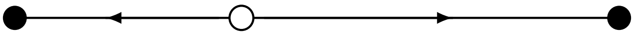
represents a real solution only when it takes values $x^* \in [0, 1]$, and it may be a stable or unstable fixed point.

The outcomes of the dynamics are summarised as:

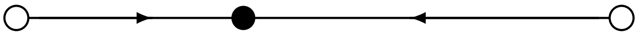
i. *Neutral stability.* If $a = b = 0$ every point in $[0, 1]$ is a rest point. In this case there is no evolution and the fraction of individuals x remains constant in time.

ii. *Dominance of one strategy.* If $ab \leq 0$ and at least one of the factors a and b is not 0, then $x^* \notin (0, 1)$, and the dynamics will lead either to $x = 0$ or to $x = 1$ depending on the sign of $\dot{x}$. This is what happens in prisoner's dilemmas (PD, defection dominates) and harmony games (HG, cooperation dominates).

iii. *Bistability.* If $ab > 0$ and $a, b < 0$ then x^* is an unstable rest point and the dynamics will lead either to $x = 0$ or to $x = 1$ if the initial fraction of individuals is below or above x^* respectively. This is what happens in stag hunt (SH) games.



iv. *Coexistence.* If $ab > 0$ and $a, b > 0$ then x^* is a stable attractor, and whenever the initial composition contains a mixture of individuals, the dynamics will lead to stable coexistence of strategies in proportions x^* for A and $1 - x^*$ for B. This is what happens in snowdrift (SD) games.



Thus, in this case in which the replicator dynamics represent the evolution of the system (it happens the same for most dynamics in the mean field limit), the PD –and the PG as its n-players generalisation– is the most difficult case for the evolution of altruism, as the evolutionary outcome is dominance of defection.

1.6 Mechanisms for the evolution of altruism

The study of the prisoner's dilemma and the public goods game has led to the discovery of a set of mechanisms allowing for the survival and expansion of altruism, which might be classified in two groups: structural and behavioural mechanisms.

Structural mechanisms imply the existence of some factor which does not depend directly on the behaviour of the individuals, as

- *kin selection* [11, 12, 40], which allows for the evolution of cooperation whenever altruistic behaviours are linked to genes, as explained in previous sections.
- *network structures*, as space or interaction networks, which depending on the properties of the network may allow for the evolution of cooperation both for prisoner's dilemmas [41, 42] and public goods games [43].
- *multilevel or group selection* [44,45], which happens whenever there are groups of individuals, and the individuals interact according to a prisoner's dilemma only with individuals of their group, and there is also competition between groups. In some situations this allows for cooperation to thrive [44].
- *green beards*, which happens when the altruistic behaviour is genetically coded and preferentially directed towards individuals carrying the altruistic trait [46,47].
- *linking payoffs to ecological variables*, which has been proven to allow for the evolution of cooperation in the competition for oviposition sites in insects [48].

Behavioural mechanisms imply the addition of new behavioural types, which may require the use of higher cognitive abilities, as memory or recognition capacity. Behavioural mechanisms found to promote altruism in a well-mixed prisoner's dilemma, where every individual interacts with any other, include

- *reciprocity –direct [49] and indirect [50]–*, where individuals choose to cooperate or not according to some previous information about the co-player, as for instance if he cooperated with you previously (direct reciprocity [49]), or if he cooperated previously with others (indirect reciprocity [50]). The most famous example of a behaviour that allows for the evolution of altruism through direct reciprocity is Tit For Tat, a strategy which cooperates the first time it interacts with someone, and then it simply imitates the behaviour displayed by the co-player in their last interaction together. This very simple behaviour turned out to be the surprising winner of a series of computer tournaments [49], showing that one time step memory is enough to promote cooperation whenever the game is an iterated prisoner's dilemma, i.e. played repeatedly between the same two players for many rounds.

- *punishment and reward* [51–59], when altruistic individuals may choose to pay some extra cost in order to punish (impose a cost on) a free-rider partner with whom they interacted, or to reward other altruistic individuals. Although the relative importance of both mechanisms is debated, it is generally accepted that they are able to increase cooperation levels.
- *similarity donation*, which happens whenever individuals choose to cooperate if they find a certain level of similarity between them and their interaction partners [60–62]. This mechanism is similar to a non-genetically determined green beard, explained above.

In addition to reward and punishment, behavioural mechanisms promoting cooperation in the public goods game include

- *loner strategies*, which do not to play the public goods game and get some benefit on their own [63]. The inclusion of loners in addition to cooperators and defectors allows for neutrally stable cycles in the absence of mutations, and for stable coexistence with cooperative and defective individuals whenever mutations between strategies happen.

All previous mechanisms enable the evolution of altruism, either promoting the invasion of the entire population by altruistic individuals, or allowing for their survival in a coexistence state with free-riders. However, for a well-mixed prisoner's dilemma or public goods game –where every individual interacts with any other individual with equal probability– without repeated interactions, and in the absence of higher cognitive abilities, cooperation cannot evolve. Being this case the most restrictive for cooperative behaviours to evolve (see appendix 1.5.1), I will use it in order to, first, prove that resource constraints may allow for the evolution of cooperation in a prisoner's dilemma (chapters 3, 4 and 5), and second, prove that destructive behaviours allow for evolutionary cycles in a public goods game (chapters 6 and 7). Before that, however, I will discuss in chapter 2 the concepts of altruism and cooperation, and prove that the interactions of parasites and free-riders also determine a prisoner's dilemma, not explicitly studied in the game theoretical literature. This case, which is more appropriate for the representation of resources use and exchange, as it allows for a conservation law, will be the one studied in subsequent chapters.

Appendices

1.A The prisoner's dilemma

The PD is named after the dilemma in which two prisoners are asked to incriminate the other as participant in a robbery. If both individuals do, each one is charged with 5 years of imprisonment. If only one of them incriminates the other, they are charged respectively with 0 and 7 years imprisonment. If none of them denounces the other, both are charged with 1 year imprisonment. Thus, it is better for them if none incriminates the other, and both get free after one year, than if both testify against the other. However, rational behaviour leads to mutual defection, as from a self-maximising point of view, it is always better to incriminate: if the other one does not, incriminating is worth freedom, if the other does, incriminating reduces in two years the time in prison.

1.B Extinction of cooperation in prisoner's dilemmas and invariance of the dynamics

If the dynamics favour the increase of the proportion of individuals with higher payoff and there are only two types of individuals in the population, cooperators and defectors, then cooperators will extinguish. If the proportion of individuals are x_C and x_D for cooperators and defectors respectively, then the average payoffs obtained by each strategy after many interactions in a well-mixed population (where every individual interacts with any other individual with equal probability) according to matrix (1.4) are

$$\begin{aligned} \pi_C &= Rx_C + Sx_D \\ \pi_D &= Tx_C + Px_D \end{aligned} \tag{1.9}$$

as for the PD one has $T > R$ and $P > S$, then the mean payoff of defectors is higher than that for cooperators, and evolution leads the cooperative strategy to extinction.

Note that if the evolutionary dynamics depend on payoff differences between strategies, or between strategies and mean population payoff, as for the replicator equation (1.3), the dynamics is invariant under the addition of a constant to any column in the payoff matrix. Let us prove it for the general case of N different strategies.

For payoff differences between two strategies, writing M_{ij} for the element in row i, column j of the payoff matrix, i.e. the payoff of strategy i interacting with j)

$$\pi_i - \pi_j = \sum_{k=1}^{N} x_k M_{ik} - \sum_{k=1}^{N} x_k M_{jk} = \sum_{k=1}^{N} x_k (M_{ik} - M_{jk}) \tag{1.10}$$

and as the difference in the last term is for payoffs in the same column, i.e. column k, the addition of any constant to the entire column leaves the result invariant.

For dynamics ruled by the difference of strategies payoff and the mean population payoff,

$$\pi_i - \overline{\pi} = \sum_{k=1}^{N} x_k M_{ik} - \sum_{j=1}^{N} x_j (\sum_{k=1}^{N} x_k M_{jk}) \tag{1.11}$$

then, if one adds a constant t to all payoffs in column m, one gets an extra term $x_m t$ from the first summation, and $-\sum_{j=1}^{N} x_j(x_m t) = -x_m t$ from the second one; both vanish as they have different sign.

Chapter 2

The tower of Babel of cooperation

Summary

The evolution of altruism, where individuals incur costs to provide benefits to others, represents a dilemmatic situation, as behaviours that enjoy the benefits without paying costs are promoted by natural selection. Many recent studies have focused on this problem. However, its behavioural roots are sometimes missing, and contribute to misunderstandings in the use of concepts such as altruism and cooperation [64–73]. Although altruism is a form of cooperation, there exist other cooperative behaviours. I start this chapter providing a relative definition of such and related concepts.

Then, I show that pairwise interactions and additive fitness resulting from individual behaviours determine always Prisoner's Dilemma's (PD's) and Harmony games, property which –to my knowledge– has not been previously pointed out, and which allows for an easy understanding of situations in which interactions determine PD's, which has been recently questioned given the difficulties to measure payoffs experimentally [74–77].

To finish, I show that in addition to the altruists vs. free-riders setting, the combination of free-riders and parasites determines a fundamentally different PD, included in the general framework of the relative definition. I show using numerical simulations that the combination of parasites, free-riders and altruists, enables coexistence of the three strategies whenever mutations occur, which may help understand the infrequent punishment directed towards free-riding non-aggressive individuals observed in nature and society.

2.1 Introduction

The most widely studied case of the evolution of cooperation stands for altruism [11, 12]. An act is said to be altruistic if it confers a benefit b_a to a partner at a cost c_a to oneself. The interactions between altruists and passive individuals, that receive the benefits of the altruistic acts but do not pay any cost nor confer benefits to others, determine a prisoner's dilemma (PD) whenever the provided benefits are higher than the costs $b_a > c_a > 0$. Such neutral or passive individuals, called free-riders as they receive the benefits at no personal cost, are expected to increase in number until altruism extinguishes (see section 1.5). The study of the free-riding problem has been a major task in the last decade, leading to the discovery of some mechanisms allowing for the evolution of altruism, as those in section 1.6.

However, the development of our knowledge carried attached some problems, as the controversy on the definition and use of altruism, cooperation and related concepts [64–73], which have been mixed and occasionally used without distinction. According to the classic definitions, altruistic behaviours are always cooperative, but not all cooperative behaviours are altruistic, although some recent redefinitions of the concepts map the entire range of cooperative behaviours within weak or strong altruism [73]. In order to clarify this issue, at the beginning of the present chapter I provide a classification of concepts based on relative definitions of selfishness and cooperativeness, which comprises previous ones found on the literature, and intends to flatten the path towards a unified semantic framework. These definitions will be adopted in the rest of the present work.

Then, in section 2.3 I analyse the range of application and behavioural roots that lead to PD's. The usefulness of the PD has been recently questioned. The difficulty to measure payoffs in nature [74–77] did not allow for a clear assessment of whether some situations are PD's or snowdrift games. I prove that, whenever interactions are carried out by one individual, received by another, and if payoffs are additive, only PD's and harmony games emerge, from which the PD is the most difficult case for the evolution of altruism. I further illustrate the necessity of identifying the behavioural roots that lead to PD's by showing that two altruists interacting together may determine one, in which both are cooperative individuals, but differing in their level of cooperativeness and selfishness.

After that, I show that in addition to the case of altruists vs. free-riders, interactions between parasites, who pay a cost c_p to parasitise a benefit b_p from the co-player, and free-riders (passive individuals receiving the actions of the co-player) also determine a PD, both PD's belonging to different categories of the tragedy of the commons [66]: the first case (altruism), to social goods formed by cooperation; the second case (parasitism), to social goods formed by restraining from conflict. I also discuss the usefulness of some of the mechanisms for the evolution of altruism in the free-rider vs. parasite case.

To finish, I define a generalised PD where neutral individuals define the null point of the reference system, altruists increase the mean population fitness, and parasites reduce it. I show that whenever the three strategies are mixed, mutations enable coexistence of the three strategies, which does not happen whenever only two of the strategies are present in the population. Thus, the combination of altruists and free-riders allows for their survival in the presence of parasites, and provides an intuitive explanation for two important questions related to the evolution of cooperation. First, the observation that animals punish much more often thieves than lazy individuals [78]. Second, the emergence and survival of cooperation in strictly defective populations, as those composed of parasites.

2.2 A relative definition of cooperative behaviours, a general definition of cooperation

The concept of cooperation, rather than a fixed concept that allows for a clear definition of what cooperative individuals are, is a contextual dependent concept, as strategies can be defined as cooperative or not only in relation to other strategies involved in the evolutionary process [79,80] (see sections 2.3 and 2.B). This suggests that, instead of trying to define strategies as cooperative or defective, a gradual definition for cooperation might be established according to the following two principles:

- *A strategy A is more cooperative than another one B whenever it is more beneficial* *to interact with A than with B from a receiver's point of view.*

- *A cooperative act does not reduce the fitness of the recipient of the act.*

Note that this is a relative definition for a cooperative behaviour or act, as it is based on the perception of benefits of one individual when interacting with others, and that this definition is completely consistent with the general definition of *cooperation*, which might be stated as *the non-forced act of working together for a common purpose or benefit*; if two individuals that are regarded as cooperative interact together, it defines a cooperative act.

Note also that this defines cooperation in the short-term, i.e. interaction after interaction, as well as in the medium term (a certain number of interactions) and in the long term (lifetime consequences of the behaviour [67]), but that such time frame should always be specified [72,78], as past semantic misunderstandings originated on the confusion of acts (short term) and lifetime behaviour, as illustrated by the discussion on the so called reciprocal altruism [81]. According to the definitions above, some acts that might be seen as altruistic may turn to be mutually beneficial in the long term, as it happens for behaviours that reciprocate altruistic acts; they might be called mutually beneficial (selfish and cooperative) in the long term, but altruistic (non-selfish and cooperative) in the short, whenever individuals cannot predict the outcome of the next interaction. Note however that independently of the time frame, both are cooperative acts.

The second requirement states that the benefits of cooperation must be at least the absence of fitness losses due to aggressions, and from this ground, any positive benefit, as those created by altruists; a slightly more stringent definition requires positive effects (even if infinitesimal) on the partner [70]. However, the definition given above accounts for peace as a social good [66], and thus conflict-avoiding, pacific and pacifist behaviours as cooperative. Note that, although when compared with altruism, free-riding strategies (neutral individuals) are regarded as defective, the cost paid by altruists is not a consequence of the free-riding strategy, but of the altruistic behaviour itself; furthermore, as I will show (section 2.6), in a context in which there exist aggressive, parasitic strategies, the existence of free-riders and altruists allows for their survival, preventing the sure extinction of any of those strategies when interacting

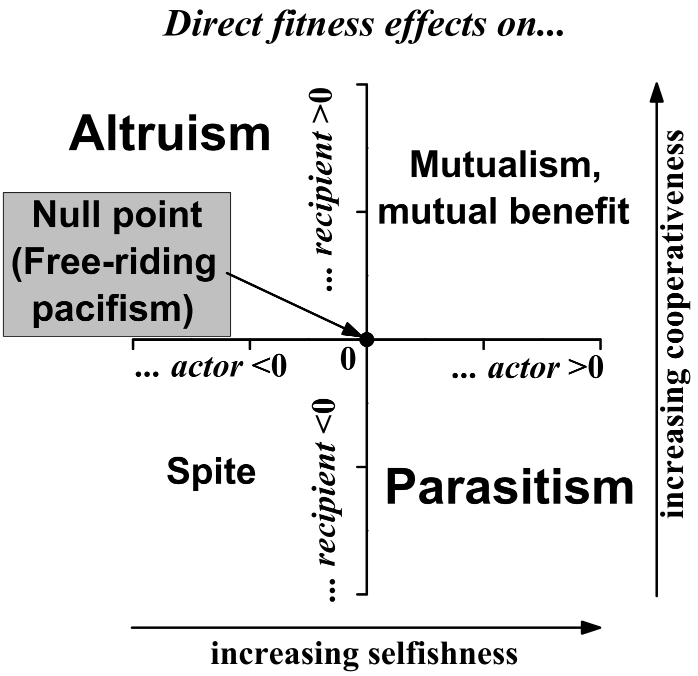


Figure 2.1: *Classification of strategies in the case of direct interactions as a function of the direct fitness effect of the action on the actor itself and on the recipient. The arrow on the right shows the increase in cooperativeness; increase in selfishness shown by the lower arrow. According to the definition, only non-damaging strategies (upper quadrants including the x-axis) should be called cooperative, while only strategies increasing their own fitness should be called selfish. Neutral individuals (free-riders) determine the null point, altruism is non-selfish cooperation, mutualism is selfish cooperation, spite is non-selfish and damaging, and parasites are selfish non-cooperative individuals. The combination of any two of these strategies determines either a Prisoner's Dilemma or a Harmony Game.*

with parasites in well-mixed populations, i.e. in the mean field limit in which every individual interacts with any other with equal probability.

If one assumes a relative definition for the concept of selfishness, calling a strategy more selfish than another if it is more costly or less beneficial for the actor, and truly selfish if it provides positive benefits to the actor, a complete classification of strategies can be done, including cooperative behaviours in which the cooperator gets a self-benefit for cooperating, e.g. behaviours determining snowdrift games, which might be regarded as selfish cooperation (figure 2.1). In this way, 'cooperativeness' ('relative selfishness') refers to fitness variations in co-player (oneself), requiring for absolute cooperation (selfishness) such effects to be non-negative (positive) when compared to the neutral case, i.e. the null point of the reference system (figure 2.1). I show in the following two sections that the entire ladder of cooperation due to direct interactions, with its lower level being parasitism and its higher altruism, may be illustrated with the well known Prisoner's Dilemma. The problem on how to choose the null point of such reference system (figure 2.1) is discussed in section 2.7.

2.3 The prisoner's dilemma, a controversial example

The PD game has been widely used as a mathematical metaphor representing the problem of the evolution of altruism and cooperation during the last 20 years. However, its study by theoretical scientists has been surrounded by controversy since the very beginning, as some scientists claim that other games, as the snowdrift, in which coexistence is the evolutionary outcome (see appendix 1.5.1), are more suitable to represent real interactions. The controversy has not been solved, as difficulties arise when trying to measure payoffs in nature, which usually does not allow to assess if the payoff ordering is that of a PD or of a snowdrift [74–77]. I show in sec.2.3.1 below a special feature that allows for a clarification of this problem in some contexts: If individual behaviours produce a fixed fitness variation on the actor, a fixed fitness variation on the receiver of the act, and fitness is additive, only PD structures or harmony games emerge, being cooperation the nontrivial solution only for the PD. However, I also show a limitation of the PD: the widely spread belief that any PD structure of the interactions involves altruists and non-altruists is wrong. As I show in sec.2.3.2, two altruists interacting together may also define a PD, in which they differ in their cooperativeness degree.

2.3.1 Direct interactions and additive payoffs lead either to prisoner's dilemmas or to harmony games

Suppose that in a habitat there are two interacting species, or in a population two different behavioural types; let's call them A and B. Suppose also that during any interaction individual A produces a fitness change A_s on itself and A_r on the recipient, and B produces B_s and B_r on itself and on the co-player respectively. The interaction matrix is

$$\begin{array}{c|cc} & \text{A} & \text{B} \\ \hline \text{A} & R = A_s + A_r & S = A_s + B_r \\ \text{B} & T = B_s + A_r & P = B_s + B_r \end{array} \tag{2.1}$$

Let us assume in the following that individual A is the cooperative individual, and B the non-cooperative one, also called defector. Then, the first requirement in the definition of cooperative behaviours (see section 2.2) –it is better to interact with the more cooperative individual– turns into $T, R > P, S$, and the second requirement –absolute cooperative individuals do not reduce the recipient's fitness– into $A_r \geq 0$. Defining $\Delta_s = A_s - B_s$ (relative selfishness degree of A), and $\Delta_r = A_r - B_r$ (relative cooperativeness degree of A), the two requirements for the definition of a behaviour as cooperative reduce to

$$\begin{aligned} &\Delta_r > Abs(\Delta_s) \\ &A_r \geq 0. \end{aligned} \tag{2.2}$$

The first of equations (2.2) implies that, for individual A to be a relative cooperator and B a relative non-cooperator, the relative cooperativeness degree of A must be bigger than its relative selfishness degree. The second equation requires the action of A on B to have neutral or positive effects in order to call A an absolute cooperator. As we will see below in section 2.3, A being an absolute cooperator does not imply that B is necessarily a non-cooperator; they may perfectly be both absolute cooperators, and still determine a PD, as I show in section 2.3.2. For that reason, in the following cooperative and defective individuals should be interpreted according to the relative scale defined by equations (2.2).

There are four possible games that are consistent with equations (2.2) (see appendix 1.5.1), and thus one of the interacting individuals is regarded as more cooperative than the other:

$$\begin{array}{llcl} \text{Game} & \text{Payoff ordering} & \rightarrow & \text{requirement} \\ \text{Prisoner's Dilemma (PD)} & T \geq R > P \geq S & \rightarrow & \Delta_s \leq 0 \\ \text{Harmony Game (HG)} & R \geq T > S \geq P & \rightarrow & \Delta_s \geq 0 \\ \text{Snow Drift (SD)} & T \geq R > S \geq P & \rightarrow & \Delta_s = 0 \\ \text{Stag Hunt (SH)} & R \geq T > P \geq S & \rightarrow & \Delta_s = 0 \end{array} \tag{2.3}$$

For a PD, being A the cooperative individual, the relative selfishness degree of A is positive. This means that it is better to be a non-cooperator than a cooperator, as $\Delta_s \leq 0 \rightarrow A_s \leq B_s$ implies that changing strategy from A to B in any interaction increases ones own payoff in a quantity Δ_s, while getting the same payoff from the co-player. In this case, Darwinian payoff self-maximisation promotes the increase of the relative non-cooperative individuals, which have a higher payoff, leading to populations where everyone earns a payoff P, though populations of relative cooperative individuals do have a higher mean payoff, as $R > P$. Note that whenever $P = 0$ we face the so called tragedy of the commons [39], i.e. the exhaustion of common goods due to selfishness.

If one imposes the payoff ordering for a Harmony Game, then $\Delta_s \geq 0$, i.e. $A_s \geq B_s$. In this case cooperative individuals (A) are more selfish, getting the higher self-payoff, and any defector increases its own payoff in a quantity Δ_s in any interaction by changing to cooperate. Cooperators are thus favoured by natural selection and their evolution does not represent a dilemma, as self-maximisation of payoffs equals mean population-payoff maximisation.

For the snow drift (SD) and the stag hunt (SH) games, the payoff ordering imposes $A_s = B_s$, which means that, if payoffs are assumed to be additive and interactions direct, both dilemmas only exist at the boundary between PD and HG regions, and might be seen as limit cases of them. It is not possible to have a SD or SH with fixed additive fitness variations due to direct interactions; only PD and HG structures emerge in this case, i.e. all possible combinations of behaviours present in figure 2.1 give rise to PD's or HG's.

2.3.2 Cooperative and defective altruists in a PD

The payoff ordering in equation (2.3) implies that whenever there are two altruistic behaviours interacting together, i.e. $A_s = -c_a$, $A_r = b_a$, $B_s = -c_b$, $B_r = b_b$, and both behaviours fulfil a PD, i.e. $c_a \geq c_b$, $b_a \geq b_b + c_a - c_b$, then A is regarded as cooperator and B as defector. This has led to the false and widely spread belief that PD structures always include absolute cooperative and non-cooperative individuals, as an altruist and a non-altruist. However, according to the definition of cooperation given in section 2.2

and formalised in equation (2.2), altruistic behaviours are always absolute cooperative behaviours when compared to neutral individuals defining the origin of the reference system (see figure 2.1, although one of them is more cooperative and less selfish than the other. It seems thus necessary to address the behavioural roots that lead to PD. In the next section I show that, whenever one of the individuals is a neutral one, two different PD's arise, one in which the cooperator increases the social goods above zero, another one in which the defector decreases them below zero.

2.4 Two prisoner's dilemmas: Altruists, free-riders and parasites.

The PD may represent two different situations, one related to social goods formed by cooperation, another to social goods created by refraining from conflict [66]. One may prove this using a free-rider (passive, neutral individual) to define the null point of the reference system (figure 2.1); then, altruists that pay a cost c_a to give a benefit $b_a > c_a$ to the co-player are more cooperative and less selfish, creating social goods that increase the mean population fitness at a cost to themselves, while if compared to parasites that pay a cost c_p to parasitise a fitness amount b_p from the co-player, free-riders are cooperative individuals (relative and absolute). In this case the social good is the non-competitive environment created by free-riders, while parasites decrease the mean population fitness. In short:

$$\begin{array}{ll} \text{Altruists:} & \text{Pay } c_a\text{, give } b_a \text{ to the co-player.} \\ \text{Free-riders:} & \text{Receive the action of the co-player.} \\ \text{Parasites:} & \text{Pay } c_p\text{, parasitise } b_p \text{ from the co-player.} \end{array} \tag{2.4}$$

The interaction matrices determined by altruists and free-riders, and by free-riders and parasites

$$\begin{array}{l|cc} \text{(a)} & \text{C} & \text{D} \\ \hline \text{C (altruist)} & b_a - c_a & -c_a \\ \text{D (free-rider)} & b_a & 0 \end{array} \qquad \begin{array}{l|cc} \text{(b)} & \text{C} & \text{D} \\ \hline \text{C (free-rider)} & 0 & -b_p \\ \text{D (parasite)} & b_p - c_p & -c_p \end{array} \tag{2.5}$$

determine a PD according to equation (2.3) whenever

$$b_i > c_i > 0 \tag{2.6}$$

Although in recent years some evolutionary game theorists have carried out work on the study of cooperation using generic payoffs T, R, P, S, most work on the evolution of altruism has focused on the study of altruists vs. free-riders. Specifically, most mechanisms found for the evolution of cooperation refer to the evolution of altruism. Thus, we may ask ourselves if this rules work in the free-rider vs. parasite case.

2.4.1 Mechanisms promoting cooperation in the free-rider vs. parasite case

Some of the mechanisms for the evolution of altruism in populations of altruists and free-riders require [65]

$$q > c_a/b_a \tag{2.7}$$

where q is a constant related to the mechanism. For direct reciprocity q is the probability of playing a next round with the same player, for indirect reciprocity it is the probability of knowing the reputation of the other individual, and for kin selection $q = r$ is the genetic relatedness.

The previous rule (equation (2.7)) makes cooperation –at least– evolutionary stable [65,82], i.e. altruists resist invasion attempts by free-riders, but, do the mechanisms for the evolution of altruism work for the evolution of non-aggressive societies (i.e. the free-rider vs parasite case)? In order to answer to this question, note that, if the evolutionary dynamics of the two cases are identical for some parameters combination, the result must be the same. In appendix 2.A I address this question for the case in which the evolutionary dynamics depends either on the difference between individual payoffs, or between individual and mean population payoffs. I find equations (2.17), which applied to the altruist vs. free-rider and free-rider vs. parasite cases (equations (2.5)) results in

$$b_a = b_p \tag{2.8}$$

$$k = \Delta b_a = c_p. \tag{2.9}$$

Using the previous equations, we may write equation (2.7) in terms of the parameters referring to the parasite vs. free-rider case. Then, the mechanisms for the evolution of non-aggressive free-riding societies require

$$q > 1 - c_p/b_p. \tag{2.10}$$

Thus, cooperation is enhanced whenever the costs for defecting increase or its benefits decrease.

Mechanisms for the evolution of cooperation based on structural properties –group selection, kin selection, network reciprocity– work for the free-rider–parasite dilemma without modification. However, some of the mechanisms for the promotion of altruism require conditional behaviours, i.e. altruists may decide not to pay the cost in relation to some previous information about the co-player, and thus yield no benefit to the free-riders. For these mechanisms to work in the "non-aggressions dilemma", when the active individual paying the cost is the parasite, free-riders would need the development of either some defence ability to stop the losses (at least partially), or some ability to act as a parasite when interacting with such individuals. This would increase the assortment between free-riders [14, 83, 84], giving them the opportunity to enjoy a non-competitive environment, and reject parasites in it. It seems thus plausible that punishment directed towards parasites evolved in nature parallel to emerging conflict-avoiding animal groups or societies, in order to ensure such free-riders assortment, which matches the observations in nature of punishment of thieves (parasites), and the few punishment observed directed towards lazy but non-aggressive individuals [78].

Note to finish that equation (2.9) requires k to equal the synergistic benefit ΔB_s produced by the altruistic action, and the cost of the selfish act. This excludes the possibility of having the same situation in the altruist and parasite cases if $k = 0$, as according to equation (2.6) $c_p > 0$. Thus, even if we can compare both situations and the dynamics might be identical, they are fundamentally different, one representing social goods formed by restraining from conflict, i.e. not decreasing others individuals fitness (free-riders vs. parasite), and the second representing goods formed by cooperation (altruist vs. free-riders), which increase the mean population fitness.

Furthermore, every time altruists interact, they produce a benefit which is bigger than the cost paid, i.e. create a positive synergistic benefit. However, two parasites interacting together create a net cost, i.e. a negative synergy. In order to have the same evolutionary dynamics in both cases, the negative synergistic effect has to be compensated with a higher baseline fitness (equation (2.9)). This suggests that, although in a PD cooperators always do worst than defectors, populations of altruists (active cooperators), might have some advantage over parasites (active defectors) due to the fact that the first create positive synergistic effects while parasites create a negative synergy.

As I show in the next section, in well-mixed populations of altruists, free-riders, and parasites, the combination between the first two allows for their survival in higher levels than predicted by the mutation terms, providing a first step towards the emergence of cooperation.

2.5 Generalised prisoner's dilemma

The altruist and parasite strategies are defined in reference to a passive or neutral one, called free-rider. The generalised PD matrix including interactions between the three strategies is in this case

$$\begin{array}{c|ccc} & \text{Altruist} & \text{Neutral} & \text{Parasite} \\ \hline \text{Altruist} & b_a - c_a & -c_a & -b_p - c_a \\ \text{Neutral} & b_a & 0 & -b_p \\ \text{Parasite} & b_a + b_p - c_p & b_p - c_p & -c_p \end{array} \tag{2.11}$$

Note that any two strategies in this matrix determines a PD if $b_i > c_i > 0$ (for altruists vs. parasites this condition may be relaxed).

2.6 Altruist–free-riding assortment to survive parasitism

In any mixed population of two strategies determining a PD, defectors perform better than cooperators, i.e. have higher fitness, and thus the final population will consist only of defective individuals. Let us see what happens when the three strategies are mixed in the population. For this purpose I will assume that the replicator dynamics hold, i.e. the variation of x_i, the fraction of i individuals in the population, follows the equation,

$$\frac{dx_i}{dt} = x_i(f_i - \overline{f}) \tag{2.12}$$

where f_i is the payoff of strategy i and $\overline{f}$ is the mean population payoff.

The payoffs for altruists, free-riders (neutral individuals) and parasites in a well-mixed population with proportions of individuals x_i, $i = a, n$ or p, are

$$\begin{aligned} f_a &= 1 - s + s[x_a b_a - x_p b_p - c_a] \\ f_n &= 1 - s + s[x_a b_a - x_p b_p] \\ f_p &= 1 - s + s[x_a(b_a + b_p) + x_n b_p - c_p]. \end{aligned} \tag{2.13}$$

where the selection strength s accounts for the relative effect of the interactions on the fitness of individuals (for $s = 0$ the game is irrelevant; for $s = 1$ the game determines the entire fitness).

As $x_a + x_n + x_p = 1$, we can describe the system dynamics with two replicator equations. We will use those for altruists and parasites. The replicator equations are

$$\begin{aligned} \tfrac{dx_a}{dt} &= s x_a[(b_a x_a - c_p)x_p - (1 - x_a)c_a], \\ \tfrac{dx_p}{dt} &= s x_p[x_a(c_a + b_a(x_p - 1)) + c_p(x_p - 1) - b_p(x_a + x_p - 1)], \end{aligned} \tag{2.14}$$

and the rest points (x_a, x_p) for such dynamics are (0,0), (0,1), (1,0), corresponding to homogeneous populations of one of the strategies. However, as it can be observed in figure 2.2, the dynamics leads to populations of parasites whenever the initial conditions include individuals of all types.

The situation changes drastically if mutations appear. In this case, if the cost associated with altruism is not too big, and the one associated with parasitism is big, the dynamics leads to coexistence of the three strategies, with fractions of altruists, free-riders and parasites approaching 1/3 for high mutation rates (figure 2.3(c)) or extreme costs ($b_a \gg c_a, b_p \approx c_p$, figure 2.3(f)).

One observes that decreasing altruists costs increases slightly the fraction of altruists and appreciably that of parasites (figures2.3(b),(d)), while increasing costs for parasites increases the fraction of altruists and free-riders in the population (figures2.3(b),(e)), and thus the mean cooperative level. Decreasing altruists costs and increasing costs of parasites increases greatly the levels of cooperative strategies (free-riders and altruists) in the population (figures2.3(b),(f)).

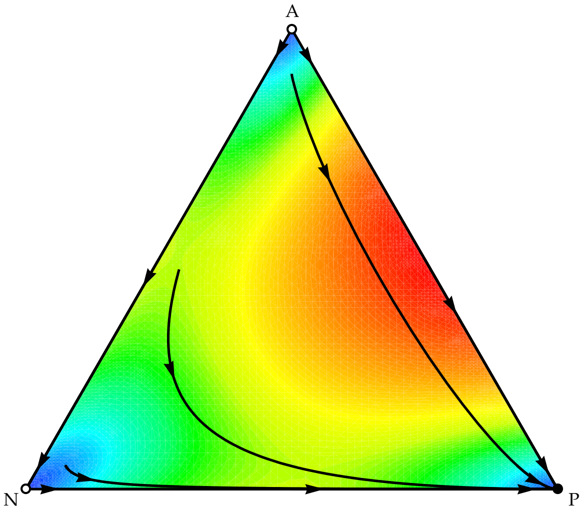


Figure 2.2: *Replicator dynamics in well-mixed populations (mean field limit) of altruists (A), free-riders (N) and parasites (P) without mutations. The simplex represents the fractions of individuals in the population; it shows the* $x_a + x_n + x_p = 1$ *plane in the three dimensional space determined by the fractions of strategies: The corners represent homogeneous populations of the corresponding individual while any other point represents mixed states. Colours correspond to different speeds* dx_i/dt*: red for the fastest, blue for the slowest. The evolutionary dynamics leads to homogeneous populations of parasites, the dominant strategy, where the fitness of any individual is* $-c_p < 0$*. This represents the worst tragedy of the commons, as homogeneous populations of free-riders possess null fitness, and populations of altruists have* $b_a - c_a > 0$ *(note that these quantities might be seen as variations on a baseline fitness). Parameters: Altruist and parasite benefits* $b_a = b_p = 2$ *and costs* $c_a = c_p = 1$*; selection strength* $s = 1$*. Images obtained using a modified version of the Dynamo Package [85].*

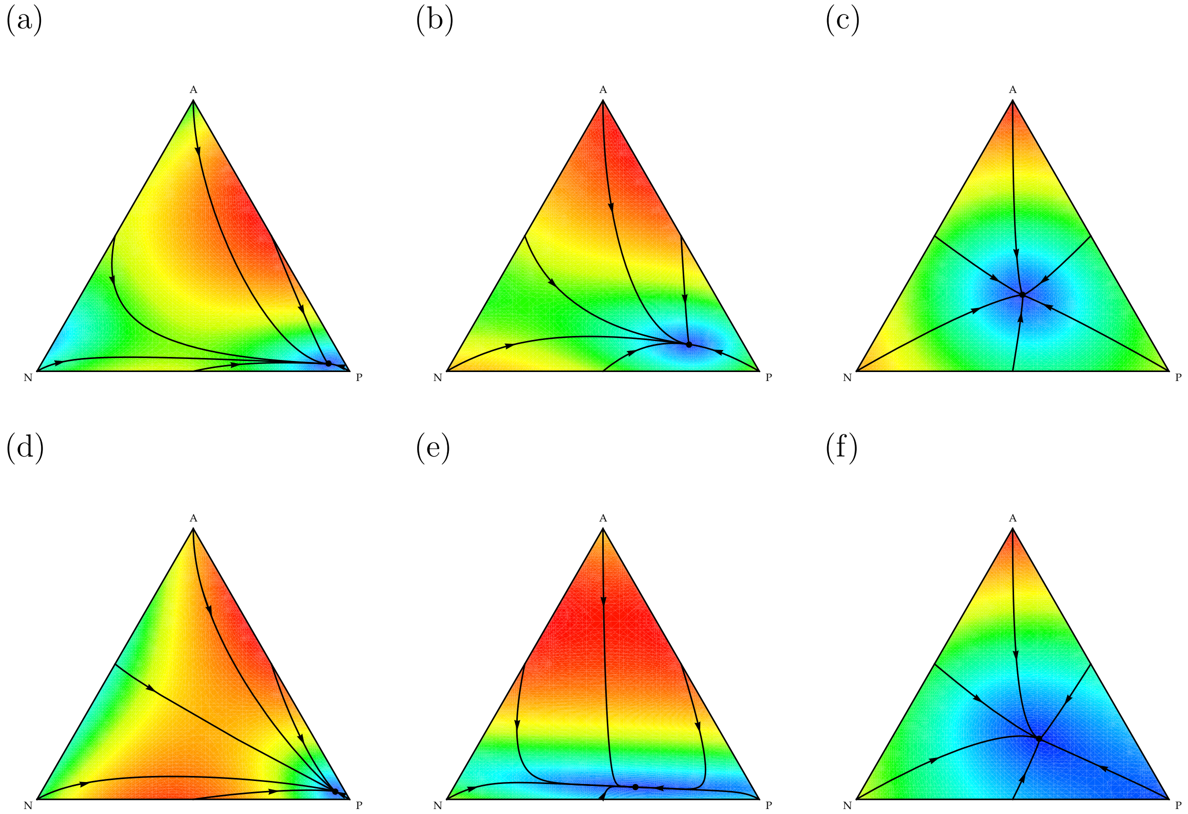


Figure 2.3: *Replicator dynamics in well-mixed populations of altruists (A), free-riders (N) and parasites (P) with mutations. Unexpectedly, altruist and free-rider individuals survive in higher proportions than expected by the mutation rate. Increasing the mutation rate increases the fractions of altruists and free-riders in the fixed point, as shown in (a)-(c). Decreasing altruists costs and increasing parasites costs favours altruism, as shown in (d)-(f), which have equal mutation rate as (a). Parameters:* $b_a = b_p = 2$, $s = 1/(1 + c_a + b_p)$, *which ensures non-negative payoffs, (a)-(c)* $c_a = c_p = 1$, *(a)* $\mu = 0.05$, *(b)* $\mu = 0.15$, *(c)* $\mu = 0.45$; *(d)-(f)* $\mu = 0.05$, *(d)* $c_a = 0.05$, $c_p = 1$, *(e)* $c_a = 1$, $c_p = 1.95$, *(f)* $c_a = 0.05$, $c_p = 1.95$.

The coexistence found cannot be explained by the mutation term alone; the presence of altruist and free-rider individuals allows for both of them to survive to the invasion of parasites, which does not happen whenever any of such strategies is mixed only with parasites. This result resembles the speciation transitions found in other models (not PD's), where evolution leads to coexistence of individuals differing in their cooperative levels [86, 87]. Thus, although free-riders lead altruism to extinction, and parasites lead free-riders to extinction, the presence of both free-riders and altruists provides an escape from the worst of the tragedies of the commons, i.e. populations where all individuals are parasites decreasing the fitness of any other individual, and where the mean population fitness decreases to its minimum value below zero.

2.7 Discussion

2.7.1 Remarks on the definitions

At the beginning of the present chapter I stated a relative definition of cooperation and selfishness, and avoided commentaries of whether cooperation is intentional or unintentional. The definition of cooperation in this way includes by-product mutualism; this situation might be regarded as a case of unintentional cooperation, which some authors have claimed to be on the limit of the scope of cooperation [67, 79], and which is important to understand the emergence of stable ecosystems and other selective units [1] from cooperative interactions, independently of their intentionality.

As an example, an elephant excreting dung is acting beneficially for itself, and for beetles feeding on such dung. Some authors argued that such behaviour is out of the scope of cooperation, as the situation is a one-way byproduct benefit, and the elephant behaviour does not deviate from the behaviour found in the absence of beetles, which in this case represents the null point [67,72,79]. However, it is known that baby elephants eat other elephants dung in order to obtain some bacteria that feed on it, and which they need to digest the vegetation present in the savannahs and jungles. According to the same reasoning, if an increase in dung leads to an increase of such bacteria, which in turn allows elephants to produce more dung, this second situation might be classified as cooperation.

The provided definition explicitly states that cooperation must not be forced. Other authors require it to be voluntary to prevent some exploitative or slaver behaviours and acts to be regarded as cooperative, as food in exchange for work or forced starvation otherwise, which might be found in the wrongly-classified as mutualistic interactions between ants and aphids, where ants take care of aphids as far as they provide them with food, but kill them otherwise. Requiring cooperation not to be forced allows for coherence with this argument, as well as with those in the previous paragraphs for including non-intentional behaviours.

Cooperative acts may be carried out in big groups [80], where one action has many simultaneous recipients. According to the definition, we might talk about cooperative acts of one individual directed to another, as it might happen that the action of an individual has non-negative effects and negative effects on different individuals at the same time (suppose the elephant dung falls on an ants nest and blocks the entrance). The act would be cooperative for some (beetles, bacteria), while non-cooperative for the rest (ants), and only classified as cooperation between bacteria and elephant.

Furthermore, even if intentionally directed towards cooperation and voluntary, cooperative acts may fail to produce the expected benefits [64]. In this case, the long term behaviour, influenced by the probability of success, can be used to define it as cooperative or not. Note that with this extension of the definition, acts that cannot reduce other individuals fitness are always regarded as cooperative, even if they always fail to provide benefits.

2.7.2 Discussion on the null point

Along the text I have extensively used the PD to illustrate the cases of cooperation by restraining from conflict (free-riders vs. parasitism), and that of social goods formed by cooperation (altruism vs. free-riding). However, it is good to remark that both of them, as well as the definition of cooperation provided at the beginning, are relative definitions, as they refer to fitness changes in reference to a certain behaviour, which determines the null point. In the PD examples along the text, the reference used is a passive, neutral individual, called free-rider, as it produces no fitness variations on others, nor on itself, but receives the actions of the co-players.

Whenever the null point is determined by a passive behaviour, it can be easily used as null point or reference. However, it might not be so easy to find such reference points in other situations, specially whenever all individuals are active, e.g. individuals which by refraining from reproduction reduce their own reproductive fitness and increase that of others would be altruists, while those that increase their reproductive rate and decrease the fitness of others would be parasites. However, in this case no fixed reference point can be established, as all individuals are actively reproducing and it might be the case that no fixed baseline fitness can be measured. In these cases the mean population fitness value might be used as reference.

Finally, I have analysed using computer simulations the dynamics when three strategies (altruists, free-riders and parasites) are present, and I have shown that coexistence is possible in proportions beyond those predicted by the mutation rate, even when all interactions are PD's irrespective of the two strategies involved, one of the three strategies –parasites– may be regarded as an active super defector favoured by evolution, and no previous mechanism for cooperation is present. This shows that, whenever parasites are present in a population or ecosystem, the synergy between non-competitive environment supported by free-riders and benefits provided by altruists allows for the survival of both of them, providing for an evolutionary explanation for why individuals in nature do not punish laziness, but they do punish parasitism: if lazy non-aggressive individuals were not present, cooperative populations might be easily extinguished by parasites, leading to the worst of the tragedies of the commons, while the combination of free-riders and altruists provides a mechanism for their survival, and a first step for the emergence and rise of altruistic, non-aggressive societies.

Appendices

2.A Reference strategies, dynamical equality and distinguishability

If the evolutionary rule depends on the payoff difference between strategies, as it happens for some local rules [88, 89], or between the strategy's payoff and the mean population fitness, as for the replicator equation [90], the dynamics is invariant under the addition of a constant to all payoffs (see Sec.1.B). Suppose now that there are two different situations, one represented by payoff matrix Π, corresponding to equation (2.1), the other one by Π'. We may add a constant k to the second one, and find the necessary conditions to have equal dynamics, i.e. find the parameters that fulfil

$$\Pi = \Pi' + k. \tag{2.15}$$

By doing so, one finds

$$\begin{aligned} \Delta_s &= \Delta'_s \\ \Delta_r &= \Delta'_r \\ k &= A_r - A'_r + A_s - A'_s \end{aligned} \tag{2.16}$$

This conditions tell us when the dynamics of the two situations are indistinguishable given the previous assumptions, and thus cannot be used to tell the difference between both scenarios. Note that if we are dealing with direct interactions between individuals, which produce a fitness change in actor and recipient, and fitness is additive, then equations (2.2), (2.3) must hold, which is consistent with equations (2.16).

Now, suppose that we are dealing with the more interesting case in which one of the strategies is present in both situations, and might be used as reference to establish a relative scale of cooperativeness. If this strategy is the cooperative one in both scenarios, then the only possibility that fulfils equations (2.16) is that the defective strategy is also the same, and $k = 0$. Both situations are then not only indistinguishable by looking to the dynamics, but the same indeed. There is a more interesting case, however, when the strategy present in both scenarios is regarded as defective in one case, as cooperative in the other, i.e. $B_s = A'_s, B_r = A'_r$. In this case, this strategy may be used as reference. Equations (2.16) reduce to

$$\begin{aligned} 2B_s &= A_s + B'_s \\ 2B_r &= A_r + B'_r \\ k &= \Delta_s + \Delta_r > 0 \end{aligned} \tag{2.17}$$

The fact that $k > 0$ comes from the restrictions introduced in equation (2.3), both for PD and HG. This has an important implication: Even if the dynamics of two situations are identical (given the assumptions above), we may always measure a baseline fitness difference k to tell them apart. Furthermore, the equations tells us the relationship between cooperativeness and selfishness degrees (Δ_r, Δ_s), and difference in mean population fitness k.

It might not seem really surprising the fact that we can always find a difference when the systems are not equal. However, the fact that we may quantify such difference measuring differences in baseline fitness, and relate it to higher or lower cooperativeness and selfishness of the interactions between the different behaviours or species, allows us to define a relative scale for cooperation.

2.B Some definitions along the literature and commentaries on them

- "*The degree of co-operation observed in nature varies along a continuum, from the one extreme of severe parasitism/virulence to the other extreme of mutual benevolence. [. . .] An observed level of co-operation requires evolutionary explanation only in so far as that level deviates from a level representing the "null" point for the species interaction, and calculation of this null point is somewhat subjective. [. . .] Our designation of a phenotype as cooperative need only imply that it is more co-operative than some feasible alternative.*" [79]

  This definition refers to relative cooperation.

- “*Cooperation is an outcome that –despite potential relative costs to the individual– is ”good” in some appropriate sense for the members of a group, and whose achievement requires collection action. But the phrase ”to cooperate” can be confusing, as it has two common usages. To cooperate can mean either: (1) to achieve cooperation–something the group does, or (2) to behave cooperatively, that is, to behave in such a manner that renders the cooperation possible (something the individual does), even though the cooperation may not actually be realised unless other group members also behave cooperatively.*” [80]
  The difference between cooperative behaviour and cooperation is clear in this definition.

- “*The key distinction we wish to make is between cooperation (an interaction between two or more individuals) and cooperative behaviour (an action or actions taken by a single individual). [. . .] We define cooperation as an interaction between individuals that results in net benefits for all of the individuals involved*” [70]
  This definition is slightly more restrictive than the one in the main text, though both overlap if one accounts for peace as a social good or benefit.

- Referred to lifetime consequences: “*Cooperation: A behaviour which provides a benefit to another individual (recipient), and which is selected for because of its beneficial effect on the recipient*” [67]
  This definition mixes cooperation, which is something carried out by at least two interacting individuals (see the definition by Dugatkin above), and cooperative behaviour, i.e. individual behaviour which allows for cooperation.

- “*- Cooperative behaviour: a behaviour that on average increases the fitness of a recipient and which is under positive selection if it on average increases the inclusive fitness of the actor via direct fitness benefits. [. . .] - Altruistic behaviour: a behaviour that on average increases the fitness of a recipient and which is under positive selection if it on average increases the inclusive fitness of the actor via indirect fitness benefits. [. . .] - Cooperation: two (n) partners increase on average their direct fitness due to the interaction.*” [72]
  The first definition above accounts always for cooperative behaviours (behaviours

that, when interacting together, create direct fitness benefits for all interacting individuals). However, the above definitions are blurry in some situations, as when behaviours are counter-selected, e.g. if an actor provides a benefit to a recipient, and the inclusive fitness of the actor increases due to direct fitness benefits, but less than the average increase in the population, it would be under negative selection, and the above definition cannot be applied to call it cooperative or not. Furthermore, the definitions above are not self-consistent: a behaviour which provides benefits to the recipient, which produces negative direct fitness effects on the actor, and which is selected for due to positive inclusive fitness effects, would be called altruistic but not cooperative according to the above definitions.

Part II

Resource constraints in the evolution of cooperation

Since 1859, when Darwin published the theory of natural selection [91], the question on how cooperation is established and evolves has centred the attention of many scientists, as it seems to contradict the principle of fitness self-maximisation. The first mechanism found to promote cooperation, kin selection [11, 12], states the conditions that make beneficial from a genetic point of view to help individuals sharing your own genes, even if it is costly for yourself. More recent studies pay attention to how cooperation evolves in the absence of genetic relatedness. Two frameworks are widely used for this purpose.

The first framework is evolutionary game theory (EGT) [15, 16, 90], which models the interactions from an individual point of view, regarding to the strategies of the interacting agents, but usually not including ecological dynamics; the second framework –called here the ecological, resource based or just resources framework– includes Lotka-Volterra models and resource-ratio theory [92–94]. This framework models the ecological systems as a whole, including environmental features, as the existence of limiting resources, but does not usually regard to the microscopic interaction dynamics.

As explained in section 1.6, the evolutionary game theoretical framework allowed to find mechanisms for the evolution of cooperation. However, most models used implicitly assume that the limitation of resources does not modify payoffs, and thus does not affect directly the dynamics. On the other side, recent studies using the ecological framework have shown that the limitation of resources may play an important role in the evolution of cooperation [95–97], and might be important to explain cooperative behaviours in bacteria, plants and animals. As an example, the trade off between rate and yield of metabolic pathways, as that of aerobic and anaerobic bacteria, has been proposed to help cooperation thrive in a two dimensional world [95,96], and as a possible mechanism for the emergence of undifferentiated multicellularity. Furthermore it has been shown that if trade of resources is possible [97], long term relationships allow cooperative plants to evolve.

In chapters 3, 4 and 5 I present some models aiming to ascertain some implications of the limitation of resources in the survival of cooperation. The stylised models are a first step towards this understanding, where the dynamics of the system is ruled by a limiting resource necessary for reproduction. Two cases are studied: One in which the limiting resource is also necessary for survival –this is dealt in chapter 3 – and a second one, where it is not necessary for survival –treated in chapter 4. These agent-based models are shown to fulfil an a priori PD game, but in some conditions the limitation of resources allows for the survival of cooperation, thus providing a scenario not previously addressed in the evolutionary game theoretical literature, where resource limitation is usually assumed just to impose a constant population size. Chapter 5 provides simplified analytical models for the agent based models studied in chapters 3 and 4.

Chapter 3

Resources necessary for reproduction and survival

Summary

In this chapter I first present a model of a population of individuals whose strategies fulfil a PD and where a limiting resource is necessary for their survival and reproduction. In the ideal situation where all individuals possess resources, the interactions between cooperators and defectors leads to a PD –as determined by their strategies– and thus cooperators extinguish. Remarkably enough, the dynamics changes when resources are limited: the game is modified and a region of dominance of cooperation appears.

After that, I present the equations that connect resources and fitness as defined in evolutionary game theory, and test the validity of the replicator equation [18] to predict the mean time evolution of the system, opening a way to connect resource based models and evolutionary game theory.

3.1 A game theoretical model including resource consumption

The model presented here includes three basic features of alive organisms under natural selection: reproduction, interactions and death. It consists of an agent based model of a well-mixed population of self-replicating individuals that receive resources from the environment and exchange resources during interactions. Each individual is represented by its internal amount of resources and its strategy, namely to cooperate or defect: defectors parasite resources from the interaction partner at a cost to themselves, cooperators do not. In order to maintain living functions, every time step individuals dissipate an amount of resources E_l. If an the amount of resources of an individual surpasses a certain bound, E_s, it splits into two identical copies with half its internal amount of resources; if it is depleted, the individual dies. Neither genetic relatedness nor special abilities are assumed. Next I provide the details of the model.

3.1.1 Environment and resource allocation

In order to study the influence of resource limitation in the evolution of cooperation, let's assume for simplicity that the environment supplies resources at a constant rate. Every time step, the environment generates an approximately constant amount of resources E_T to be shared among all individuals in the population. Each individual receives a random portion E_p uniformly distributed on the interval $[0, 2E_T/N]$, where N denotes the number of individuals in the population. In this way, we allow for variations in the resource intake of individuals while keeping an approximately constant total yield E_T in the population. Other resource assignation methods were also tested providing the same results, as shown below.

In contrast to most models, where the number of individuals in the population is kept constant, in the present one it evolves in time and its equilibrium value depends on the composition of the final population. The reason for this is that, in equilibrium, the resources that enter the system compensate the ones that are dissipated. Since defectors dissipate resources at a higher rate than cooperators (see next subsection) the amount of individuals that the environment is able to sustain depends on the fraction of defectors in the final population. In the simple case when it only contains cooperators, the equilibrium size is $N = E_T/E_l$.

3.1.2 Interactions

The defective strategy is characterised by two quantities: the cost spent E_c for getting a reward E_r from the co-player. Both quantities are inherited without mutation and supply the interaction payoffs whenever the internal resources of the two players surpass the corresponding values, E_c and E_r. For simplicity, interactions are considered as simultaneous, though results are the same for not simultaneous interactions (see Appendix 3.A) If resources were unlimited, the internal resources of individuals would be high and those values would describe the amount of resources actually exchanged, leading to a payoff matrix

$$\begin{array}{c|cc} & \text{C} & \text{D} \\ \hline \text{C} & R = 0 & S = -E_r \\ \text{D} & T = E_r - E_c & P = -E_c \end{array} \tag{3.1}$$

which fulfils the requirements for a simplified prisoner's dilemma between parasites (D) and pacific individuals (C) as in equations (2.2)-(2.3), whenever $E_r > E_c > 0$; note that the reproduction rate is proportional to resource intake and whenever no resource constraint is influencing the game, evolution will lead to homogeneous populations of parasites.

However, if resources are limited, individuals may posses resources below E_r and E_c. We thus assume: (i) if the internal resources of a defector are smaller than the cost E_c, it does not pay the cost nor receives the reward; and (ii) if the interaction partner of the defector has internal resources below E_r, the defector extracts the entire amount of resources of the co-player. Some modifications of the rule were also tested, such as allowing parasites to spend lower costs than E_c if their internal resources are smaller than this amount and then getting proportional rewards; they yield similar results to those presented below.

Interactions with cooperators whose internal resources are lower than E_r make the average reward actually obtained by defectors E_r' fall below the value expected from their inherited strategy, $E_r' < E_r$. Since E_r' depends on the distribution of resources within the population of cooperators, which in turn depends on the action of defectors, its value is not known a priori. The change in E_r' modifies accordingly the average net reward got by defectors in an interaction $\Delta E' = E_r' - E_c$. Therefore, resource limitation modifies the interaction payoffs. If eventually $\Delta E'$ became negative, the game would turn into a Harmony Game and cooperation would become dominant (see chapter 2). Because E_r' is not known, but determined by the dynamics, it turns out quite difficult to predict analytically the fate of the population. Instead, we have performed extensive numerical simulations.

3.1.3 Numerical simulations

Simulation runs started with population compositions ranging from 5% to 90% of cooperators, and sizes close to the estimated equilibrium values for such proportion of individuals. The initial internal resources of individuals was taken from a uniformly random distribution on the interval $[0, E_s]$, whereas other initial distributions have been analysed yielding the same results. The value of E_T was chosen to ensure big populations ($N \sim 10^4$ individuals) in order to avoid finite size effects while keeping feasible simulation times. The amount of resources required for splitting was taken $E_s = 1000$.

The dynamics is implemented as follows. Every interaction time step, six individuals are chosen at random: (a) two of them receive an amount of resources E_p from the environment, independently calculated for each one, (b) two of them interact and (c) two of them dissipate an amount of resources E_l. This process is repeated $N/2$ times for, in average, all individuals to have captured resources, interacted, and dissipated resources, once. This defines one time step of the simulation. Simulations run a maximum of 1000 time steps and stop if a homogeneous population is reached before.

The latter dynamics describes a completely asynchronous updating method with overlapping generations in order to prevent spurious correlations (see [98]). Note that asynchronous updating mimics the dynamics observed in nature where, with few exceptions, individuals do not feed, interact and reproduce at the same time, but with fixed mean ratios between the different actions (we are excluding seasonal reproduction in this way). Other updating methods were also tested obtaining the same results (see Appendix 3.A).

Finally, let us note that the model presented here contains 5 parameters. One of them, say E_s, sets the scale of resources, and E_T only affects the number of individuals in equilibrium (provided it is big enough), and not its composition. Therefore, the fate of the population in the model is characterised by three parameters: the a priori defector's cost E_c and net benefit $\Delta E = E_r - E_c$, and the amount of resources dissipated by the individuals to keep alive E_l. We have performed simulations covering the whole parameters space.

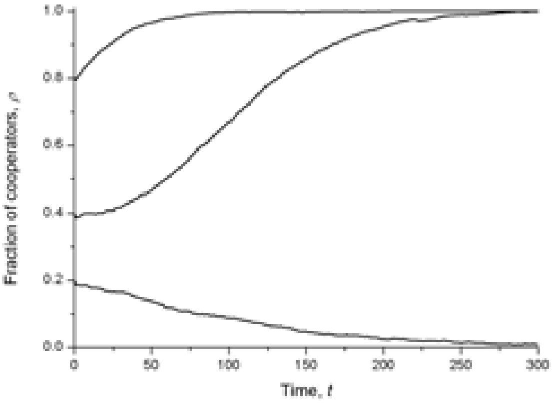


Figure 3.1: *Time evolution of the fraction of cooperators for several parameter values and initial conditions of the model. The genetically determined strategies of the individuals fulfil a simplified PD (see equation* (3.1)*). However, the limitation of resources may modify the payoff structure of the interactions, allowing cooperators to invade the entire population. Stable coexistence is not observed. While the invasion capacity of cooperation depends on its initial frequency in some situations, this dependence is very small for small* E_l*, being cooperation the dominant strategy in many situations (see figure 3.2).*

3.2 Peace or parasitism

3.2.1 Agent based simulations results.

Simulations show that, when resources are limited, there exist situations in which selfish individuals die out despite the genetically inherited strategies determine a PD under unlimited resources (figure 3.1).

The dynamics leads to two different regions in the parameter space: one where the system ends up in a population of only cooperators at essentially large costs E_c, and another with a population of defectors only (figures 3.2). The biggest regions of cooperation are found for dissipation of resources around $E_l \sim 0.4E_s$, while increasing or decreasing it diminishes the region of cooperation. There is little dependence on the initial fraction of cooperators; the bigger the fraction, the bigger the region of cooperation. This dependence increases as E_l approaches the splitting bound E_s. However, except for extreme cases of very high resource dissipation, $E_l \sim E_s$, and very low initial fraction of cooperators, $\rho_{C0} < 0.1$, one observes regions where cooperators invade the entire population.

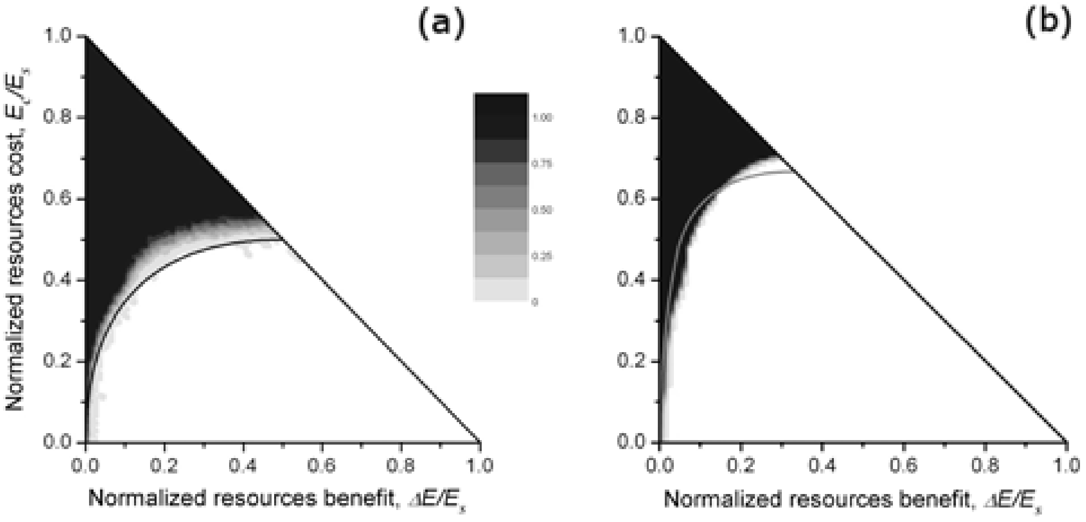


Figure 3.2: *Regions of cooperation and defection. The final fraction of cooperators ρ is displayed as a function of the parasite strategy, i.e. resources cost (E_c) and net benefit ($\Delta E = E_r - E_c$). In black, the fraction of cooperators is 1; in white it is 0. Whenever costs and net benefits are small enough, i.e. when the limitation of resources does not influence the payoffs, defectors invade the entire population, as expected for a PD. However, one observes a well defined region where cooperation overcomes defection. In this region the initial PD is modified by the limitation of resources, which leads to negative net benefits for defectors and allows the system to evolve towards homogeneous populations of cooperators. Solid lines show the analytical prediction for the frontier between both regions. In (a) the dissipation of resources for keeping alive is $E_l = 0.4E_s$; in (b) $E_l = 0.02E_s$. In all cases, simulations start with a $\rho_0 = 0.5$. Results have been averaged over 50 realisations.*

Modifications in the updating method as well as in the definitions of interactions and resource allocation were also tested: distributing the resources in identical portions among all individuals $E_p = E_T/N$; giving portions of a constant size E_p with a probability $p = E_T/(NE_p)$; allowing defectors to get a proportional reward to the cost spent in case their internal amount of resources was lower than E_c; or defining not simultaneous interactions (see Appendix 3.A). The results obtained in all cases showed similar or slightly bigger regions of cooperation. In the case in which individuals may spend lower costs than E_c and get proportional rewards, the regions of cooperation do not depend on the initial fraction of cooperators.

Some modifications in the updating were tested too, as distributing the resources in portions $E_p = E_T/N$, giving portions of a constant size E_p with a probability

$p = E_T/N$, allowing defectors to get a proportional reward to the cost spent in case their internal amount of resources was lower than E_c, or defining not instantaneous interactions. The results obtained in all cases showed similar or bigger regions of cooperation. In the case in which individuals may spend lower costs than E_c and get proportional rewards, the regions of cooperation do not depend any longer on the initial fraction of cooperators.

3.2.2 Analytical description

The genetically determined prisoner's dilemma structure of the resource exchanges among cooperators and defectors, which matches the real resource exchanges in the absence of limitation of resources, may lead to the prediction that selfish individuals have a larger resource intake than cooperative ones and thus reproduce quicker. However, as the simulation results show, the existence of a limiting resource modifies the outcomes of the interactions allowing unconditional cooperators to invade defectors in the case of a well-mixed population and with non-iterated interactions. In the following, I show analytical methods to explain such results and to model the dynamics of the system.

Depletion of resources and survival of cooperation

The invasive capability of cooperators when there is a limitation in the available resources is due to the subsequent distribution of internal resources in the population. This distribution of internal resources modifies the outcome of the interactions by lowering the average reward E_r' actually obtained by defectors from cooperators, because some cooperators have internal resources below E_r. If the average reward E_r' turns to be smaller than the defector's cost E_c, the net reward $\Delta E' = E_r' - E_c$ becomes negative and defection is not favoured any more by natural selection. In this case the resource payoff matrix is modified and it is no longer a prisoner's dilemma, but a Harmony Game (see chapter 2). This is what happens in the regions where cooperation invades the entire population in figures 3.2.

Analytic expressions

As mentioned before, an exact analytical treatment of the model is quite difficult because of the interdependence of E_r' and the cooperator's distribution of internal resources. We next provide a quantitative analysis that allows for an estimation of the region in the parameter space where cooperation becomes dominant.

The condition for cooperation to outperform defection is

$$E_c > E_r' \tag{3.2}$$

i.e. the cost per interaction for the selfish individual must be bigger than the average amount of resources obtained from a cooperative individual. Let us call $P(E < E_r)$ the probability that a cooperator has an internal amount of resources lower than E_r. The mean payoff for a defector playing against a cooperator can be written as $E_r' = P(E > E_r)E_r + P(E < E_r)\bar{E}_r$, where $\bar{E}_r$ is the mean internal amount of resources of cooperators in the region $E < E_r$. This may be rewritten as

$$E_r' = E_r - P(E < E_r)(E_r - \bar{E}_r). \tag{3.3}$$

If the distribution of resources is known, one could derive from this equation the analytic expression for the region where cooperation is dominant. As an example, for the case shown in figure 3.2a the distribution of resources may be taken at a first approximation as uniform (see figure 3.3a). For uniform distributions, the mean amount of resources that selfish individuals steal from cooperators is $E_r' = E_r - E_r^2/(2E_s)$, which after a few calculations yields

$$E_c > (2E_s\Delta E)^{1/2} - \Delta E. \tag{3.4}$$

figure 3.2a shows that this approximation is in good agreement with simulation results. For other values of the dissipation of resources E_l the internal distributions cannot be approximated as uniform (figure 3.3b). Then, stepwise distributions are already good approximations to calculate the region where selfishness is suppressed (figure 3.2b).

3.2.3 Connecting resources and fitness

The usual framework in evolutionary game theory expresses the payoffs in terms of fitness, and assumes that the cooperative individual is the one incurring the costs. This

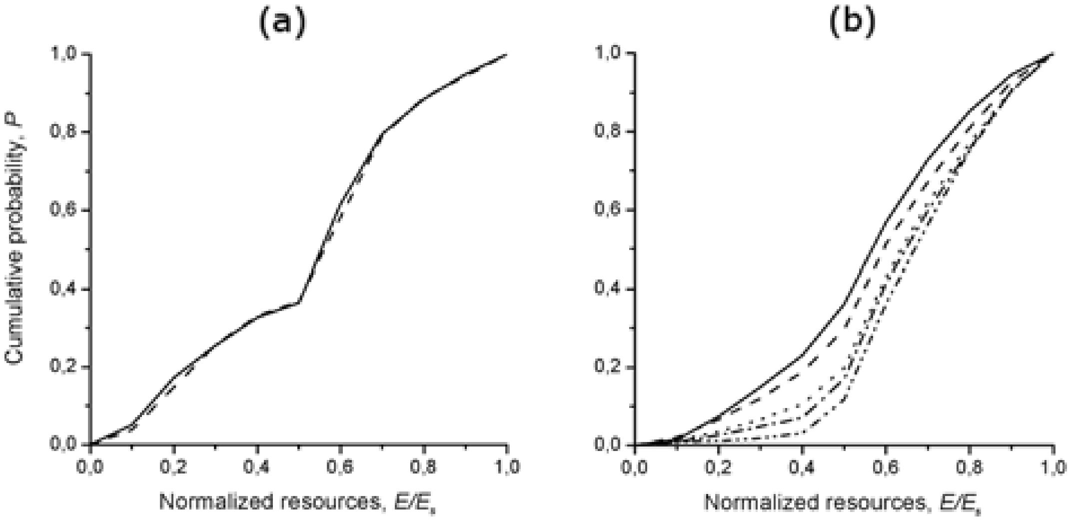


Figure 3.3: *Internal distribution of resources for cooperators. Cumulative resource histograms for parameter values close to the boundaries of cooperation and defection (see figure 3.2). In (a)* $E_l \approx 0.4E_s$ *and (b)* $E_l \approx 0.02E_s$. *In (a) the histograms do not depend on the point of the boundary chosen (only two points are displayed for clarity), and can be approximated by a straight line, i.e. a uniform distribution. This approximation is used to derive the analytical prediction shown in figure 3.2a. In (b) the histograms are point dependent. To derive the analytical prediction of the boundary in figure 3.2b a mean histogram was obtained and approximated by a stepwise distribution. This rough approximation is again in good agreement with the results.*

framework can be recovered in the resource scenario by comparing the fitness matrix, in which cooperators pay a cost c in order to provide a benefit b to the co-player, with the one in terms of resources (equation (3.5)), in a similar manner as done in chapter 2. To do so, let us notice that in the model, the greater the resource intake by an individual, the faster it reaches the splitting bound E_s and reproduces. Therefore, the resource income rate is proportional to the reproductive rate and may be translated into fitness. The matrixes in both scenarios and relationships obtained are

(a) Resources framework

	C	D
C	E_0	$E_0 - pE'_r$
D	$E_0 + p\Delta E'$	$E_0 - pE_c$

(b) Fitness framework

	C	D
C	$k+b-c$	$k-c$
D	$k+b$	k

(c) Relationship between both frameworks

$$b = apE'_r,\ c = ap\Delta E',\ k = a(E_0 - pE_c),\ \Delta E'/E_c = c/(b-c) \tag{3.5}$$

where a is the proportionality factor between resources and fitness and k a constant. Note that b, c are independent of such constant, and the cost to benefit ratios in both frameworks are independent of k, a and p.

In appendix 3.A we derive the values of the terms in equation (3.5)(a). As expected, the interaction terms are described by the cost E_c and the average rewards E'_r and $\Delta E' = E'_r - E_c$. All these terms, however, appear multiplied by the factor $p \equiv P(E_D > E_c)$, namely the probability that a defector actually performs a parasitic action. Naturally, being factor p in all terms of the payoff matrix, it does not modify the structure of the game (see appendix 3.A for more details); it only affects the temporal scale of the dynamics.

The relationships in equation (3.5)(c) can be used to check the validity of the replicator equation (equation (1.3)) on its evolutionary game theoretical form to describe the dynamics in the model [18]

$$\frac{d\rho}{dt} = \rho(\pi_c - \bar{\pi}) \tag{3.6}$$

where ρ is the fraction of cooperators, π_c their fitness and $\bar{\pi}$ the mean population fitness. According to equation (3.5), this equation writes

$$\frac{d\rho}{dt} = -a'\Delta E'\rho(1-\rho) \tag{3.7}$$

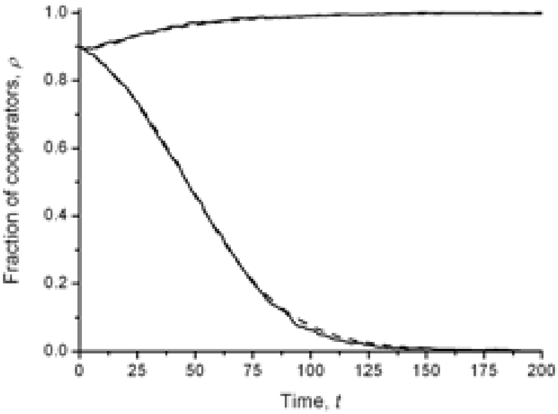


Figure 3.4: *Connection between resource and fitness frameworks and test of the replicator equation. The decreasing solid line shows the time evolution for simulations with* $\Delta E = 16$*,* $E_c = 1$*; in this case (*$Ec, \Delta E \ll E_s = 1000$*) the payoffs are not altered and the dynamics results in the extinction of cooperation, as expected for a well-mixed PD. The increasing line shows the time evolution in a region where the distribution of internal resources modifies the payoffs and drives the extinction of defectors (*$\Delta E = 16$ *and* $E_c = 161$*). In this case,* ΔE *must be substituted by* $\Delta E' = E'_r - E_c$ *in the replicator equation. Solid lines show the mean time evolution averaged over 20 realisations. Dashed lines show the analytical predictions by using the best fit value for parameter* a' *in equation* (3.7)*.*

with $a' = ap$. The factor $p = P(E_D > E_c)$ depends on the distribution of internal resources in the population of defectors. By assuming that stationary distributions are rapidly achieved (this is confirmed by simulations), the factors $\Delta E' = E'_r - E_c$ and a'can be approximated as constants. In our simulations we do not know these values in advance. However, good agreement between the replicator equation and the simulations can be observed in figure 3.4, where E'_r has been calculated according to equation (3.3), and a' has been obtained by a numerical fit using the simulation data.

However, as the genetically determined quantities (in the sense that they are fixed before starting the game) are the values of E_r and E_c related to the selfish strategy, which might be measured in experiments designed to avoid external influences on the payoffs, it would be useful to find a rule for the evolution of cooperation based only on these a priori determined quantities. Using the equations in equation (3.5) one may find the corresponding fitness values for these quantities associated to the parasitic strategy, namely $b = apE_r$ for the reward, $c = ap\Delta E$ for the cost. Then, writing the constant a in units of E_s equation (3.4) reduces to

$$b > (2apc)^{1/2} \tag{3.8}$$

This inequality is similar to previously found rules to describe the evolution of cooperation (see section 2.4.1). Indeed, the rules relating to kin selection [11, 12], direct and indirect reciprocity, network reciprocity and group selection can be written as: $b/c > 1/r$ [99]. Equation (3.8) suggests that, as a first order approximation, a general rule for the evolution of cooperation based on statistical analyses and including the effect of environmental or morphological constraints might be written as

$$b/c^S > (\lambda a)^S \tag{3.9}$$

where λ, S and a are constants related to the statistical properties of the system under study and the reproductive dynamics of the population.

3.2.4 Conclusions

We have analysed the influence of the limitation of resources in the evolution of cooperative behaviours in the case in which selfish individuals perform parasitic acts, and have shown that, although the genetically inherited strategies define a PD under unlimited resources, resource constraints may modify the structure of the game so that cooperation becomes the dominant strategy. Thus, resource limitation permits the survival of cooperation in well-mixed populations, without repeated encounters between the same two individuals and in the absence of either genetic relatedness, memory, or other special abilities. This suggests that the limitation of resources is an important element to be taken into account when studying the evolution of cooperation in simple entities, such as viruses, unicellular organisms or even plants, and makes the present results suitable for studying the evolution of cooperation in early evolutionary stages, and thereafter the associated transitions in evolution, as those from prokaryote to eukaryote cells or from unicellular to multicellular organisms. More generally, these results might be applicable to any system in which reproduction and death are ruled by the same limiting resource, and with the restrictions that the strategies are fixed before starting the game and that the benefits and costs for defecting are disassociated.

Two different frameworks were used in this chapter, the resources framework and the (evolutionary game theoretical) fitness framework (equation (3.5)). In the first one the selfish individuals pay the cost, while in the latter the cooperators are the individuals paying it. This might seem contradictory, however, selection is totally unaware of who is the individual acting and selects behaviours by the results of the actions. Therefore, as both matrixes determine the same outcome, a PD, there is no contradiction on it, and individuals that seem not to pay the cost in some situations might be seen as cooperators paying a cost in the fitness framework. Indeed, our simulations show that the dynamics in the model is well described by the replicator equation of evolutionary game theory both, when resource exchanges satisfy a PD so that cooperators die out, and also when resource constraints make cooperation dominant and defectors are extinguished.

Finally, we have found a simple rule for the evolution of cooperation based only on the fitness translation of the inherited strategies. The use of equations connecting resources and fitness may facilitate the design of experiments to test evolutionary game theoretical predictions and we hope they will help in establishing the necessary communication between evolutionary game theoretical researchers and experimental biologists, as well as to introduce more detailed behavioural and ecological features in the models, all of this in order to continue expanding our knowledge on how altruistic, mutualistic and parasitic behaviours evolved and gave rise to the diversity present in the natural world.

Appendices

3.A Payoff matrix calculation

The average payoff obtained by each player in a time step is calculated here. Interactions are defined as simultaneous between both players. Defectors pay a cost E_c to steal a maximum reward E_r from the co-player. Furthermore (i) if the internal resources of a defector are smaller than the cost E_c, it does not pay the cost nor receives the reward; and (ii) if the interaction partner of the defector has internal resources $E_{int} < E_r$, the defector extracts the entire amount of resources of the co-player. Thus, the reward obtained by a defector when interacting with individual i is $E_r^i = min(E_r, E_{int}^i)$. Accordingly, if individuals j and k interact, the variation of their internal resources after interacting can be written as

$$\begin{aligned} \Delta E^j &= q^j(E_r^k - E_c) - q^k E_r^j \\ \Delta E^k &= q^k(E_r^j - E_c) - q^j E_r^k \end{aligned} \tag{3.10}$$

Here $q^i = 1$ if individual i is a defector with resources above the cost E_c, i.e. it is an individual able to perform a parasitic action, and $q^i = 0$ otherwise. Below we provide the variation of internal resources of the players as supplied by equation (3.10) for all possible interaction couples:

i. Interaction CD:

$$\Delta E^C = -q^D E_r^C, \ \Delta E^D = q^D(E_r^C - E_c). \tag{3.11}$$

ii. Interaction CC:

$$\Delta E^{C1} = 0, \ \Delta E^{C2} = 0. \tag{3.12}$$

iii. Interaction DD:

$$\Delta E^{D1} = q^{D1}(E_r^{D2} - E_c) - q^{D2}E_r^{D1}, \ \Delta E^{D2} = q^{D2}(E_r^{D1} - E_c) - q^{D1}E_r^{D2} \tag{3.13}$$

Averaging these equations over the entire population one finds the average payoffs obtained by each player in a time step, i.e. the terms in the payoff matrix. The average of E_r^C is, by definition, E_r'; the average of q^D supplies $P(E_D > E_c)$, the fraction of defectors that possess resources above the cost. Then, by calling $p \equiv P(E_D > E_c)$ the terms in the payoff matrix write:

i. Interaction CD:

$$\Delta E^C = -pE_r', \ \Delta E^D = p(E_r' - E_c). \tag{3.14}$$

ii. Interaction CC:

$$\Delta E^C = 0 \tag{3.15}$$

iii. Interaction DD:

$$\Delta E^D = -pE_c \tag{3.16}$$

Therefore, the payoff matrix of resource exchanges due to interactions in a time step reads

$$\begin{array}{c|cc} & \text{C} & \text{D} \\ \hline \text{C} & R = 0 & S = -pE_r' \\ \text{D} & T = p\Delta E' & P = -pE_c \end{array} \tag{3.17}$$

The condition for cooperators to dominate defectors (Mesterton-Gibbons 1991, Nowak 2006) is then $E_c > E_r'$ (equation (3.2)).

The decrease of defectors rewards due to the distribution of internal resources of cooperators is included in the term E_r', while the decrease in the capacity of defectors to act as parasites is included in the term $p = P(E_D > E_c)$, related to their distribution of internal resources. Note that the first term may alter the structure of the payoffs, meanwhile the last term only affects the time scale of the simulations by reducing the net number of effective interactions, i.e. interactions in which defectors actually behave as parasites. To obtain the total exchange of resources for individuals in a time step, one must add the average portion E_p received from the environment and subtract the dissipated resources E_l, i.e one must add $E_0 = E_p - E_l$. This provides the resource payoff matrix displayed in equation (3.5).

Note that, if the interactions are defined with one individual as actor and one as recipient of the act, which would model not simultaneous interactions, the calculation of the payoffs is similar but a 0.5 factor appears multiplying the term p. This happens because the individuals act only half of the times and receive the act the other half. However, as this factor multiplies each matrix element, it does not modify the structure of the game but only the time scale of the dynamics, which now becomes slower. We have checked that the use of this method does not modify the simulation results. Nevertheless, since our extensive simulations over the parameter space are very time consuming, they have been carried out using simultaneous interactions.

Chapter 4

Limiting resources constraining reproduction

Summary

In this chapter I modify the agent-based model in the previous chapter and show that whenever the limiting resource is only necessary for reproduction, the resource limitation may drive a self-organising process that allows for stable coexistence between cooperators and defectors. In contrast to previous EGT studies including ecological features, in which coexistence happens only in public goods games with variable interaction group sizes [100], it is transient [101] or requires spatial structure [102,103], here stable coexistence for pairwise interactions without population structure is found. This stable coexistence resembles the homeostatic equilibrium in the daisy world [104,105], as both are mediated by environmental factors driving the system out from equilibrium.

4.1 The model

In order to study the situation in which resources are only necessary for reproduction, the model presented in chapter 3 is modified here. The model consists again of an evolving well-mixed population of self-replicating individuals that receive resources from the environment and exchange resources during interactions. No population structure, memory, learning abilities or any other sensory inputs are assumed. The difference with the model in chapter 3 is that now the limiting resource necessary for reproduction provides no advantage for keeping alive; therefore, no resource dissipation for keeping alive is assumed ($E_l = 0$) and deaths occur at random with a frequency (rate) f relative

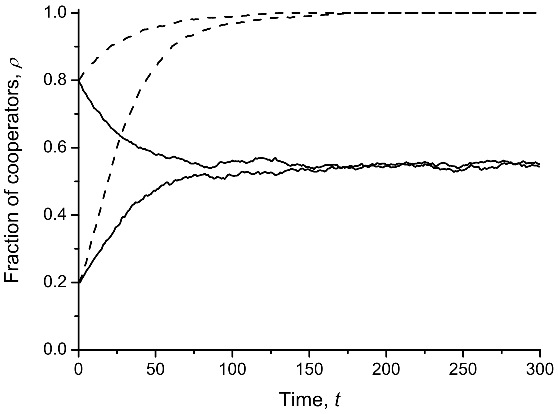


Figure 4.1: *Simulation results for the evolution of the fraction of cooperators* ρ *for two different values of the reward* E_r *and cost* E_c *associated to the selfish strategy (averaged over 10 runs). In some cases the simplified PD payoff structure is modified by the limitation of resources, which allows for coexistence of cooperation and defection (solid line) and dominance of cooperation (dashed line). The final stable states are independent of the initial* ρ *and* N*. Parameters:* $f = 1$*,* $E_s = 1000$*,* $E_T = 8200000$*,* $E_c = 660$*; solid line,* $\Delta E = 310$*; dashed line,* $\Delta E = 10$*.*

to receiving resources and interacting –which happen equally frequently– irrespective of the strategy.

As before, the PD structure of resource exchanges predicts a larger resource intake of defectors and their quicker reproduction –fitness is proportional to resource exchanges. Therefore one would expect homogeneous populations of defectors as the outcome of the evolutionary process. However, the nonlinearities of the model modify this simple picture allowing for a region of dominance of cooperation, as in chapter 3. Simulations show that the present model, where deaths are not linked to payoffs, yields this behaviour and also stable coexistence of cooperation and defection (figure 4.1). This result is quite surprising, since coexistence is the expected outcome in games with a snowdrift payoff structure (see appendix 1.5.1), different from the one here. As shown below, coexistence in the present model is the result of a complex self-organising process.

4.2 Emergent coexistence of cooperators and defectors.

Coexistence in this scenario requires a complex feedback process whose exact analysis is quite difficult because of the complex nonlinearities involved in the dynamics. However, a simple quantitative reasoning exhibits the logic of this feedback and allows for an analytic estimation of the final stable state of the system. Let us note that an increase in the number of defectors over the equilibrium value would cause an overexploitation of cooperators, thus reducing their resource content. This would have two effects: (i) it would reduce the reproduction rate (fitness) of cooperators because they become farther from the splitting bound E_s, and (ii) it would also decrease the average reward obtained by defectors, which thereby reduces their fitness. If the second effect dominates over the first one, then stable coexistence becomes possible, as the feedback pushes the system back to equilibrium. A similar argument applies for a decrease in the number of defectors.

The entire system is in equilibrium when the resource influxes and out fluxes in the populations of both cooperators and defectors cancel out. The balance of resources in these subpopulations contains three contributions: environmental supply, deaths, and interactions. They are expressed in the following equations

$$\frac{dE^C}{dt} = N_C[E_0 - f\overline{E}^C - pE'_r(1-\rho)] \tag{4.1}$$

$$\frac{dE^D}{dt} = N_D[E_0 - f\overline{E}^D - pE_c + pE'_r\rho] \tag{4.2}$$

E^j, $\overline{E}^j$ and N_j denote, respectively the total resource content, average resources per individual and number of individuals of the subpopulations $j = C, D$; $E_0 = E_T/N$ is the mean amount of resources received by an individual per unit time, with $N = N_C + N_D$ the instantaneous population size; $\rho = N_C/N$ is the fraction of cooperators; f is the death probability per individual and interaction, and p the fraction of the population of defectors able to pay the cost (i.e. with $E_i > E_c$).

In equilibrium, the populations of cooperators and defectors become constant in time so that the resource pools E^D and E^C reach a constant value. One thus finds the equilibrium condition

$$p(E'_r - E_c) = f[\overline{E}^D - \overline{E}^C] \tag{4.3}$$

This shows that the coexistence depends on the death frequency f. For simplicity, we assume in this analytic derivation that deaths happen much less frequently than interactions, i.e. the limit $f \to 0$; this corresponds to many interactions in a lifetime, when the effects of interactions become more relevant. Other f values will be studied through simulations (figures. Since p never equals zero due to the constant resource influx, equation (4.3) reduces in this ideal limit to

$$E_c = E'_r \tag{4.4}$$

Remarkably this means that for coexistence to exist in the limit $f \to 0$ it is necessary that the system tunes the value of the benefit E'_r to match the cost E_c.

In order to analytically predict the region of coexistence in the parameters space and the corresponding population composition, it is necessary to know the average reward E'_r in terms of the parameters E_r and E_c. This implies the calculation of the equilibrium distribution of resources for cooperators, which is a difficult task due to the nonlinearities involved in the dynamics. Instead, a rough heuristic estimate can be given as follows. The lower the fraction of cooperators in the population, the more frequent any cooperator meets a defector, thereby cooperators become overexploited and their average internal resources decrease. Thus the average reward E'_r is expected to decrease as ρ decreases. Now assume a linear relationship between both quantities, $E'_r = \alpha\rho$, with α a positive factor. By the moment, consider that when ρ is close to 1, the effect of defectors is expected to be small, so that at first order the resource distribution of cooperators may be approximated as uniform. For uniform distributions one finds $E'_r = E_r - E_r^2/(2E_s)$ (see equation (3.3)). With the previous assumptions

$$E'_r = \rho(E_r - \frac{E_r^2}{2E_s}) \tag{4.5}$$

By combining equation (4.5) with equation (4.4) one obtains an expression for the equilibrium fraction of cooperators

$$\rho = \frac{E_c}{E_r - E_r^2/2E_s}. \tag{4.6}$$

In order to analyse in detail the behaviour of the model, extensive numerical simulations covering the whole parameters space have been performed. They confirm the stability of the coexistence for all death frequencies (figures4.2), and show that the final stable state is independent of the initial conditions and resource influx (and thus, final population size). The analytical prediction for ρ according to equation (4.6) is shown in figure 4.3a, showing a good qualitative agreement with the outcome of the simulations. Deviations root in the linear approximation assumed in equation (4.5) (see figure 4.3b) , and in the assumption of $f \to 0$ (the accuracy of equation (4.3) is shown in figure 4.4 for $f = 0.01$) . If one assumes a quadratic dependence the agreement between predictions and simulations improves substantially (see figure 4.3c).

4.3 Novelty of coexistence states in the mean field limit: Feedback towards neutral stability.

The obtained stable coexistence between cooperators and defectors presents a new outcome in the context of two-player games, where a stable mixed state is only expected in Snowdrift (or Hawk-Dove) games, which have a different payoff structure from the one analysed here. As shown in appendix 1.5.1, symmetric two-player games can be described through the interaction matrix [106]

$$\begin{array}{c c} & \begin{array}{cc} \mathrm{C} & \mathrm{D} \end{array} \\ \begin{array}{c} \mathrm{C} \\ \mathrm{D} \end{array} & \begin{pmatrix} 0 & a \\ b & 0 \end{pmatrix} \end{array} \tag{4.7}$$

where coefficients a and b are assumed to be constant. Applying the replicator equation [18, 90, 106] to analyse the evolution of the population, three cases are possible (see section 1.5.1): (i) dominance of one strategy (when a and b differ in sign); this is the case of the non-iterated PD, where defection always wins; (ii) bistability (if both a and b are negative), in this case the final state is homogeneous and depends on initial conditions; this is what happens in stag hunt games, where coordinating with the partner pays; and (iii) coexistence (if both a and b are positive); this is what occurs in Snowdrift games, when it always pays to play the opposite of the co-player.

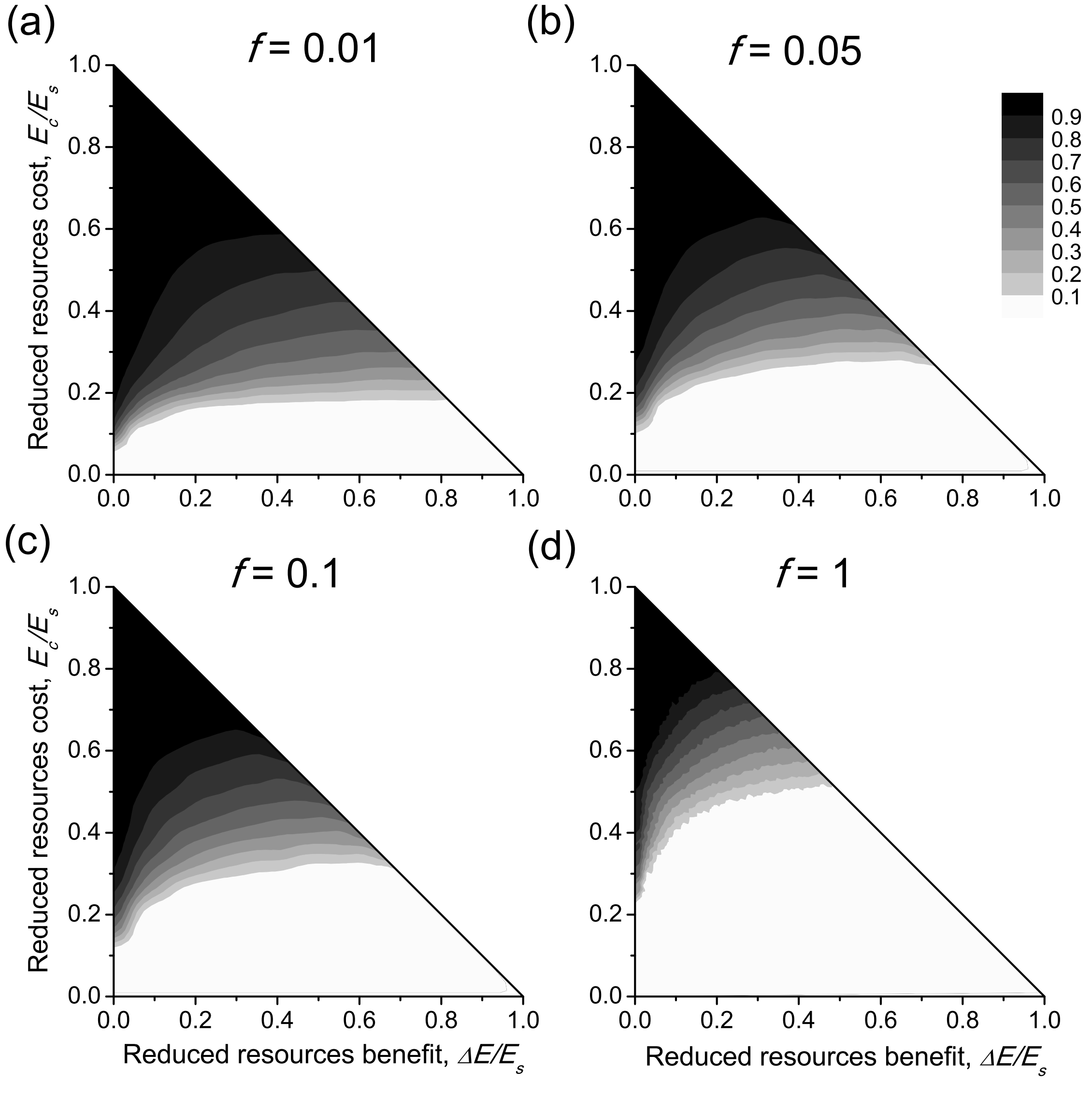


Figure 4.2: *Final fraction of cooperators* ρ *as a function of resources cost* (E_c) *and net benefit* ($\Delta E = E_r - E_c$) *of the selfish strategy. In black* $\rho = 1$, *in white* $\rho = 0$. *One observes well defined regions of coexistence of cooperation and defection, as well as regions where cooperation is the dominant strategy. The regions of coexistence and dominance increase with decreasing* f, *the death rate. Parameters:* $E_s = 1000$, $E_T = 420000$; *in (a)* $f = 0.01$, *(b)* $f = 0.05$, *(c)* $f = 0.1$ *and (d)* $f = 1$.

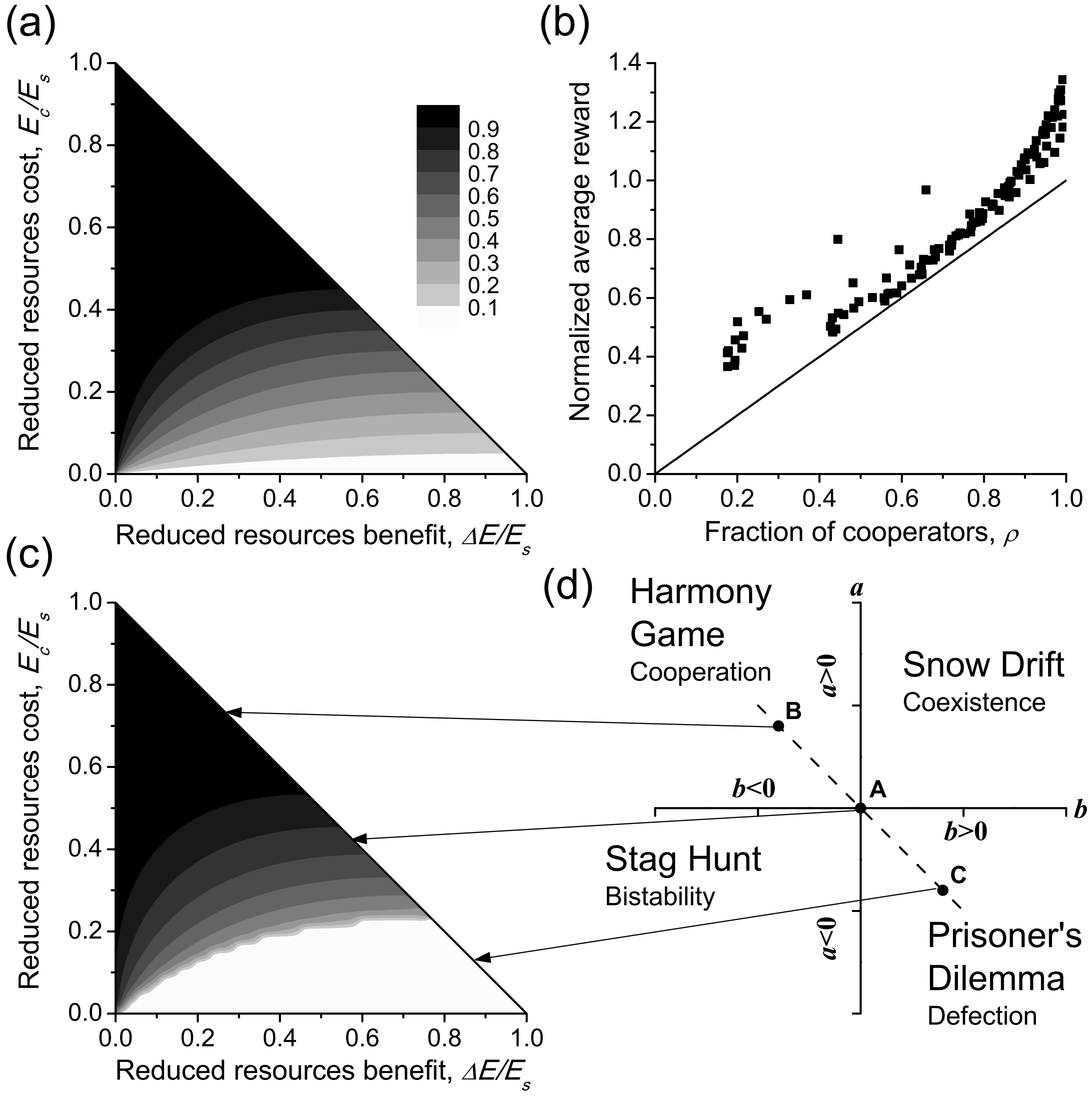


Figure 4.3: *(a) Analytical prediction according to equation* (4.6) *for the final fraction of cooperators* ρ *as a function of resources cost* (E_c) *and net benefit* ($\Delta E = E_r - E_c$) *of the selfish strategy. In black* $\rho = 1$*, in white* $\rho = 0$*. (b) Comparison of the approximation in equation* (4.5) *and the result of numerical simulations. (c) A quadratic fit between* E'_r *and* ρ *obtained from (b) is used to improve the analytic prediction in figure (a). In (d) the different games corresponding to a 2x2 matrix are shown; the dashed line shows the places where the payoffs in the model lay (see equation* (4.9)*). Point A denotes the final payoffs for coexistence states, where the payoff matrix is evolutionary neutral; points B and C are examples of final payoffs for situations where cooperation and defection are dominant, respectively.*

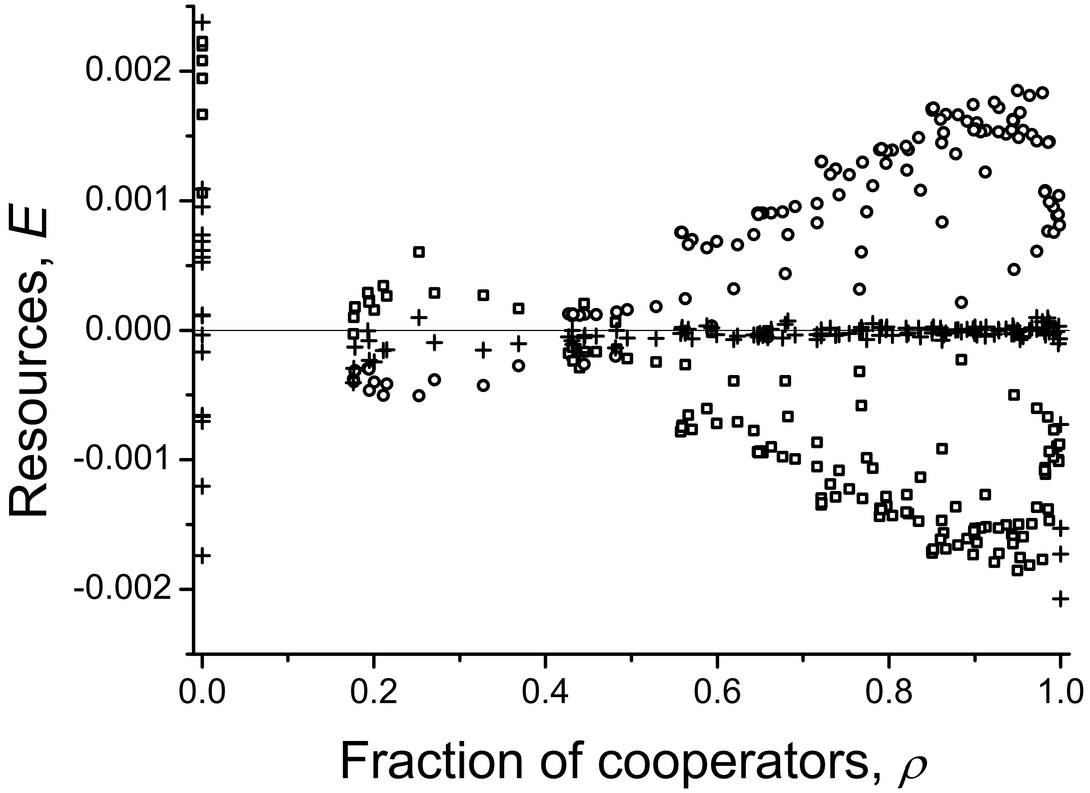


Figure 4.4: . *The figure shows the terms* $p(E_r' - E_c)$ *(squares),* $-f[\overline{E}^D - \overline{E}^C]$ *(circles) and their addition* $p(E_r' - E_c) - f[\overline{E}^D - \overline{E}^C]$ *(crosses) obtained from the simulations for* $f = 0.01$ *as a function of* ρ *(see figure 4.2(a)). The fact that the latter is very close to zero (the minimum resource unit in the simulations is 0.001) shows the accuracy of equation* (4.3).

In the model, fitness is directly proportional to resource exchanges, because individuals reproduce when their resources overcome an upper bound that is the same for cooperators and defectors. Resource exchanges come from the environment and from interactions. The resource supply from the environment is the same for defectors and cooperators; it just provides a constant to all fitness values and can be omitted in the fitness matrix. The latter is thus ruled by the average resources exchanged through interactions, which aside from a scale factor translating resource exchanges to fitness (equation (3.5)), is

$$\begin{pmatrix} 0 & -pE'_r \\ p\Delta E' & -pE_c \end{pmatrix}. \tag{4.8}$$

As stated above, p stands for the fraction of defectors whose resources exceed the cost E_c. Let us note that this factor does not change the payoff structure in any case, as it multiplies all payoffs, and it only modifies the time scale of the dynamics. The interaction matrix can be rewritten in the form of matrix (4.7) by adding pE_c to the second column (as adding a constant to a column does not affect the replicator dynamics, see section 1.B):

$$\begin{pmatrix} 0 & -p\Delta E' \\ p\Delta E' & 0 \end{pmatrix} \tag{4.9}$$

i.e. $a = -b = -p\Delta E'$. According to the classification given above, this payoff matrix leads to dominance of one strategy whenever $p\Delta E' \neq 0$. In the absence of resource limitation $\Delta E' = \Delta E > 0$ and we have a PD. If resources are limited, there exists a wide range of parameters for which the $\Delta E'$ is tuned to zero for a specific mixture of cooperators and defectors (see figures 4.2); thus, the stable equilibrium is the result of a dynamical self-organising process and not of the game structure itself (see figure 4.3d). This represents a new result in two player games.

Equation (4.9) can be used to gain further insight into the stability of the coexistence state found in the model. In equation (4.5) we proposed the rough estimate $E'_r = \alpha\rho$ for the net benefit of defectors, with $\alpha > 0$. Thus, we have $\Delta E' = \alpha\rho - E_c$. Aside from a positive factor relating fitness and payoffs in equation (4.9), the replicator equation yields

$$\frac{d\rho}{dt} = -\rho(1-\rho)p\Delta E = p\rho(1-\rho)(E_c - \alpha\rho) \tag{4.10}$$

which supplies three equilibria, $\rho = 0, 1$ and E_c/α. Since $p > 0$, the mixed state is the stable one for $0 < E_c/\alpha < 1$, in agreement with the stability of the coexistence states observed in the simulations.

4.3.1 Independence of the results on initial conditions and resource influx

As already mentioned, the simulation results presented above are very robust. In particular, they are independent on initial conditions aside from finite size effects when either N or ρ are too small. For instance, in figure 4.5 simulations starting from four different initial amounts of cooperators and defectors (N_C, N_D) lead to the same final steady state.

In addition, the results are robust with respect to changes in the resource influx and, in particular, the latter is not required to be constant for coexistence to happen. Figure 4.6 shows simulation results for a sudden reduction of E_T to its fifth. As expected, the population size N also reduces to its fifth, but the fraction of cooperators hardly changes. Indeed, it is observed a slight transient advantage for cooperators when resources are reduced, and a transient advantage of defectors when resources are increased.

Finally, figure 4.7a analyses the limit of small population sizes. One observes that both the number of individuals in the population and the fraction of cooperators reach steady states with larger random fluctuations. The other panels of figure 4.7 show the effect of oscillatory changes of the total resource influx E_T in these small populations. The population numbers are found to follow the resource influx E_T (except at fast oscillations of period $w = 10$, shorter than the time scale of the population dynamics). Remarkably, the fraction of cooperators remains essentially constant, though fluctuations may drive the system to the extinction of one strategy (figure 4.7f).

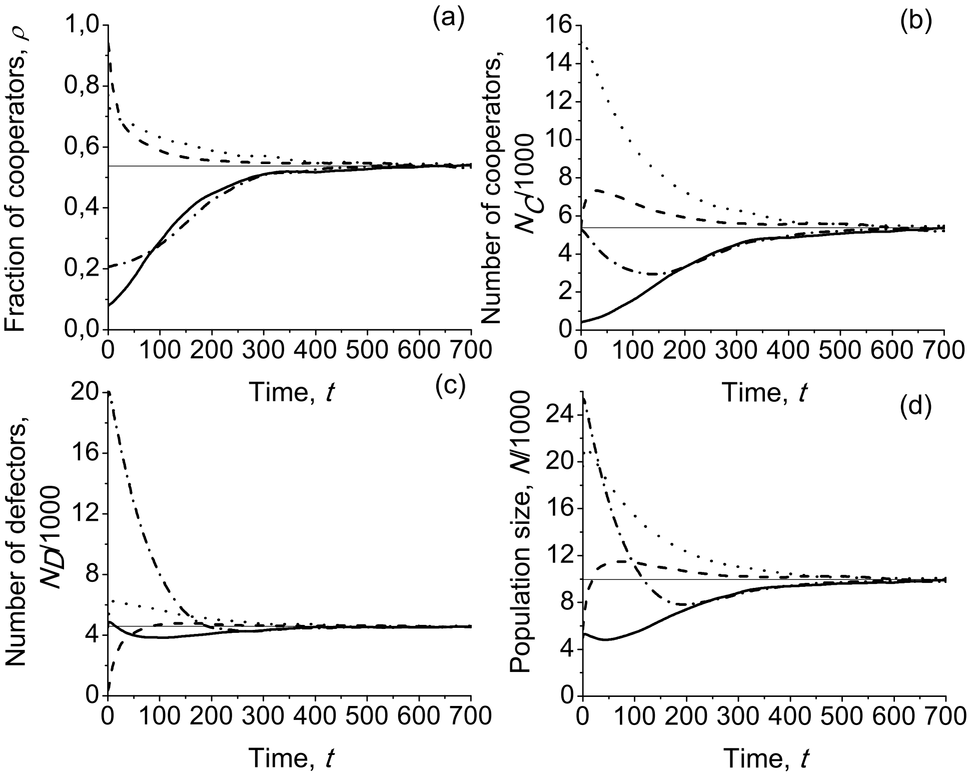


Figure 4.5: *Evolution of (a) ρ, (b) N_C, (c) N_D and (d) N, for four different initial numbers of cooperators and defectors. It can be observed that in all cases, even when the initial values are far away from the final state, the system recovers its equilibrium values given there is enough time. In the case in which the initial number of defectors is much bigger than its final stable value (five times bigger, dash-dotted lines), or that of cooperators is very small (13 times smaller, solid lines), the population of cooperators/defectors (respectively) decreases initially, and thus this situation could drive one of the populations to extinction if its initial number was small enough (see figure 4.7). Parameters:* $E_T = 420000, E_c = 300, \Delta E = 400, f = 0.01$. *Final values:* $\rho = 0.54, N_C = 5380, N_D = 4580, N = 9960$

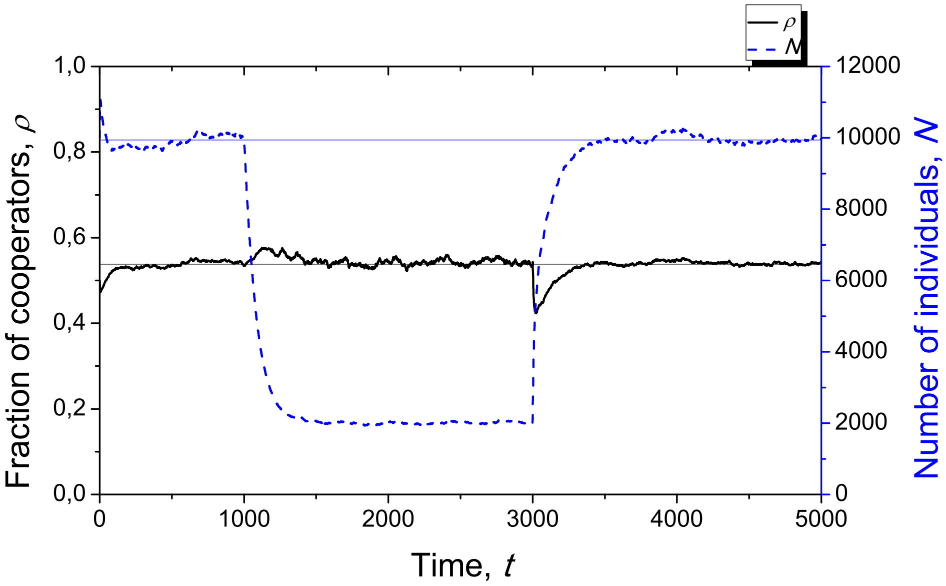


Figure 4.6: *Simulation results dividing instantaneously by five the total amount of resources* E_T *introduced into the system at* $t = 1000$*, and recovering the initial value at* $t = 3000$*. It can be observed that the population size is proportional to* E_T*, decreasing in a factor 5 during the intermediate period, while the fraction of cooperators is only slightly affected during the short time spans in which the population increases or decreases. Parameters:* $E_{T,inic} = 420000, E_c = 300, \Delta E = 400, f = 0.01$*; values in equilibrium:* $\rho = 0.54$*,* $N = 9960$

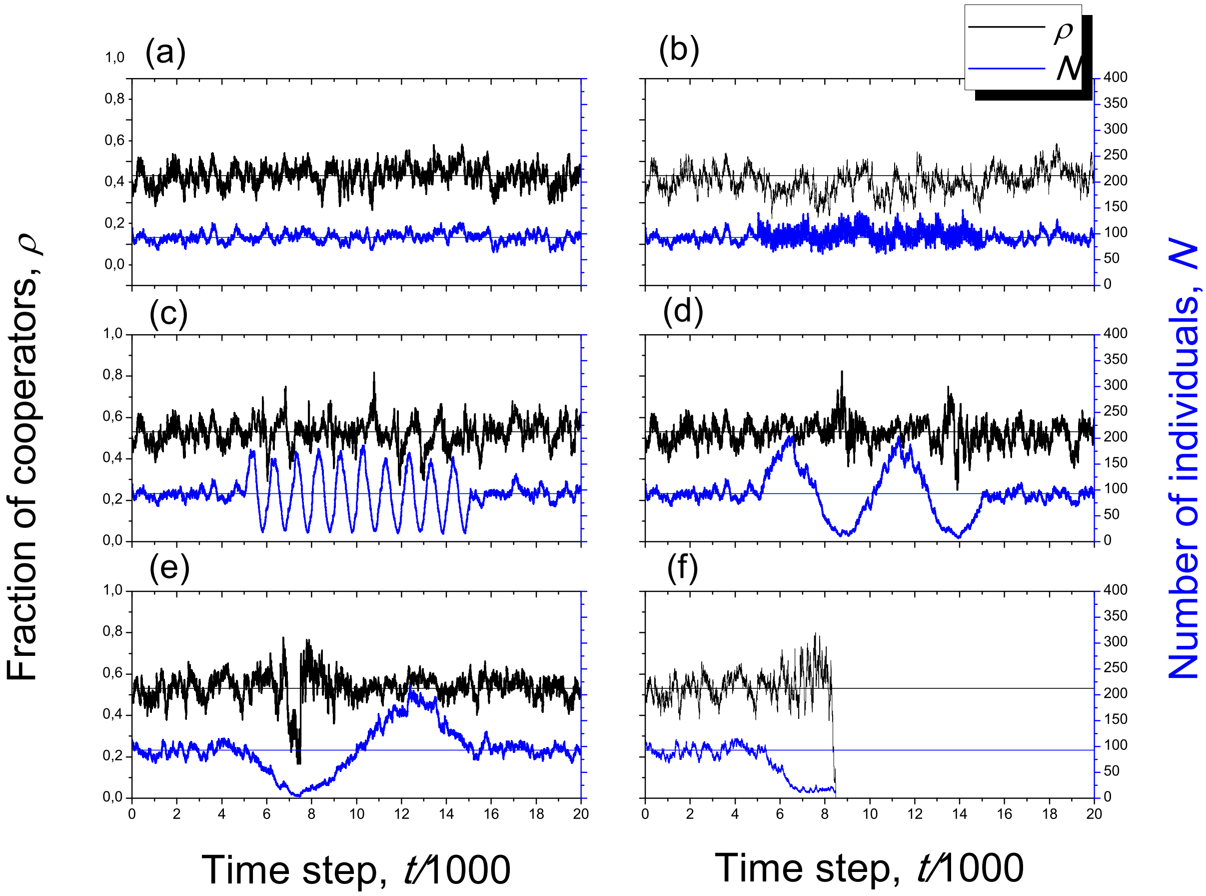


Figure 4.7: *Dynamics of small populations. Simulation results for (a) a constant* $E_T = 4000$*, and a variable* $E_T = 4000 + 3500sin(2\pi t/w)$ *in between* $t = 5000$ *and* $t = 15000$ *with periods (b)* $w = 100$*, (c)* $w = 1000$*, (d)* $w = 5000$*, (e),(f)* $w = 10000$*. It can be observed in figures (b)-(e) that the inclusion of a variable resource influx only introduces noise in the value of* ρ*, while* N *follows the behaviour of* E_T*. For values of* w *lower than 100 (the one in figure (b)),* N *does not follow* E_T *and only some noise is introduced into the system. In (f) an example of fixation of one strategy is shown: a random fluctuation makes the system remain in a state with 15 individuals during time enough as to allow for fixation of defectors. Note that typical fluctuations in the equilibrium (figure(a)) have a standard deviation on* N_C *of 8 individuals, while it is of 4 individuals for* N_D*; thus, any state in which the number of individuals is maintained in very low values during time enough will reach fixation, being fixation of defectors favoured over cooperators in this case. Mean values in equilibrium (figure(a)):* $\rho = 0.53$*,* $N = 93$*. Parameters:* $E_c = 300, \Delta E = 400, f = 0.01$*.*

4.4 Discussion

The scenario presented here, in which reproduction depends on a limiting resource, allows for stable coexistence of unconditional cooperators and defectors in well-mixed populations under pairwise interactions. This result is quite robust, since it does not depend on initial conditions, and it is also observed in small populations – though in this case fluctuations may lead to the extinction of one strategy – and under variable influx of resources. This stable coexistence roots on a self-organising process which implicitly includes the environment, and it is the feedback induced by environmental constraints and defective behaviour which turns the payoff matrix into evolutionary neutral and allows for the stability of the system. The evolutionary neutrality of the system (environment + individuals) and its stability as a whole, might be a first step towards the emergence of new units of selection by providing a self-organising mechanism preventing the spread of selfish mutants alternative to central control (see [1]).

Let us also remark that, in contrast to previous models in evolutionary dynamics, the model presented here explicitly sets the issue in a non-equilibrium context, where a (resource) flux drives the system out from equilibrium. The observed self-organised coexistence state may be seen as another example of self-organising process found in non-equilibrium systems such as, for instance, the unexpected oscillations in Belusov-Zabhotinsky reactions. This perspective may bear interest in economic contexts, another classical field of evolutionary game theory, where some authors claim that economic systems should be modelled as open, nonlinear non-equilibrium systems instead of the closed, equilibrium view dominant in traditional economics [107, 108].

Chapter 5

Analytical models of cooperation and resources

Summary

Aside from a few examples [100–103], the role played by the limitation of resources in most studies on the origin and persistence of cooperation has been just to impose a constant population size [42,49,50,60,61,65,81,109]. In the previous chapters, however, we have introduced a new viewpoint where the environment is considered explicitly by introducing a resource flux into the system that drives it away from equilibrium (chapters 3 and 4). This standpoint leads to unexpected outcomes, such as that resource limitation allows for stable coexistence between unconditional cooperators and defectors, and even dominance of cooperation, in well-mixed populations playing an a priori Prisoner's Dilemma (PD) game, where defectors are expected to drive cooperators to extinction [49]. This happens due to a self-organising process involving the environment which generates dynamical payoffs transforming the original PD structure into a different game. In the present chapter a phase transition from defection to cooperation is studied in three analytical models, two of which represent simplified versions of the agent based models in chapters 3 and 4.

In the first model, presented in section 5.1 the limiting resource constraints the ability of reproduction of individuals and their survival, similarly to the agent based model in chapter 3; in the second model, in section 5.2 the limiting resource is necessary only for reproduction, as in chapter 4. One finds that the analytical models display, with a few differences, the same qualitative behaviour of the more complex agent-based models. In addition, the analytical models allow to expand the study and identify the dimensionless parameters governing the final fate of the system, such as coexistence of cooperators and defectors, or dominance of defectors or of cooperators. We provide a detailed analysis of the occurring phase transitions as these parameters are varied. A third model is presented in section 5.3 where resources are necessary for reproduction and the population size is held constant. This situation corresponds to a case where the population size depends on a limiting resource different from the one constraining reproduction. This model allows for a description of a phase transition from defective populations to coexistence states when the amount of resources received by individuals decreases, showing the importance of the limitation of resources as a factor allowing for the survival and evolution of cooperation.

5.1 Resources constraining reproduction and survival

An analytical simplified version of the agent-based model in chapter 3 is presented below. In this model resources are necessary for reproduction and survival of the individuals, and the population size depends on the resources influx.

5.1.1 Analytical model

The model consists of an evolving well-mixed population of self-replicating individuals that receive resources from the environment and exchange resources during interactions. The internal resources of individuals are either 0 or 1. Each defector attacks at a rate α individuals chosen at random and steals its internal resources. To do so, the defector must have internal resources greater than 0 (i.e. $E_i = 1$). In every interaction, the defector loses its unit of resources with probability q, which is thus the average cost paid by a defector in an interaction. Let us note that, in an ideal situation where all individuals possess resources ($E_i = 1$), the payoffs for cooperators and defectors in an interaction between them are respectively $\pi_{CD} = -1, \pi_{DC} = 1 - q$; interactions between cooperators result in a payoff $f_{CC} = 0$ for each and between defectors in $\pi_{DD} = -q$. The payoff ordering in this situation $\pi_{DC} > \pi_{CC} > \pi_{DD} > \pi_{CD}$ corresponds to a Prisoner's Dilemma, and hence the names cooperators and defectors, and the expectation of the extinction of cooperation. However, since not all cooperators have resources $E_i = 1$, the average net reward got by defectors will be, in general, smaller than $1-q$. This reward depends on the fraction of cooperators in state $E_i = 1$, which is a dynamical quantity. As a consequence, the dynamics might lead the average reward to values smaller or equal to the cost and allow for the survival of cooperators, as shown below.

The system receives resources from the environment at a rate E_T, and they are distributed equally among the N individuals of the population independently of its strategy. In addition, individuals dissipate resources in living activities at a rate r; this is implemented as the probability of spending one resource unit per unit time. If an individual with 0 internal resources is attacked or it is required to dissipate resources it dies. On the other side, when an individual with internal resources $E_i = 1$ receives an extra unit of resources it splits into two identical copies, each one with $E_i = 1$. Again, resource allocation, reproduction and death rules are equal for both cooperators and defectors, being the strategy the only difference.

Let us note that the main differences of the model presented here and the agent-based one in chapter 3 are: (a) now there are only two resource levels $E_i = 0, 1$, instead of a much larger distribution, (b) the cost paid by active defectors in an interaction, and resource dissipation are stochastic.

We use the following notation: c_i for the number of cooperators with internal resources i and d_i for defectors; $N = c_1 + c_0 + d_1 + d_0$ represents the population size. The model equations are:

$$\begin{aligned}
\frac{dc_0}{dt} &= -\alpha d_1 \frac{c_0}{N} + \alpha d_1 \frac{c_1}{N} - \frac{E_T}{N} c_0 - r c_0 + r c_1 && (5.1)\\
\frac{dc_1}{dt} &= -\alpha d_1 \frac{c_1}{N} + \frac{E_T}{N}(c_0 + c_1) - r c_1 && (5.2)\\
\frac{dd_1}{dt} &= \alpha(1-q) d_1 \frac{c_1}{N} - \alpha q d_1 \left(\frac{c_0 + d_0 + d_1}{N}\right) + \\
&+ \frac{E_T}{N}(d_0 + d_1) - r d_1 && (5.3)\\
\frac{dd_0}{dt} &= -\alpha d_1 \frac{d_0}{N} + \alpha(1-q) d_1 \frac{d_1}{N} + \alpha q d_1 \left(\frac{c_0 + d_0 + d_1}{N}\right) - \\
&- \frac{E_T}{N} d_0 - r d_0 + r d_1 && (5.4)
\end{aligned}$$

Let us first explain the interaction terms. From the α attacks per unit time of a defector

D_1, in a fraction c_1/N the victim will be a C_1 player. Thus, $\alpha d_1 c_1/N$ describes the rate of interactions of active defectors D_1 with cooperators C_1. As a result of these interactions, individuals C_1 lose their internal resource unit after the attack of defectors and move from population c_1 to c_0; this explains the first term in the equations for c_0 and c_1. Also, in a fraction $1-q$ of these interactions the D_1 individual keeps its resource unit, which added to the stolen unit from the C_1 player, leads to its reproduction; this gives the first term in the equation for d_1. When a D_1 player attacks C_0 and D_0 individuals, a fraction q of times loses its resource unit so that it moves to population D_0 (this yields part of the second term in equations for d_1 and d_0); furthermore, in this case the C_0, D_0 individual dies. An interaction D_1D_1 produces either D_1D_0 with probability q (which reduces the D_1 population and increases D_0), or $D_1D_1D_0$ with probability $1-q$, which does not affect the population of d_1 but increases the one of d_0; these two processes describe the remaining interaction terms in the dynamic equations for d_1 and d_0. Finally, dissipation kills individuals c_0 and d_0 at a rate r and moves individuals from c_1 to c_0, and from d_1 to d_0 also at a rate r.

On the other hand, the term in $\frac{E_T}{N}c_0$ quantifies the number of individuals C_0 moving to population C_1 after getting a unit of resources from the environment. In addition, individuals in population c_1 that receive resources from the environment replicate, thus increasing the c_1 population. The same applies for the population of defectors d_0 and d_1.

This model is much simpler than the one described in chapter 4, because it contains just four independent variables, namely c_0, c_1, d_1 and d_0, in contrast to the many variables included in the resource distributions for cooperators and defectors of the latter model. However, it keeps most of its ingredients and captures the main features of its behaviour: the promotion of cooperation triggered by resource limitations.

5.1.2 Model dynamics

One can analyse the dynamical behaviour of our model equations (5.1)–(5.4). Since the right-hand side of the system equations are homogeneous functions of degree 1 on c_i, d_i, N and E_T, the stationary populations c_i, d_i are proportional to E_T. Therefore, E_T just determines the population size, but not the composition, given by c_i/N and d_i/N.

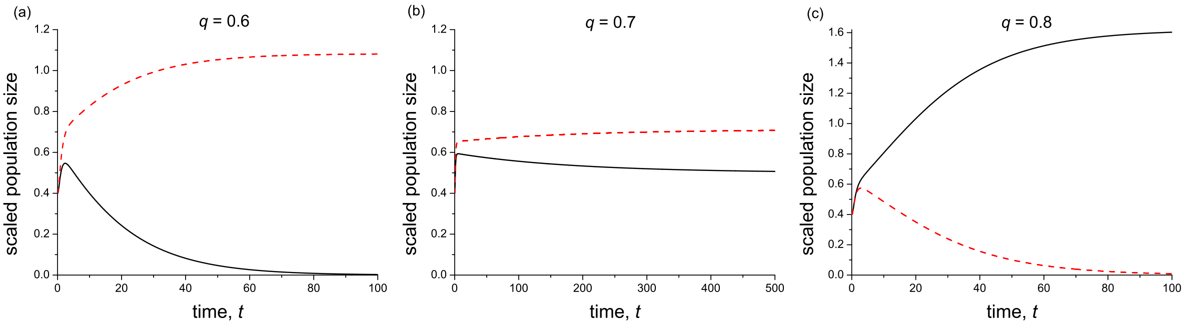


Figure 5.1: *Time evolution for the scaled number of cooperators (solid line) and number of defectors (dashed line) for three sets of parameter values:* $\alpha/r = 1$ *and (a)* $q = 0.6$, *(b)* $q = 0.7$ *and (c)* $q = 0.8$. *In (a) cooperators die out, in (b) the system ends up in a mixed state where cooperators and defectors coexist, in (c) cooperators get rid of defectors. Two phase transitions occur as* q *increases. The populations are given in units of* E_T/r *(see equation* (5.5)*).*

This is in agreement with the behaviour found in the agent-based model in chapter 3. One can also nondimensionalize the system equations by defining a nondimensional time rt. This shows that the system is ruled by three nondimensional parameters: q, α/r and E_T/r and, the stationary populations obey the scaling relation

$$c_i, d_i = \overline{g}_i(q, \frac{\alpha}{r})\frac{E_T}{r}. \tag{5.5}$$

Here, E_T/r provides the characteristic size of populations c_i, d_i; this is larger the bigger the resource influx rate E_T and the smaller its dissipation rate r. On the other hand, the composition of the final population is determined by parameters q and α/r.

The numerical resolution of the system (5.1)–(5.4) displays two main behaviours depending on the parameter values: dominance of defection and dominance of cooperation (see figure 5.1), in agreement with the behaviour of the agent-based model in chapter 3. figure 5.1b shows that coexistence of cooperators and defectors is also possible, in opposition to the behaviour of the more complex agent-based model. Again, figure 5.1 shows that the final composition of the system changes as a parameter is varied, indicating a phase transition from a population of only defectors at small costs q and a population of only cooperators at larger q values, separated by a coexistence region (see figure 5.2). Let's analyse the parameter region where each attractor becomes the stable one, i.e. let us find the phase diagram of the model.

The analytical resolution of the system reveals the existence of three stationary

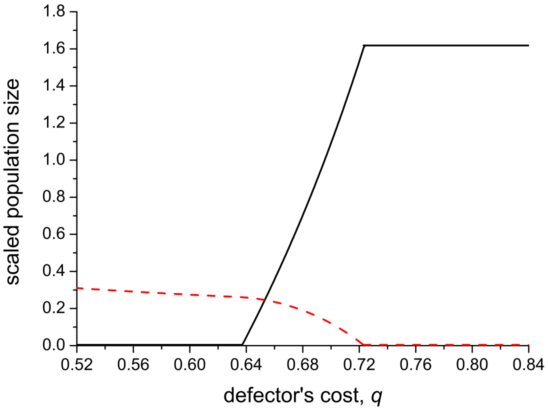


Figure 5.2: *Phase transitions for* $\alpha/r = 10$. *Population of defectors (dashed line) and cooperators (solid line) as function of defectors cost* q. *As* q *grows two phase transitions occur: first, a transition from defective to coexistence states, and a second one at* $q = 0.723$ *from coexistence to purely cooperator states.*

states: (a) one made of cooperators ($c_1 = E_T/r, c_0 = 0.62E_T/r$), (b) one made of defectors ($d_1 = E_T/(\alpha q + r), d_0 = E_T[\sqrt{\alpha^2 + 5r^2 + 6\alpha r} - r - \alpha]/2r(\alpha q + r)$), and (c) a mixed state whose solution provides positive populations only for a limited set of parameter values. The whole solution is rather cumbersome, but one can extract valuable information by focusing in some aspects of it. The solution for c_1 is ($E_T = 1$)

$$c_1 = \frac{2.62\alpha q^2 - 1.62q\alpha + 3.62qr - 2.62r}{q\alpha(1-q)}, \tag{5.6}$$

which is positive provided that

$$\frac{\alpha}{r} = \frac{1 - 1.38q}{q(q - 0.62)} > 0. \tag{5.7}$$

This shows that the mixed state can only exist in a thin range of q values between 0.62 and 0.72, in agreement with figure 5.1b. The same happens for solution c_0. Populations d_0 and d_1 become negative at $q > 0.72$. Expression (5.7) provides the separation line between dominance of defectors and coexistence; for $q > 0.72$ cooperators dominate (see figure 5.2). Therefore, the dynamics is mainly ruled by the defector cost q, being defectors dominant below $q = 0.62$ and cooperators dominant above $q = 0.72$ (figure 5.3). Aside from the thin range of coexistence in the parameter region separating both dominating behaviours, the analytical model provides the same qualitative behaviour as the agent-based model presented in chapter 3.

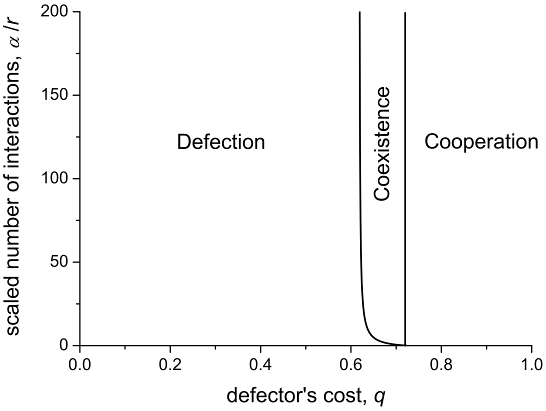


Figure 5.3: *Phase diagram. Below* $q = 0.62$ *defectors dominate. Above* $q = 0.72$ *cooperators dominate. In between there is a thin region of coexistence of cooperators and defectors.*

5.2 Limiting resource constraining reproduction

In this section the simplified analytical version of the agent-based model in chapter 4 is studied, where the limiting resource only constrains reproduction; therefore deaths are assumed to happen at random and equally for cooperators and defectors.

5.2.1 Simplified analytical model

The model studied here is similar to that developed in section 5.1, but now resources are not necessary for survival; therefore no dissipation of resources to keep alive is assumed. Again the internal amount of resources E_i is either 0 or 1 and each defector attacks at a rate α per unit time to individuals chosen at random and steals its internal resources. To do so, the defector must have internal resources greater than 0 (i.e. $E_i = 1$), otherwise it does not attack. In every interaction, the defector loses its unit of resources with probability q, which can thus be seen as the average cost paid by a defector in an interaction. If the interaction partner has no resources, no reward is obtained. Cooperators do nothing, they just eventually suffer from defector's attacks.

The system receives from the environment E_T units of resources per unit time, which are distributed equally among the N individuals of the population independently of its strategy, thus not modifying the interaction payoff structure. When an individual with internal resources $E_i = 1$ receives an extra unit of resources it splits into two identical copies, each one with $E_i = 1$. Along with reproduction, we assume that players die with a probability f per unit time, independently of its strategy. Therefore, resource allocation, reproduction and death rules are equal for both cooperators and defectors, being the strategy the only difference.

At the sight of the two models, the main differences between them are that in the simplified model the resource distribution is discrete (while it is continuous in the agent-based model), and defectors cost is stochastic.

We consider simultaneous interactions and large populations so that we can make a continuum approach. We denote by c_0 and c_1 the number of cooperators with internal resources 0 and 1, d_1 and d_0 the number of defectors with internal resources 1 and 0, respectively; $N = c_0 + c_1 + d_1 + d_0$ is then the total population size. The evolution equations according to the mechanisms involved are

$$\begin{aligned}
\frac{dc_0}{dt} &= \alpha d_1 \frac{c_1}{N} - \frac{E_T}{N} c_0 - f c_0 && (5.8)\\
\frac{dc_1}{dt} &= -\alpha d_1 \frac{c_1}{N} + \frac{E_T}{N}(c_0 + c_1) - f c_1 && (5.9)\\
\frac{dd_1}{dt} &= \alpha(1-q) d_1 \frac{c_1}{N} - \alpha q d_1 (\frac{c_0 + d_0 + d_1}{N}) + \\
&+ \frac{E_T}{N}(d_0 + d_1) - f d_1 && (5.10)\\
\frac{dd_0}{dt} &= \alpha(1-q) d_1 \frac{d_1}{N} + \alpha q d_1 (\frac{c_0 + d_0 + d_1}{N}) - \\
&- \frac{E_T}{N} d_0 - f d_0 && (5.11)
\end{aligned}$$

The equation terms are similar to those in equations (5.1)-(5.4), but with no deaths due to interactions and no dissipation of resources ($r = 0$). The terms with f just describe the number of individuals dying in each population per unit time.

5.2.2 Model dynamics

One of the properties of the model in chapter 4 is that a change in the resource influx E_T does not modify the final fate of the system, but just the final population size; more specifically, it was found in equilibrium that $N \propto E_T$. This is also what the system (5.8)–(5.11) predicts for the steady state, since the right-hand side of all the equations are homogeneous functions of degree 1 of variables c_i, d_i, N and E_T, as in the previous model. This means that the stationary states are solutions of the type

$c_i, d_i = \lambda_i E_T$, with λ_i constants depending only on α, f and q; therefore, $N \propto E_T$ as in the previous model.

As before, one can obtain a further understanding of the model through nondimensionalization. By dividing equations (5.8)–(5.11) by the death rate f and defining the dimensionless time ft, the system turns to be described by three dimensionless parameters, namely q, α/f and E_T/f. Since we have seen above that stationary populations are proportional to E_T, they can be generally written as

$$c_i, d_i = g_i(q, \frac{\alpha}{f})\frac{E_T}{f}, \qquad (5.12)$$

with g_i unknown functions of the dimensionless parameters q and α/f. Then, E_T/f sets the characteristic size of the populations, and the composition, let us say the population fractions $c_i/N, d_i/N$, comes determined by the other two parameters, q and α/f through functions g_i. Parameter α/f has a direct interpretation: since α is the attack rate of a defector and f^{-1} is the average lifetime of an individual, α/f denotes the average number of interactions performed by an active defector, and it is this quantity, along with the cost q, what determines the fate of the system. For simplicity, in the following we will assume $E_T = 1$, i.e. absolute populations c_i, d_i will be given in units of E_T.

The most interesting feature of the model in chapter 4 was the existence of situations where cooperators are able to survive in coexistence with defectors in mixed stationary states. We analyse next the dynamical behaviour of equations (5.8)–(5.11) through its numerical and analytical resolution. Figure 5.4 illustrates that the dynamic equations (5.8)–(5.11) indeed display a behaviour as the original model, namely by modifying parameters α, f and q the system ends up either in purely defective states or in coexistence states.

One can perform a systematic analysis of the dynamic behaviour of our system (5.8)–(5.11) which will allow for a better understanding of the model. Its analytical resolution shows the existence of a number of stationary states: (a) one made only of cooperators C_1, which the dynamics shows it is always unstable; (b) another one made only of defectors, which is sometimes stable (we give it here for completeness, $d_1 = \frac{1}{\alpha q + f}$, $d_0 = \frac{\sqrt{1+\alpha/f} - 1}{\alpha q + f}$); and (c) a number of mixed states of which only one provides positive values for all population variables for some parameters. The latter

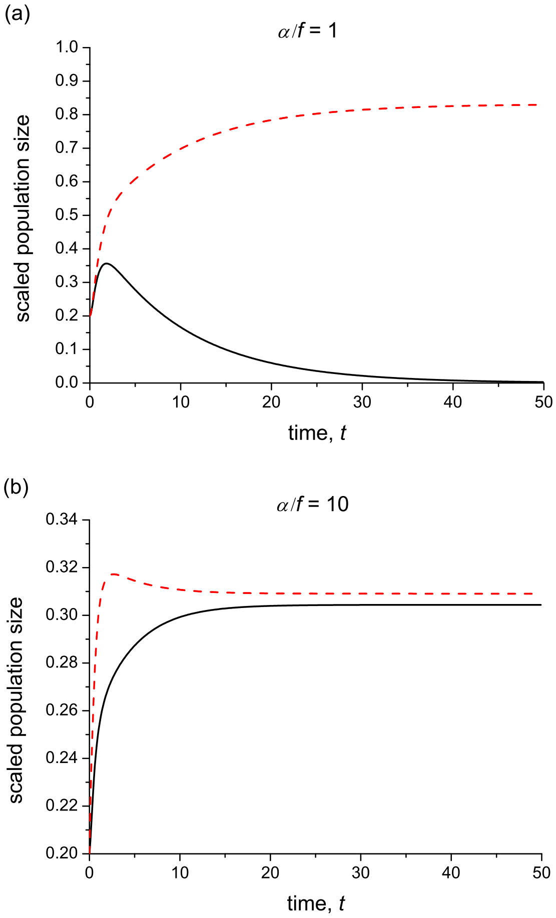


Figure 5.4: *Time evolution for the scaled number of cooperators (solid line) and number of defectors (dashed line) for two sets of parameter values:* $q = 0.7$ *and (a)* $\alpha/f = 1$ *and (b)* $\alpha/f = 10$. *In (a) cooperators die out, in (b) the system ends up in a mixed state where cooperators and defectors coexist. These two types of states are the only attractors of the dynamics. The populations are given in units of* E_T/f *(see equation* (5.12)*).*

is the mixed state that, when takes positive values, becomes stable at the same time that the defective state (b) becomes unstable. In order to study this (transcritical) transition, it is useful to realise that the populations for cooperators in the mixed state (c) have the following form (the solutions for defectors are always positive)

$$c_i = \frac{a_i}{\alpha}[\frac{\alpha}{f} - \gamma_c], \tag{5.13}$$

where a_i $(i = 0, 1)$ and γ_c are functions of q only. This expression supplies positive values for c_i only when $\alpha/f > \gamma_c$. Therefore, $\gamma_c(q)$ is the critical value over which α/f must be in order for the system to end up into a coexistence state. This indicates that the transition from defective to coexistence states depends on the parameter α/f, and not separately of parameters α and f, in agreement with equation (5.12). figure 5.5 shows the phase transition from dominance of defectors to coexistence of cooperators and defectors for two values of q. One observes that the survival of cooperation is favoured by larger defector costs (larger q), as expected, since mixed states appear at lower critical numbers of α/f. One can also display the phase transition as a function of q for two values of α/f (figure 5.6). One observes that as $q \to 1$ the mixed state tends to the stationary state made only of cooperators C_1, which is the stable state for $q = 1$.

Finally, one can obtain the phase diagram separating the two behaviours in terms of the two parameters governing the system. The separation line is found by imposing $c_i = 0$ in equation (5.13), i.e. $\alpha/f = \gamma_c$. The analytical expression for γ_c is long but it can be solved numerically (see figure 5.7).

5.2.3 Comparison with the agent-based model

The phase diagram, figure 5.7, shows that cooperation is favoured at large costs q for defecting, as expected, and also at large numbers of attacks in a lifetime, α/f. The latter behaviour is surprising, since at first sight interactions should benefit defectors versus cooperators. However, we must bear in mind that attacks are indiscriminate and then a fraction of the attacks fall on defectors themselves, thus reducing the number of defectors in active states. The dynamics of the system shows that for a large enough number of attacks in a lifetime, the number of active defectors decrease enough so as

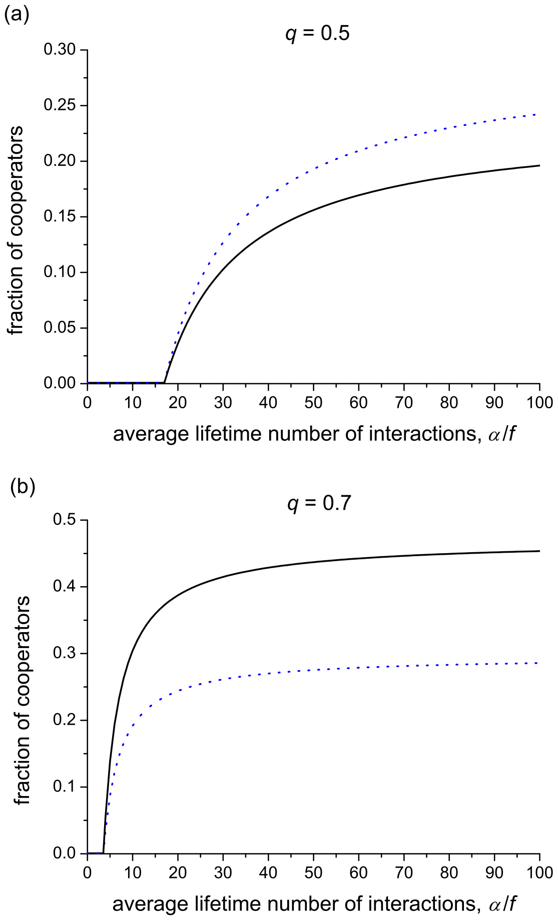


Figure 5.5: *Phase transition. Fraction of cooperators (c_1/N, solid line; c_0/N, dotted line) as a function of parameter α/f for (a) $q = 0.5$ and (b) $q = 0.7$. Below a critical value, cooperators die out.*

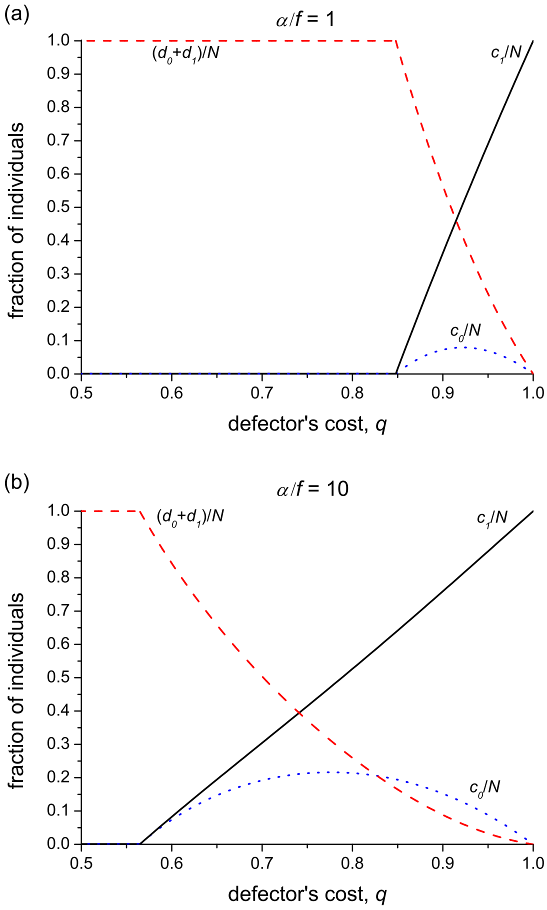


Figure 5.6: *Phase transition. Fraction of cooperators (c_1/N, solid line; c_0/N, dotted line) and defectors (dashed line) as a function of parameter q for (a) $\alpha/f = 1$ and (b) $\alpha/f = 10$. Below a critical value, cooperators die out.*

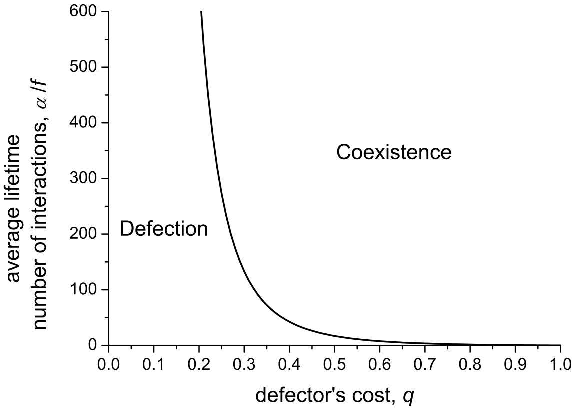


Figure 5.7: *Phase diagram. For large costs q or large average number of attacks in a lifetime, α/f, cooperators survive in coexistence with defectors.*

to allow for the survival of cooperators. This happens in a continuous phase transition as seen in figures 5.5 and 5.6. Let us note that the latter behaviour was partially observed in the original agent-based model. There, the attacking rate α was set to unity by construction of the model, so that it could not be modified. However, it was found that cooperation increased when the death rate f decreased, in agreement with the predictions of the present model.

Let us further compare the agent-based model in section 4 and the simplified analytical model presented here. As previously noticed, they show a similar qualitative behaviour, both displaying a phase transition from purely defective states at low costs and small death rates to stable coexistence states in the opposite limit. However, there exist a few differences between them. The numerical simulations of the former model predicted dominance of cooperators for large costs (see figure 4.2 in chapter 4), whereas this does not occur in the analytical model. We have checked this difference of behaviour by performing large-size simulations of the agent-based model, thus minimising finite size effects; they confirm the extinction of defectors for large costs, and the existence of a region where they extinguish due to stochastic fluctuations in coexistence states with few defectors.

5.3 Resources constraining reproduction with constant population size

One of the main results in the previous section is that a well-mixed population of unconditional cooperators extinguishes for infinite resources (where the system plays a PD game) but may survive for some parameter values when resources are finite (where the game is not a PD anymore). This suggests the possibility of a transition from a population of only defectors when resources are abundant to a population containing cooperators for more stringent environments. The existence of this transition should have great interest, since it would provide a resource-based mechanism preventing the spread of defectors and thus may shed light on the conditions under which cooperators could appear through evolution. Indeed, this effect has been recently observed experimentally in yeast cultures [110], and has also been found in a model for the survival of aerobic cells inside anaerobic cultures [95, 96]. The model depicted in sections 5.2 and 5.1, however, do not yield such a transition: in these models we considered that the population was ruled by a resource limiting reproduction, and that deaths occurred at a constant rate, so that the limiting resource influx determined the population size; as it was thoroughly discussed, a reduction in the resource flux just decreased the size of the population in the same proportion, but it did not modify its composition. In this section we consider a different situation in which the limiting resource constraining reproduction is different from the limiting factor constraining population size. For instance, limiting factors for bacteria include nutrients, as Carbon or Nitrogen, space, and light (for photosynthetic bacteria), to name some. The situation studied in this work might happen by the combination of two different nutrients or, in a simpler case, by the combination of a limiting nutrient for reproduction, and space constraining population size. If there is a flux of an available nutrient which is necessary for reproduction in a certain area or volume where the bacteria might live, bacteria will increase in number until the total habitable area or volume is occupied; further reproduction drives some of the bacteria out of the habitable area. As an example, sub-aquatic volcanoes are a constant source of nutrients for some bacteria, which live in the surrounding area, and which has very specific environmental conditions, as heat and nutrient concentration. This area is clearly limited, which constrains population size, while nutrient concentration constrains reproduction.

In this section we show that, in the situation just described, a system of unconditional players displays a phase transition from a population of defectors when the resource limiting reproduction is abundant, to the coexistence of cooperators and defectors when it is scarce. To this end, we develop a stylised model, similar to the one in section 5.2, which consists of an evolving well-mixed population of self-replicating individuals that receive resources from the environment and exchange resources during interactions. However, we focus in a limiting resource constraining reproduction while population size is constant.

5.3.1 The model

The model consists of an evolving well-mixed population of self-replicating individuals that receive resources from the environment and exchange resources during interactions. Again, no memory, learning abilities or any other sensory inputs are assumed. Each individual i is represented by its internal amount of resources, E_i, which in this simplified model is either 0 or 1, and its strategy, namely cooperate (C) or defect (D). The internal amount of resources may be interpreted as the amount that belongs to it independently of how (it may be in its surroundings, for instance). Each defector attacks at a rate α per unit time to individuals chosen at random and steals its internal resources. To do so, the defector must have internal resources greater than 0 (i.e. $E_i = 1$), otherwise it does not attack. In every interaction, the defector loses its unit of resources with probability q, which can thus be seen as the average cost paid by a defector in an interaction. If the interaction partner has no resources, no reward is obtained. Cooperators do nothing, they just eventually suffer from defector's attacks. We assume that behaviours are inherited without mutation and represent physiologic or morphological characteristics intrinsic to individuals which cannot be modified by choice.

Each individual receives from the environment γ units of resources per unit time independently of its strategy, thus not modifying the interaction payoff structure. When an individual with internal resources $E_i = 1$ receives an extra unit of resources it splits into two identical copies, each one with $E_i = 1$. Along with reproduction, we assume that players die with a probability f, independently of its strategy, in such a way that the number of individuals in the population remains constant. Therefore, resource allocation, reproduction and death rules are equal for both cooperators and defectors, being the strategy the only difference.

Let us note that, in this model, an increase in the environmental resource supply leads to an increase in γ, the amount of per-capita resources obtained by individuals. This contrasts with the models in sections 5.1 and 5.2, where an increase of resources leads to a proportional increase in the population size while keeping the same per-capita value.

We consider simultaneous interactions and large populations so that we can make a continuum approach. We denote by c_0 and c_1 the fraction of cooperators with internal resources 0 and 1, and d_1 and $d_0 = 1-c_0-c_1-d_1$ the fraction of defectors with internal resources 1 and 0, respectively. The equations governing the evolution of cooperators are the following

$$\frac{dc_0}{dt} = \alpha c_1 d_1 - \gamma c_0 - f c_0 \tag{5.14}$$

$$\frac{dc_1}{dt} = -\alpha c_1 d_1 + \gamma(c_0 + c_1) - f c_1 \tag{5.15}$$

The $\alpha c_1 d_1$ term shows the fraction of cooperators C_1 that lose their internal resource unit after the attack of defectors (the latter pertaining to the population d_1); these individuals move from population c_1 to c_0. The term in γc_0 quantifies the fraction of individuals C_0 that change to population c_1 after getting a unit of resources from the environment. In addition, individuals in population c_1 that receive resources from the environment replicate, thus increasing the c_1 population. The terms fc_i describe the fraction of individuals dying in each population per unit time.

To describe the evolution of defectors is enough to write the equation for population d_1 because d_0 is just the remaining fraction of the whole population. The dynamic equation for d_1 is

$$\frac{dd_1}{dt} = -\alpha q d_1 + \alpha c_1 d_1 + \gamma(d_0 + d_1) - f d_1. \tag{5.16}$$

The terms related to deaths and resource allocation from the environment are analogous as for cooperators. The interaction term is as follows. On the one hand, with probability q individuals D_1 lose its resource unit when interacting with individuals C_0, D_0 and D_1; this leads to a decrease in the population of d_1 in an amount $\alpha q d_1(c_0+d_0+d_1)$. On the other hand, when interacting with individuals C_1, individuals D_1 sequester their resource unit; therefore, either the population of D_1 does not change, with probability q, or it increases due to reproduction at a rate $\alpha c_1 d_1(1-q)$.

To complete the equations of the model, we need an expression for the death rate f. In order to have a constant population size, the frequency of deaths must equal the frequency of reproductions. This leads to

$$f = \gamma(c_1 + d_1) + \alpha(1-q)(c_1+d_1)d_1. \tag{5.17}$$

The first term denotes reproductions due to resource allocation and the second one to reproduction of D_1 individuals when attacking individuals with $E_i = 1$ and not paying the cost. equations (5.14)–(5.17) are the equations of our model. They can be further simplified by noticing that one can divide all the equations by parameter γ and absorb it into the time parameter; therefore, there are just two dimensionless parameters in the model, q and $\beta = \alpha/\gamma$. A large β value indicates either large defector attack rates or small resource influxes from the environment; conversely, large resource influxes or small attacking rates yield small β values. The dimensionless equations are the same equations (5.14)–(5.17) replacing α by β, and γ by 1.

The numerical resolution of the model shows that the system is attracted to a globally stable fixed point independent of initial conditions. Depending on the parameter values, the final fate is either a population of defectors (an expected solution) or, interestingly, a stable mixture of cooperators and defectors. Remarkably enough, for fixed q, small β values, i.e. large resource influxes, provide a population of just defectors, but when β exceeds a critical value β_c a mixed state appears, thus providing a smooth phase transition from defective states to mixed states as resources become scarce (see figure 5.8). The existence of stable mixed states in the model may be explained in terms of the overexploitation mechanism discussed in chapter 4: an excess of defectors may reduce the resources owned by cooperators and, as a result, the average reward obtained by defectors; eventually, rewards decrease below costs and cooperators recover. Interestingly, we can obtain simple analytical expressions for the composition

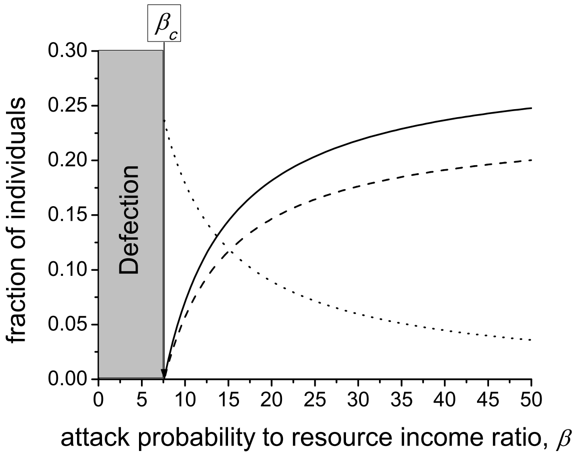


Figure 5.8: *Phase transition for q=0.5. The fraction of cooperators* c_0*,* c_1 *and defectors* d_1 *above the threshold are denoted with solid, dashed and dotted lines, respectively. Below the critical value* $\beta_c = 7.58$ *cooperators die out.*

of the mixed state as a function of parameter β above the threshold:

$$c_i = a_i(1 - \frac{\beta_c}{\beta}), \qquad d_1 = \frac{a_2}{\beta}, \tag{5.18}$$

with a_i and β_c functions of parameter q.

Remarkably, the dynamics in coexistence states self-organises defectors rewards to be (almost) equal to costs thus turning the payoff matrix to neutral. According to the model, the payoff matrix for an average interaction is

$$\begin{array}{c c} & \begin{array}{cc} \text{C} & \text{D} \end{array} \\ \begin{array}{c} \text{C} \\ \text{D} \end{array} & \begin{pmatrix} 0 & -E_r' \\ E_r' - E_c & -E_c \end{pmatrix} \end{array} \tag{5.19}$$

with E_r' the average reward obtained when a defector attacks a cooperator, and $E_c = q$ the average cost paid when a defector attacks. Then, the average reward received by defectors when interacting with cooperators is $E_r' = c_1/(c_0+c_1)$. equation (5.18) shows that $E_r' = a_1/(a_0 + a_1)$ and then it is a function dependent only on q, and not on β. figure 5.9 displays the reward E_r' as obtained numerically versus the cost q showing that $E_r' \simeq q$. They are not exactly equal because, as explained in equation (4.3) of chapter 4, they may differ when death frequencies f are not small compared with resource intake.

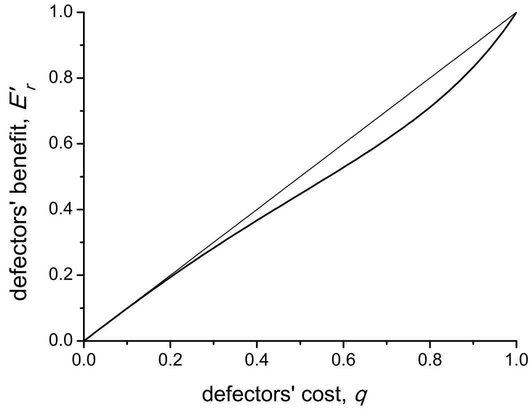


Figure 5.9: *Defectors benefit versus costs in coexistence states. It equals the frequency rate function $f(q)$ (see text). The dashed line $E'_r = q$ is a guide to the eye.*

In the present model, f cannot be arbitrarily chosen because of the constant population condition. Indeed, equations (5.14)–(5.15) readily show that $f = c_1/(c_0 + c_1) = E'_r$ and then figure 5.9 also displays $f(q)$. One observes that f is generally of order 1 (this is the cause of the small deviations found in figure 5.9). At small q, however, f is also small and E'_r and q match perfectly.

One can further study the transition by drawing a phase diagram $\beta - q$ with the regions where each behaviour dominates. It is possible to obtain an analytical expression for the critical curve $\beta_c(q)$ by performing a stability analysis. To do so, let us recall that for a fixed point to be stable in three dimensions the trace and determinant of the Jacobian matrix must be negative, since all three eigenvalues must be negative. Our model system given by equations (5.14)–(5.17) has at least two fixed points, corresponding to pure populations of cooperators and defectors: (A) $c_1 = 1$ (the remaining variables equal to 0), and (B) $c_0 = c_1 = 0$ and $d_1 \neq 0$ obeying, according to equation (5.16),

$$d_1(f + \beta q) = 1. \tag{5.20}$$

As we know, it may also have a mixed fixed point, given by equation (5.18), but it need not be considered for our present purpose. Linear stability of fixed point A leads to the jacobian matrix

$$\begin{pmatrix} -2 & 0 & \beta \\ \\ 1 & -1 & -1-2\beta+\beta q \\ \\ -1 & -1 & \beta(1-q)-1 \end{pmatrix}, \tag{5.21}$$

with determinant $D = 4\beta(1-q) > 0$. The positive sign shows that at least one of its three eigenvalues is positive. Then point A is always unstable for $q < 1$ and cooperators never occupy the whole population. Fixed point B provides the following jacobian matrix

$$\begin{pmatrix} -1-f_* & \beta d_1^* & 0 \\ \\ 1 & 1-\beta d_1^*-f^* & 0 \\ \\ -1 & -1-d_1^*\dfrac{df}{dc_1}+\beta d_1^* & -\beta q-f_*-d_1^*\dfrac{df}{dd_1} \end{pmatrix}, \tag{5.22}$$

where d_1^* and f_* are the values of these quantities in fixed point B. To be compact, let us call $J_{33} = -(\beta q + f_* + d_1^*(1+2\beta(1-q)d_1^*)) < 0$. The trace is $T = J_{33} - 2f_* - \beta d_1^* < 0$, and the determinant can be written as

$$D = J_{33}(-1+\beta d_1^* f_* + f_*^2). \tag{5.23}$$

Then, for point B to be stable the term inside parenthesis has to be positive. Although this is not a sufficient condition to prove that point B is stable, the numerical resolution of equations (5.14)–(5.17) shows that this is the case; this is the region where defectors are dominant. When the parenthesis in equation (5.23) is negative point B becomes unstable, which means that a small fraction of cooperators will grow and survive (notice that point B is the only fixed point with only defectors). Then, since point A is also unstable, in this situation there must exist a third (mixed) fixed point in the dynamics. equation (5.18) supplies the solution for this mixed fixed point and numerical solutions show it is a stable attractor, the one describing the stationary coexistence of cooperators and defectors found at large β values. In order to obtain the curve $\beta_c(q)$ separating the regions of dominance of defectors from the mixture of cooperators and defectors we should find d_1^* from equations (5.17) and (5.20) and solve the equation

$$-1+\beta_c d_1^* f_* + f_*^2 = 0. \tag{5.24}$$

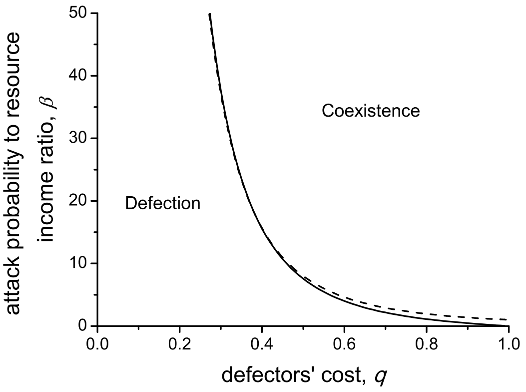


Figure 5.10: *Phase diagram. The solid line indicates the numerical solution, the dashed line the analytical approximation* $\beta_c = q^{-3}$. *Cooperation is favoured at large* β, *i.e. small resource fluxes or large attacking rates (see text).*

The exact analytical solution of this transition curve is very cumbersome, so that we try two alternative routes. One is to obtain a numerical solution (see figure 5.10, the other one is to find an approximate analytical solution. In this sense, let us note that, if $\beta^2 q^3 \gg 1$ equations (5.17) and (5.20) show that $d_1^* \simeq (\beta q)^{-1}$, because $\beta q \gg f_* \simeq (\beta q^2)^{-1}$. In this limit, the instability condition (5.24) just gives

$$\beta_c = q^{-3}, \tag{5.25}$$

which provides an excellent approximation not only for $\beta_c^2 q^3 \simeq q^{-3} \gg 1$ (say $q \lesssim 0.5$) but over the whole range $0 \leq q \leq 1$ as shown when compared with the exact numerical solution (figure 5.10).

figure 5.10 shows that cooperation is favoured at large costs q and large β, whereas defectors dominate in the opposite limit. The origin of the dependence on the average cost q is rather direct: the larger the cost, the less favourable for defectors to reproduce. The dependence on parameter β is, however, counterintuitive since (at first sight) one would expect that large attack rates (large β) should benefit defectors. The explanation is not easy due to the nonlinearities involved in the model. One might think that the origin of the observed behaviour relies on the exploitation mechanism that explains the existence itself of coexistence states, and accordingly reason that large attacking rates would cause a great damage on cooperators, which would reduce rewards over costs, ultimately harming defectors. However, this is not what happens, since we have seen above that the average reward E_r' is a function of q only, and then it does not change when increasing β at fixed q.

One explanation of why large β favour cooperators is that it leads to a small fraction of defectors in the active state (D_1), thus reducing the damage on cooperators. In effect, if resources are abundant individuals receive them frequently and there will be large populations of D_1 individuals; if resources are scarce, only a few individuals will be in state $E_i = 1$. The same occurs if attacking rates are large. Since attacks are indiscriminate, defectors are also victim of the attacks, which decrease the number of D_1 individuals; conversely for small attacking rates. This explanation is consistent with the behaviour of d_1 displayed in figure 5.8. Indeed d_1 decreases yet from $\beta = 0$, i.e. below the transition, as it can be seen from our approximate solution $d_1^* \simeq (\beta q)^{-1}$. Below some critical population value depending on q (around q^2) the reduced population of defectors in the active state is not capable of extinguishing cooperators. It is worthwhile to point out that parasites continuously receive resources from the environment and interact, and then, they change from active to inactive states continuously. In the stationary state, the fraction of defectors in the population is $d_0 + d_1$. These defectors spend a fraction of time $d_0/(d_0 + d_1)$ in inactive states and $d_1/(d_0 + d_1)$ in active states.

5.4 Conclusions

In this chapter, we have studied the dynamics of three analytical models describing the evolution of well-mixed populations of unconditional cooperators and defectors under limiting resources. These models try to capture and expand the essence of the agent-based models presented in previous chapters. The main differences of the models introduced here and the agent-based models are, on the one hand, that the distribution of internal resources is limited to two states, instead of a continuous distribution and, on the other, that the cost paid by defectors is now a stochastic process. Furthermore, the third model deals with constant population sizes, which was not implemented in the agent based models.

Analytical models have the advantage with respect to simulation models of allowing for a complete and more compact analysis of their behaviour. Indeed, we have expanded the study of the agent-based models by separating the time scales of all the mechanisms in the model. In effect, in the agent-based models, we assumed equal rates for attacks of defectors and the feeding process. Here, in contrast, we consider different rates for each process. This increases in one the number of parameters. However, the nondimensionalization of the models has permitted us to identify the dimensionless parameters ruling the model dynamics, a study which is not easy to perform in agent-based models. As a result, we have easily seen that in sections 5.1 and 5.2 the resource influx from the environment determines the steady state size of the final population, but not its composition, a result that was observed in the simulations of the agent based models. Furthermore in the three models (sections 5.1–5.3) the final composition is ruled by just two parameters: the average cost paid by defectors and the number of attacks in a characteristic time.

The behaviour of the analytical models resemble very much the ones obtained in the corresponding more complex agent-based models, remarkably allowing for the survival of cooperators in some regions of the parameter space. When resources limit only reproduction, cooperators are able to coexist with defectors at larger defectors cost and larger number of interactions in a lifetime. The latter behaviour may seem surprising, as one would expect defectors attacks to benefit defectors and harm cooperators. However, since attacks are indiscriminate, a large number of interactions in a lifetime reduces the number of defectors in active states and eventually allows for the survival of cooperators. Remarkably, this process occurs following a phase transition, so that cooperators are able to survive only when parameters surpass some critical value. When resources restrict reproduction and survival the fate of the system is essentially a population of defectors at small defector costs, and a population of cooperators at large costs, separated by a thin region of coexistence at intermediate costs. Aside from the coexistence region in the second model (resources constraining also survival), this is the behaviour found in the agent-based model. The origin of this difference is probably due to the different resource distribution in both models (discrete in the analytical model, and continuous in the agent based model).

Finally, we have developed a simple model describing a phase transition from defective parasitic populations when resources are abundant to the survival of pacific cooperators when resources are scarce. In contrast to the models in chapters 3 and 4, and sections 5.1 and 5.1, where the same limiting resource ruled reproduction and population size, and which do not display this transition, the model studied here assumes that the factor limiting reproduction is different from the one limiting the population size. The simplest case for the latter is space limitation. Thus, the results presented here may represent a first step in the route towards the emergence of undifferentiated multicellularity by cooperative aggregation triggered by resource or energetic constraints.

Part III

Destruction as a source of regeneration

In this block we study the effect of destructive behaviours in the promotion of cooperation. To this end, we introduce destructive agents –called Jokers in the following– in a population of unconditional cooperators and defectors fulfilling a prisoner's dilemma. We will show that the introduction of this third agent is able to induce robust evolutionary cycles in the presence of mutations, where Defectors beat Cooperators (as it corresponds to a PD), which are overcome by Jokers which, in turn, are defeated by Cooperators, in a Rock-Paper-Scissors (RPS) dynamics. To this end, the three strategies are engaged in a Public Goods (PG) game, a standard generalisation of the PD for more than two agents. The joker behaviour represents the first simple behaviour (it does not require any special feature or cognitive ability) which allows for the existence of cycles when mutations are present.

In chapter 6 we analyse the dynamics generated by Jokers in infinite populations through the study of the replicator-mutator equation. In chapter 7, we expand the analysis to finite populations obeying several selection rules, showing the robustness of the cyclic dynamics.

Chapter 6

Destruction and regeneration, the altruism cycle

Summary

The study of the effect of Jokers (destructive agents) in the evolution of cooperation in infinite populations is carried out in this chapter. The chapter is organised as follows. Section 6.1 motivates the study and presents biological and social systems where the effect studied might be observed. In section 6.3 the model is presented and the existence of cycles shown. Section 6.4 is devoted to analyse the replicator dynamics for infinite populations. Finally, section 6.5 compares the joker model with other RPS dynamics and discusses the results.

6.1 Introduction

Piotr Kropotkin supported the idea that the evolution of mutual aid is an important factor for the evolution of individuals facing a common risk or danger, as it might be the entropy, an inclement weather or a common enemy. A metaphorical example of such danger–induced cooperative behaviours can be found in the recent Hollywood movie *The Dark Knight* (2008), where the comic character known as the Joker jeopardises a whole society spreading chaos and destruction with no aim of benefit at it. The situation is so critical that even the mob is willing to cooperate with honest people to stop the Joker–created nonsensical catastrophe. This fiction provides a visual metaphor of how an event like this can force exploiters of society to collaborate temporarily to fight the common enemy. Society is an emergent structure resulting from the cooperation among its members, and exploiters need society to survive, even if they do not contribute to it. Thus they are specially sensitive to the destruction of society precisely because, being selfish agents, society is their only source of survival. The appearance of the Joker provides a strong incentive for cooperation.

Beside situations like the one depicted by the Joker metaphor, the importance of the inclusion of malicious agents on the game is also illustrated in other scenarios. Here are a few examples. Temporary coalitions of rival parties are constantly formed whenever a common enemy arises, only to restore their old rivalry once this enemy has been wiped out. During the Second World War U.S.A. and U.S.S.R. were allied in fighting Hitler, but they got engaged in the Cold War for decades after the danger of Nazism had been ruled out. It is also well known that strong affective links between humans are created when they face a common difficult situation. Biology is another source of potential examples. For instance, it has been shown that the perception of an increase in the risk of predation can induce cooperative behaviour in some bird species [111]. Indeed, prey species frequently form groups to increase the survival rate against predator attacks [112, 113]. In some cases, this has been proven to happen even in the absence of kinship among its members, as in the collective defence of spiny lobsters [114].

The existence of these temporary coalitions for defence against a common danger in rational and irrational agents alike calls for an evolutionary explanation. In this section a stylised evolutionary game [115] is presented, aimed at studying theoretically this enhancement of cooperation driven by the emergence of purely destructive agents. The game does not try to model any specific situation, but it proposes an abstract setting in which the role of the indiscriminate destructive action of these agents in enhancing cooperation is made clear.

The model presented here is a modification of the standard Public Goods (PG) game [116], the n-players version of the Prisoner's Dilemma and a paradigm of the risk of exploitation faced by cooperative behaviour [39]. It has been shown that several mechanisms involving reputation [117], allowing for volunteer participation [118, 119], punishing defectors [120, 121], rewarding cooperators [53] or structuring agents [122–124], can enhance cooperation. Here, we present a different mechanism for the enhancement of cooperation based on the existence of destructive agents.

The game involves n players who belong to one out of three different types: cooperators, who contribute to the public good at a cost for themselves; defectors, who free-ride the public good at no expense; and jokers, who do not participate in the public good —hence obtain no benefit whatsoever— and only inflict damage to the public good. Remarkably, the appearance of jokers promotes a rock-paper-scissors dynamics, where jokers outbeat defectors and cooperators outperform jokers, which are subsequently invaded by defectors. In contrast to previous models [118,119], the cycles induced by jokers are limit cycles, i.e. attractors of the dynamics, and exist in the presence of mutations; these properties make them robust evolutionary outcomes.

Therefore, paradoxically, the existence of destructive agents acting indiscriminately promotes cooperation.

6.2 The public goods game

The public good (PG) game is a generalisation of a prisoner's dilemma to the case in which interactions happen in groups of size n instead of between pairs of individuals (see section 1.5). In a PG game there is a population of M individuals. Then, $n \leq M$ individuals are extracted at random out from the total population and are engaged in the game: each individual contributes to a common pool according to its strategy, this pool is multiplied by some synergistic factor and, finally, the pool is equally shared among the n players. This provides the payoff of each individual for one round. It is usually assumed that interactions happen many times, and the averaged payoff results in the fitness variation –it is usually added to a constant baseline fitness– of each strategy. The evolutionary dynamics depends on the particular imitation rule chosen.

In a typical PG with cooperators (altruists) and defectors, each cooperator in an interaction group contributes with a cost c to the common enterprise, which turns into a benefit $b = rc$ to the group, being $r > 1$ the synergetic gain factor (for simplicity, one can take $c = 1$); defectors do nothing. Therefore, if there are m cooperators in the group the common good ascends to mr and each player (cooperator or not) receives a benefit of mr/n. The payoff for each defector is $\Pi_D = mr/n$, and that for a cooperator, $\Pi_C = \Pi_D - 1$, since the latter pays a cost $c = 1$. Thus, defectors have a higher payoff than cooperators in any interaction group.

For large populations, if $r < n$, it can be seen (see appendix 6.A) that the average payoff of cooperators is smaller than that of defectors, $P_C < P_D$, so that defectors get rid of cooperators and the final common good vanishes (i.e. the tragedy of the commons happens). In contrast, if all of them cooperated, they would obtain a common good of $n(r-1)$. Then, the case $r < n$ is a dilemmatic situation similar to the PD. On the contrary, if $r > n$, the situation is the opposite, $P_C > P_D$, and it always pays to cooperate.

In what follows, we analyse the fate of a population of Cooperators, Defectors and Jokers in the dilemmatic situation, $r < n$, and show that robust cycles may appear in the presence of mutations.

6.3 A public goods game with jokers: existence of limit cycles

The public goods game with Jokers works as follows: Groups are formed randomly, and each player's strategy is established before the group is selected. Hence, players have no memory. Every cooperator yields a benefit $b = rc$ $(r > 1)$ to be shared by cooperators and defectors alike, at a cost c for herself (this cost can be set to $c = 1$ without loss of generality: all other payoffs are given in units of c), and defectors produce no benefit at all but get their share of the public good. As for the new agents (jokers), every joker inflicts a damage $-d < 0$ to be shared equally by all non-jokers and gets no benefit. In a given game $0 \le m \le n$ denotes the number of cooperators, $0 \le j \le n$ the number of jokers, and $n - m - j \ge 0$ the number of defectors; $S = n - j$ expresses the number of non-jokers. In this group, the payoff of a defector will be $\Pi_\mathrm{D}(m, j) = (rm - dj)/S$, and that of a cooperator $\Pi_\mathrm{C} = \Pi_\mathrm{D} - 1$. Then, in each group, defectors will always do better than cooperators. The payoff of Jokers is always 0. In summary, we have

$$\begin{aligned} \Pi_{\mathrm{D}}(m,j) &= \frac{rm-dj}{S}, && 0 \le m \le S-1 \le n-1, \\ \Pi_{\mathrm{C}}(m,j) &= \frac{rm-dj}{S}-1, && 1 \le m \le S \le n, \\ \Pi_{\mathrm{J}}(m,j) &= 0, && 0 \le S \le n-1. \end{aligned} \tag{6.1}$$

A usual requirement of PG games is that $r < n$. Without this requirement the solution in which all n players are defectors is no longer a Nash equilibrium —hence the dilemma goes away. As shown later, the evolutionary dynamics for infinite populations yields the same constraint, i.e., if $r < n$ the dynamics asymptotically approaches the tragedy of the commons. However this is no longer true for finite populations, where the upper bound of r for which the tragedy of the commons takes place grows as M, the population size, decreases. In this case the tragedy of the commons arises whenever $r < r_{\max} = n(M-1)/(M-n)$ (see appendix 6.A; notice in passing that for a population of $M = n$ individuals, the evolutionary dynamics yields a tragedy of the commons for every $r > 1$).

An invasion analysis provides the clue as to why a rock-paper-scissors (RPS) cycle is to be expected when jokers intervene in the game. We shall assume that we have a population of M players of the same type and will consider putative mutations of one individual to any of the other two types. The mutation will thrive if the average payoff of the mutant after many interactions overcomes the average payoff of a non-mutant player. The result of this analysis (see appendix 6.A) is summarised in figure 6.1, which represents the three different patterns of invasion that can be observed within the region of interest $1 < r < r_{\max}$, $d > 0$:

I **Rock-paper-scissors cycle:** It arises whenever $r > 1 + d(n-1)$. This condition expresses the fact that a single cooperator gets a positive payoff in spite of the damage inflicted by $n-1$ jokers and therefore being a cooperator pays (jokers get no payoff whatsoever).

II **Joker-cooperator bistability:** If $1 + d/(M-1) < r < 1 + (n-1)d$ neither jokers nor cooperators can invade each other. Nonetheless defectors always invade cooperators, and jokers always invade defectors, so eventually only jokers survive,

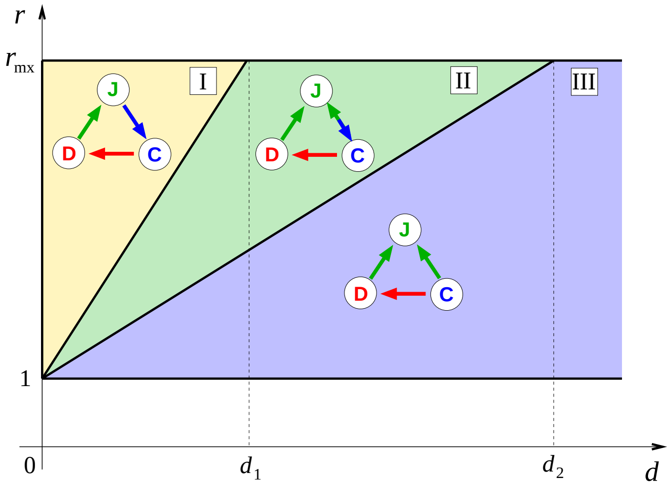


Figure 6.1: **Dynamics of invasions in a Public Goods game with jokers.** *The axes represent the gain factor* r *of the Public Goods game (i.e., the payoff each cooperator yields to the public good) and the "damage"* $d > 0$ *that every joker inflicts on the public good. The tragedy of the commons occurs for* $1 < r < r_{max} = n(M-1)/(M-n)$ *(see text), which includes the dilemmatic region* $1 < r < n$ *characteristic of PG games. Different colours are assigned to different invasion patterns: Light blue corresponds to a region where J invades both C and D (III); light green corresponds to a region where neither C nor J invades each other (there is bistability on the J–C line) but D invades C and is in turn invaded by J, so again everything ends up in J (II); finally, light yellow corresponds to a region where D invades C, J invades D, but C invades J back, thus generating a rock-paper-scissors cycle (I). The latter behaviour is the essence of the* Joker effect. *The equations of the straight lines separating the three regions are (from top to bottom)* $r = 1 + d(n-1)$ *and* $r = 1 + d/(M-1)$. *Notice that this scheme is valid for arbitrary* $n > 1$. *Also, for fixed* r, *all three regions are crossed upon varying* d, *whereas vice-versa is only true provided* $d < d_1 = M/(M-n)$. *The Joker effect does not occur if* $d > d_1$. *For large populations,* $M \gg 1$, *the region for the rock-paper-scissors cycle simplifies to* $n > r > 1 + (n-1)d$ *and* $d < 1$.

either because they are initially a majority or indirectly through the emergence of defectors.

III **Joker invasion:** If $r < 1 + d/(M-1)$ jokers will invade any homogeneous population, so a homogeneous population of jokers is the only stable solution. Notice that this region disappears for large populations ($M \to \infty$) because $r > 1$.

The RPS cycle C→D→J→C occurring in region I is the essence of the Joker effect.

6.4 Infinite population dynamics

We can gain further insight into this effect by studying a replicator-mutator dynamics [16]. We assume a very large population in which the three types are present at time t in fractions x (cooperators), y (defectors), and $z = 1-x-z$ (jokers). Agents interact with the whole population by engaging in the above described game within groups of n randomly chosen individuals [125]. Average payoffs of a cooperator, a defector, and a joker are denoted $P_{\mathrm{C}}(x,z)$, $P_{\mathrm{D}}(x,z)$, and $P_{\mathrm{J}}(x,z)$, respectively. Assuming individuals of a given type mutate to any other type at a rate $\mu \ll 1$, the replicator-mutator equations for this system will be

$$\begin{aligned} \dot{x} &= x(P_{\mathrm{C}} - \bar{P}) + \mu(1-3x), \\ \dot{y} &= y(P_{\mathrm{D}} - \bar{P}) + \mu(1-3y), \\ \dot{z} &= z(P_{\mathrm{J}} - \bar{P}) + \mu(1-3z), \end{aligned} \tag{6.2}$$

where $\bar{P} = xP_{\mathrm{C}} + yP_{\mathrm{D}} + zP_{\mathrm{J}}$ is the mean payoff of the population at a given time. Explicit expressions for P_{C}, P_{D}, and P_{J} can be obtained by averaging over all samples of groups of n players extracted from a population containing Mx cooperators, My defectors, and Mz jokers, in the limit of very large populations ($M \to \infty$); the derivation can be found in 6.B. Let us recall that the parameters of the game in the infinite population limit satisfy $1 < r < n$ and $d > 0$; the first condition enforces the public goods dilemma, and the second one implies that jokers beat defectors in the absence of cooperators, because defectors receive the damage inflicted by jokers thus obtaining a negative payoff.

The stability analysis of the dynamical system (6.2) recovers the picture displayed in figure 6.1 (taking $M \to \infty$). When $r < 1+(n-1)d$ the system is in region II. The only stable equilibrium is a population of only jokers and any trajectory of equation (6.2) is asymptotically attracted to it. Thus, in this region the destructive power of jokers is high enough to wipe out the populations of both cooperators and defectors. But the most interesting situation takes place when

$$r > 1 + (n-1)d, \tag{6.3}$$

i.e., in region I. In the absence of mutations the dynamical system (6.2) has three saddle points at the corners of the simplex as well as an unstable mixed equilibrium

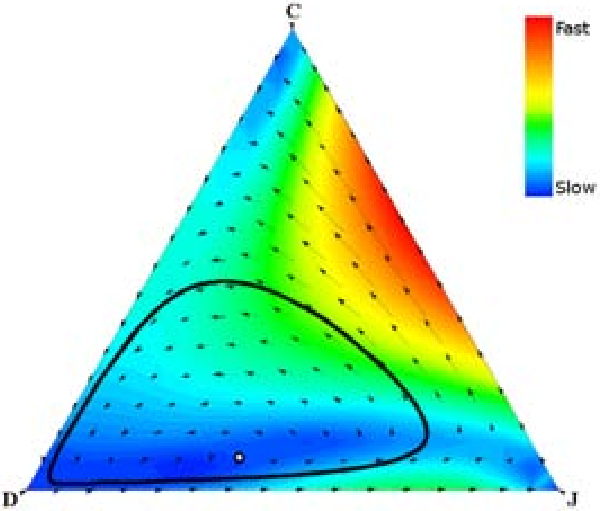


Figure 6.2: **The Joker effect in public goods games for large, well-mixed populations.** *The simplex describes the replicator-mutator dynamics, equation* (6.2)*, for a population of cooperators, defectors and jokers with parameter values satisfying* $n > r > 1+d(n-1)$*, for which a rock-paper-scissor dynamics is expected (yellow region in figure 6.1). When mutation rates are small, the only equilibrium is a repeller (white dot), and trajectories end up in a stable limit cycle (black line). Thus the presence of jokers induces periodically a burst of cooperators. Cooperators abound during short time spans, as shown by the small fraction of cooperators in the equilibrium point. Parameters:* $n = 5$*,* $r = 3$*,* $d = 0.4$ *and* $\mu = 0.005$*. (Images generated using a modified version of the Dynamo Package [127]).*

(see appendix 6.C). As a consequence, the attractor of the system is the heteroclinic orbit C → D → J → C. The period is infinite because the system delays more and more around the saddle points. When mutations occur the corners of the simplex are no longer equilibria, and one is left with the interior fixed point, which for small mutations is a repeller (see appendix 6.C). Since trajectories are confined within the closed region of the simplex, they are attracted to a stable limit cycle for any $r > 1$ (a direct consequence of the Poincaré-Bendixon theorem [126]), as shown in figure 6.2.

The size of the cycle depends on the parameter values. It grows as d increases —i.e., when jokers play a more important role (figure 6.3)— and as the mutation rate decreases (figure 6.4). For both, large values of d [compatible with condition (6.3)]

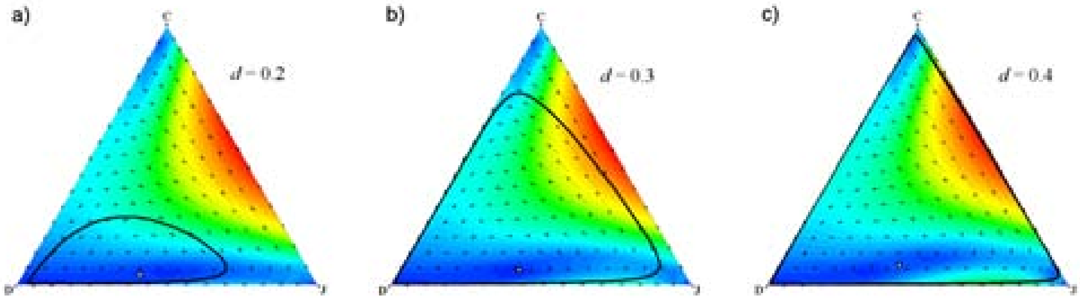


Figure 6.3: **Replicator-mutator dynamics as a function of the damage d inflicted by jokers**. *For a fixed mutation rate, the size of the cycles increases as the damage increases. Parameters: $n = 5$, $r = 3$ and $\mu = 0.001$.*

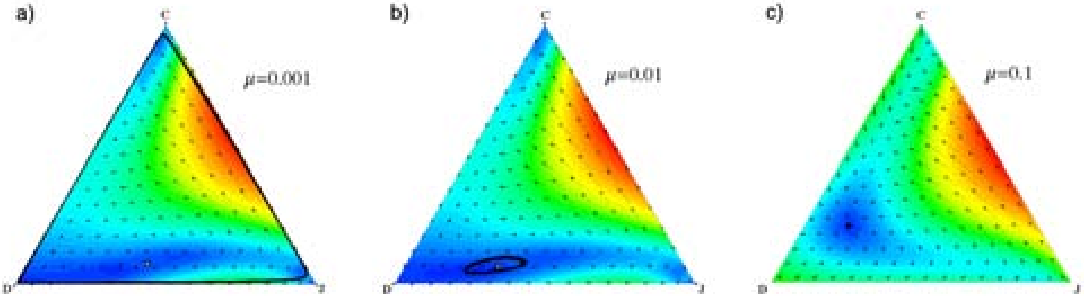


Figure 6.4: **Replicator-mutator dynamics as a function of the mutation rate μ**. *(a) For very small mutation rates cycles approach the boundary of the simplex. (b) As μ increases, the cycle amplitude decreases and, above a critical value (typically, $\mu_c \simeq 0.01$), cycles disappear in a Hopf bifurcation yielding a stable mixed equilibrium (c). Parameters: $n = 5$, $r = 3$ and $d = 0.4$.*

and very small mutations, the cycle closely follows the boundaries of the simplex (see figure 6.4a). By increasing the mutation rate (typically over 0.01), cycles disappear in a Hopf bifurcation yielding a stable mixed equilibrium (figures 6.4b-c).

6.5 Discussion on Jokers in infinite populations

The evolutionary scheme presented in the last section has some resemblances with the effect of volunteering in a PG game [118, 119]. There, the introduction of a third agent (so called loner), which does not participate in the game but receives a constant payoff, is able to generate cycles. However, the two games are fundamentally different. This can be told from the dynamic behaviour of the system. In both cases, the existence of a third agent which does not participate in the game is the ultimate reason why cooperators periodically thrive through a Rock-Paper-Scissor dynamics. However, while the loners game leads to neutrally stable cycles around a centre, trajectories in the Joker model are attracted by the heteroclinic cycle C–D–J–C. The difference is even more striking if mutations are included. Mutations replace the cycles in the loner model by a stable mixed equilibrium. In contrast, in the Joker model mutations substitute the heteroclinic orbit by a stable limit cycle, which undergoes a transition (Hopf bifurcation) to a stable mixed equilibrium above a threshold mutation rate.

These two scenarios can be understood from the analysis of general RPS games [115]. In the absence of mutations there are three situations: (a) orbits are attracted towards an asymptotically stable mixed equilibrium (the case of the loners game with mutations), (b) orbits cycle around a neutrally stable mixed equilibrium (the case of the loners game without mutations), and (c) orbits go away from an unstable mixed equilibrium and approach the heteroclinic orbit defined by the border of the simplex (the case of the Joker game without mutations). If mutations are added to the latter type of RPS games, limit cycles and a Hopf bifurcation upon increasing the mutation rate are also found [128]. Limit cycles are robust to perturbations and have a well defined amplitude irrespective of the initial fractions of players (as long as it is not at the border of the simplex). Therefore, they are true attractors of the dynamics, and can thus be regarded as a robust evolutionary outcome, in contrast to neutrally stable cycles.

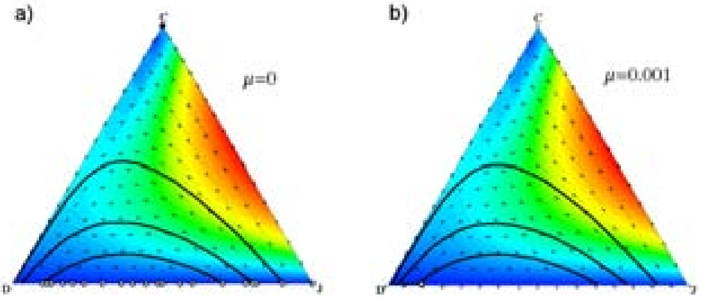


Figure 6.5: **Replicator-mutator dynamics for** $d = 0$. *If jokers are just passive agents cooperators go extinct. (a)* $\mu = 0$. *The system ends up in a point of the line DJ with a majority of defectors. (b)* $\mu = 0.001$. *Mutation generates one single stable state made up mostly by defectors. Parameters:* $n = 5$, $r = 3$ *and* $d = 0$.

In contrast to loners, which do not participate in the game but receive a benefit outside of it, jokers do not receive any benefit at all and cause damage to players. Both loner and joker models coincide —in the absence of mutations— when the damage inflicted by jokers and the benefit obtained by loners are both zero. In this case both become simply non-participants in the game, and the only effect they produce is a reduction in the effective number of players in the game, which is not enough to induce an oscillatory dynamics (see figure 6.5). In other words, the appearance of the RPS cycle which periodically increases the population of cooperators in the presence of jokers can only happen, remarkably, provided $d > 0$, i.e., if jokers are truly destructive agents.

6.6 Conclusions

In this chapter light has been shed on a still unexplored aspect of evolutionary game theory (the presence of a destructive strategy) in the prototypical PG game. It has been shown, both theoretically and by numerical simulations, that the addition of purely destructive agents (jokers) to a standard PG game has, paradoxically, a positive effect on cooperation. Bursts of cooperators are induced through the appearance of a RPS cycle in which jokers beat defectors, who beat cooperators, who beat jokers in succession. The evolutionary dynamics provoked by the Joker, with periods of cooperation, defection and destruction of the PG, may help understand the appearance of cognitive abilities that allow individuals to foresee the destructive periods, promoting in advance the necessary cooperation to avoid them.

As shown, the "Joker effect" occurs both in finite and infinite populations, discarding the possibility of its being an artificial size-depending phenomenon. The study of finite populations by means of stochastic methods is carried out in the next chapter.

Appendices

6.A Finite populations: invasion analysis

We shall consider the situation in which in a homogeneous population of M individuals with the same strategy Y, one of them mutates (changes) to a different type X. The new individual will invade provided its average payoff after many interactions, P_{X}, is larger than the average payoff of a Y individual, i.e., $P_{\mathrm{X}} > P_{\mathrm{Y}}$. Average payoffs can be evaluated as follows. The population is made of one X player and $M-1$ Y players. Thus, when playing the game, the X player will always interact with $n-1$ Y players. Therefore

$$P_{\mathrm{X}} = \Pi_{\mathrm{X}}(1X, (n-1)Y). \tag{6.4}$$

On the other hand, the $n-1$ opponents of a Y player can be of just two types: either all $n-1$ are Y players, or $n-2$ are Y players and one is the single X player. The latter situation occurs with probability $(n-1)/(M-1)$. Therefore the average payoff of a Y player will be

$$P_{\mathrm{Y}} = \Pi_{\mathrm{Y}}(nY)\frac{M-n}{M-1} + \Pi_{\mathrm{Y}}(1X, (n-1)Y)\frac{n-1}{M-1}. \tag{6.5}$$

Next we derive the invasion conditions for homogeneous populations of three types of players. In this new scenario we must consider the six different situations arising form the pair interactions that can be formed:

(a) $1\mathrm{D} + (M-1)\mathrm{C}$.

$$P_{\mathrm{C}} = r - 1 - \frac{r}{n}\frac{n-1}{M-1}, \qquad P_{\mathrm{D}} = r - \frac{r}{n}. \tag{6.6}$$

The tragedy of the commons occurs when defectors overcome cooperators, i.e., $P_{\mathrm{D}} > P_{\mathrm{C}}$. This happens iff

$$r < n\frac{M-1}{M-n}. \tag{6.7}$$

We will henceforth assume (6.7) to hold. This condition contains the dilemmatic region $1 < r < n$ of PG games. In the limit $M \to \infty$, the inequality (6.7) reduces to $r < n$ and both, the conditions for the dilemma and the tragedy of the commons coincide.

(b) $1\mathrm{C} + (M-1)\mathrm{D}$.

$$P_\mathrm{C} = \frac{r}{n} - 1, \qquad P_\mathrm{D} = \frac{r}{n}\frac{n-1}{M-1}. \tag{6.8}$$

Because of (6.7) $P_\mathrm{D} > P_\mathrm{C}$, so *C never invades D.*

(c) $1\mathrm{J} + (M-1)\mathrm{C}$.

$$P_\mathrm{C} = r - 1 - \frac{d}{M-1}, \qquad P_\mathrm{J} = 0. \tag{6.9}$$

Since $P_\mathrm{J} > P_\mathrm{C}$ iff

$$r < 1 + \frac{d}{M-1}, \tag{6.10}$$

then *J invades C iff* (6.10) *holds.*

(d) $1\mathrm{C} + (M-1)\mathrm{J}$.

$$P_\mathrm{C} = r - (n-1)d - 1, \qquad P_\mathrm{J} = 0. \tag{6.11}$$

Since $P_\mathrm{C} > P_\mathrm{J}$ iff

$$r > 1 + (n-1)d, \tag{6.12}$$

then *C invades J iff* (6.12) *holds.*

(e) $1\mathrm{D} + (M-1)\mathrm{J}$.

$$P_\mathrm{D} = -(n-1)d, \qquad P_\mathrm{J} = 0. \tag{6.13}$$

As long as $d > 0$ we will have $P_\mathrm{J} > P_\mathrm{D}$, then *D never invades J.*

(f) $1\mathrm{J} + (M-1)\mathrm{D}$.

$$P_\mathrm{D} = -\frac{d}{M-1}, \qquad P_\mathrm{J} = 0. \tag{6.14}$$

As long as $d > 0$ we will have $P_\mathrm{J} > P_\mathrm{D}$, then *J always invades D.*

Figure 6.1 illustrates the different regions of interest in this game. The most interesting one is that in which there is a rock-paper-scissor rotation between C, D, and J, which corresponds to

$$1 < r < n\frac{M-1}{M-n}, \qquad 0 < d < \frac{r-1}{n-1}. \tag{6.15}$$

6.B Infinite populations: average payoffs

We evaluate here the average payoffs P_{X} obtained by each strategy (i =C, D, J) in this game when the population is very large. These functions will determine the dynamics of the population through the replicator equation. As before, sample groups of n individuals playing the game are randomly formed, and it is assumed that each player is sampled a large number of times before payoffs are compared in order to update strategies. The payoff for a given strategy is therefore proportional to the average payoff that a player using this strategy obtains playing against the whole population. This average payoff will depend only on the player's strategy and the composition of the population, described by a fraction x of cooperators, z of jokers and $y = 1 - x - z$ of defectors. Notice that $P_{\mathrm{J}} = 0$ for any composition of the population, so only payoffs of cooperators and defectors need to be calculated.

6.B.1 Defectors

The average payoff of a defector is

$$P_D = \left\langle \frac{rm - dj}{S} \right\rangle, \tag{6.16}$$

where the symbol $\langle \cdots \rangle$ denotes an average over samples of $n - 1$ opponents randomly selected from the population. The average $\langle m/S \rangle$ can be obtained as in [119], yielding

$$\left\langle \frac{m}{S} \right\rangle = \frac{x}{1-z}\left(1 - \frac{1-z^n}{n(1-z)}\right).$$

Since $j = n - S$, the second term in equation (6.16) can be written as $n\langle 1/S \rangle - 1$, where

$$\left\langle \frac{1}{S} \right\rangle = \sum_{S=1}^{n} \binom{n-1}{S-1} (1-z)^{S-1} z^{n-S} \frac{1}{S},$$

the factor in front of $1/S$ in the summation being the probability of having $S - 1$ non-jokers in a group of $n-1$ randomly chosen players. By using the identity $a\binom{a-1}{b-1} = b\binom{a}{b}$, the latter expression becomes

$$\left\langle \frac{1}{S} \right\rangle = \frac{1-z^n}{n(1-z)}.$$

Joining the two averages one gets the average payoff of a defector,

$$P_{\mathrm{D}} = r\frac{x}{1-z}\left(1 - \frac{1-z^n}{n(1-z)}\right) - d\left(\frac{1-z^n}{1-z} - 1\right), \tag{6.17}$$

the first term arising from the exploitation of cooperators and the second one being the damage inflicted by jokers.

6.B.2 Cooperators

The difference $P_\mathrm{D} - P_\mathrm{C}$ can be written as

$$P_\mathrm{D} - P_\mathrm{C} = \left\langle 1 - \frac{r}{S} \right\rangle \tag{6.18}$$

because in a group of $S-1$ opponents switching from cooperation to defection yields a payoff increment of $1 - r/S$: the defector's payoff gets reduced by r/S because there is one cooperator less in the group, but adds 1 to her payoff because she does not pay the cost of cooperating [119]. The average in the r.h.s. of equation (6.18) just contains $< 1/S >$, thus yielding

$$P_\mathrm{D} - P_\mathrm{C} = 1 - \frac{r}{n}\frac{1-z^n}{1-z}. \tag{6.19}$$

Finally, from equations (6.17) and (6.19) one gets

$$\begin{aligned} P_C = & r\frac{x}{1-z}\left(1 - \frac{1-z^n}{n(1-z)}\right) + \frac{r}{n}\frac{1-z^n}{1-z} - 1 \\ & - d\left(\frac{1-z^n}{1-z} - 1\right). \end{aligned} \tag{6.20}$$

6.C Infinite populations: proof of existence of limit cycles

To complete the proof that the system ends up in a limit cycle it remains to show that the interior equilibrium of Eqs ((6.2)) is a repeller, i.e., its two eigenvalues have positive real parts. The interior equilibrium and its stability can be evaluated in the limit of small mutation rates, the one we are interested in. In this case, one can neglect the dependence of μ in the position of the fixed point. We are thus faced with the solution of the dynamical system ((6.2)) without the mutation term. The calculation becomes simple for $n = 2$, and tractable for $n > 3$. The proofs are treated separately in the next subsections.

6.C.1 Interior fixed point for $n = 2$

The interior fixed point (x_0, y_0, z_0) satisfies $P_{\mathrm{C}} = P_{\mathrm{D}} = 0$. According to equation (6.19), the first equality requires $(1 + z_0)r = 2$, yielding

$$z_0 = \frac{2-r}{r}.$$

Since $n = 2 > r > 1$, one has $0 < z_0 < 1$, as it should. The second equality, $P_{\mathrm{D}} = 0$, produces

$$x_0 = 2d\,\frac{2-r}{r^2}.$$

Condition $r > 1 + d$ from expression (6.3) guarantees that $0 < x_0 < 1$ and $0 < y_0 = 1 - x_0 - z_0 < 1$. In order to analyse the stability of this equilibrium, we consider frequencies x and z as the independent variables of the two-dimensional system. To prove that the equilibrium is a repeller it suffices to show that the trace and determinant of the Jacobian matrix at the fixed point are both positive. For $n = 2$, equations ((6.2)) become

$$\dot{x} = -\frac{1}{2}x(2dz^2 - rz + 2 - r - 2x + rx), \tag{6.21}$$

$$\dot{z} = z[(1-r)x + dz(1-z)]. \tag{6.22}$$

The Jacobian matrix in the interior equilibrium is

$$\begin{pmatrix} \dfrac{d(2-r)^2}{r^2} & \dfrac{d(2-r)(r^2+4dr-8d)}{r^3} \\ -\dfrac{(2-r)(r-1)}{r} & \dfrac{d(2-r)(3r-4)}{r^2} \end{pmatrix}, \tag{6.23}$$

whose trace, T, and determinant, D, are

$$T = \frac{2d(2-r)(r-1)}{r^2} > 0, \tag{6.24}$$

$$D = \frac{d(r-2)^2(r^2 + r(d-1) - 2d)}{r^3} > 0. \tag{6.25}$$

T is positive because $n = 2 > r > 1$. To prove that the determinant is positive, we should realise that the second bracket in its expression can be written as $r(r-1) - d(2-r)$, which is larger than $2(r-1)^2 > 0$ because $r > 1 + d$.

6.C.2 Interior fixed point for $n > 3$

We use the same procedure as in the previous case. The fraction of jokers z_0 of the interior equilibrium arises from $P_{\text{C}} = P_{\text{D}}$, namely equation (6.19). Once it is found, x_0 follows from $P_{\text{D}} = 0$, c.f. equation (6.17).

Calculation of z_0

z_0 is obtained as the solution to

$$1 - \frac{r}{n}\frac{1 - z^n}{1 - z} = 0, \tag{6.26}$$

which is equivalent to

$$\sum_{i=0}^{n-1} z^i = n/r. \tag{6.27}$$

The latter equation has exactly one solution, namely the crossing of the polynomial in the l.h.s of equation (6.27) with the constant $n/r > 1$. Since $r > 1$, this occurs at $0 < z_0 < 1$, consistent with the meaning of z_0. There is no analytical solution to equation (6.26) for arbitrary n. There exists, however, a simple analytical solution in the limit of large n, which is indeed an excellent approximation for all $n > 3$. It can be obtained neglecting z^n as compared to 1 in (6.26), which leads to

$$z_0 \approx 1 - \frac{r}{n}. \tag{6.28}$$

Since $r < n$, one has, of course, $0 < z_0 < 1$. For consistence, $z_0^n = (1 - \frac{r}{n})^n \approx e^{-r} \ll 1$, which holds, say, for $r > 3$. Notice that if $r \ll n$ the equilibrium approaches allJ, so that cycles get very close to this state in this limit.

Calculation of x_0

Let us impose $P_{\text{D}} = 0$. Introducing (6.26) into (6.17) one finds

$$x_0 \approx \frac{d}{r-1}\left(\frac{n}{r} - 1\right)(1 - z_0). \tag{6.29}$$

Conditions $d > 0$, $n > r > 1$, and $r > 1 + (n-1)d$ yield $0 < x_0 < 1$ and $0 < x_0 + z_0 < 1$, so that the three fractions are smaller than 1. Substituting z_0 from expression (6.28) into (6.29) one finally obtains

$$x_0 \approx \frac{d}{r-1}\left(1 - \frac{r}{n}\right). \tag{6.30}$$

Stability of the interior equilibrium

We need to determine the Jacobian matrix for the equilibrium (x_0, z_0) given by equations (6.29) and (6.28). The dynamical system ((6.2)) can be written as

$$\begin{aligned}\dot{x} = &-\frac{x}{n(1-z)^2}\Big(-r+n-rnxz-dnz^{n+1}+2nxz\\&-nxz^2-2nz+rx-rxz^n+dnz^2-nx+rz^n \qquad (6.31)\\&+nz^2+rz-rz^{n+1}+rnxz^2+dnz^{n+2}-dnz^3\Big),\\\dot{z} = &-(-dz+rx+dz^n-x)z. \qquad (6.32)\end{aligned}$$

The first equation is very cumbersome. Fortunately, as already explained, in the limit of large n and if $r > 3$ one can neglect terms of order z^n and above. Using expressions (6.28) and (6.30), the Jacobian matrix J can be written as $J = Yd(n-r)/n$, where

$$Y = \begin{pmatrix} \dfrac{n-r}{r} & \dfrac{nr(r-1)+d(r-n)(r^2-r+n)}{r^2(r-1)^2} \\ -\dfrac{r-1}{d} & 2 \end{pmatrix}. \qquad (6.33)$$

(Notice that the factor $d(n-r)/n > 0$.) As the diagonal elements of this matrix are positive, the trace is positive. Also $Y_{zx} < 0$ and, as we show next, $Y_{xz} > 0$, therefore the determinant turns out to be positive, and the interior equilibrium is a repeller. To see that $Y_{xz} > 0$ we must show that the numerator is positive. This can be shown by writing it as

$$nr(r-1)+d(r-n)(r^2-r+n) > (r-1)^2\frac{(n-r)^2+nr}{n-1} > 0.$$

The first inequality follows from condition $r-1 > (n-1)d$.

Chapter 7

Destruction towards altruism in finite populations

Summary

The analysis of the effect of destructive behaviours in chapter 6 is expanded here to finite population sizes and different updating (or selection) rules. In order to carry out such analysis, stochastic methods are used, which allow for a precise description of the dynamics of the system. The structure of the chapter is as follows: Section 7.1 provides the stochastic equations describing the evolutionary dynamics for finite populations. In section 7.2 we analyse the joker dynamics in finite populations using different selection dynamics in order to check the existence of cycles. Section 7.3 is devoted to discuss the dynamics in finite populations.

7.1 Stochastic dynamics in finite populations

The deterministic evolution represented by the replicator-mutator equation is an idealisation of the system behaviour in the limit of infinite populations. To get a deeper insight into the model we need to address the question what happens when populations have a finite size M. To begin with we need to describe the microscopic dynamics in more detail. Hauert et al. [57] have proposed a protocol in which random selections of n players are gathered together to play the game. After receiving their corresponding payoffs the group dissolves and a new one is sampled. This sampling is made a sufficient number of times so that on average each player receives a payoff proportional to the mean payoff she can obtain given the composition of the population.

Suppose there are m cooperators, j jokers, and $M-m-j$ defectors in the population. The probability that the sampling of n individuals contains k cooperators, l jokers, and $n-k-l$ defectors is given by the extended hyper-geometric distribution

$$p(k,l|n,m,j,M) = \frac{\binom{m}{k}\binom{j}{l}\binom{M-m-j}{n-k-l}}{\binom{M}{n}}. \tag{7.1}$$

The average payoff of strategy X within this population, $P_{\mathrm{X}}(m,j)$, is obtained by averaging formulae (6.1) with this probability distribution. This is done in Appendix 7.A, where explicit expressions for $P_{\mathrm{C}}(m,j)$ and $P_{\mathrm{D}}(m,j)$ are obtained —obviously $P_{\mathrm{J}}(m,j) = 0$ irrespective of the population composition.

Once payoffs are obtained evolution proceeds by imitation. Different payoff-dependent rules have been proposed in the literature [98]. All of them describe a process of birth and death which is defined by the transition probability $T(m',j'|m,j)$ from a population with composition (m,j) to another one with composition (m',j') within the set

$$\begin{aligned}\mathcal{N}_{m,j} = &\{(m,j),(m\pm 1,j),(m,j\pm 1),\\ &(m+1,j-1),(m-1,j+1)\}.\end{aligned} \tag{7.2}$$

If now $\Pi(m,j;t)$ denotes the probability that the population has a composition given by (m,j) at time t, then this probability evolves according to

$$\Pi(m,j;t+1) = \sum_{(m',j')\in\mathcal{N}_{m,j}} T(m,j|m',j')\Pi(m',j';t), \tag{7.3}$$

or in matrix notation

$$\mathbf{\Pi}(t+1) = \mathbf{T}\,\mathbf{\Pi}(t). \tag{7.4}$$

7.1.1 Stationary state

If the process undergoes mutations then matrix $\mathbf{T}$ is ergodic and equation (7.4) has got a unique stationary state, $\boldsymbol{\pi}$, which is obtained by solving the linear system

$$\boldsymbol{\pi} = \mathbf{T}\boldsymbol{\pi}. \tag{7.5}$$

In the absence of mutations, though, there are three absorbing states corresponding to the three homogeneous populations. A homogeneous population remains invariant because the imitation process cannot change its composition. We will denote these vectors $\mathbf{e}_{\mathrm{C}}$, $\mathbf{e}_{\mathrm{D}}$, $\mathbf{e}_{\mathrm{J}}$, the index denoting the strategy of the homogeneous population. Clearly $e_{\mathrm{C}}(m,j)=\delta_{m,M}\delta_{j,0}$, $e_{\mathrm{D}}(m,j)=\delta_{m,0}\delta_{j,0}$, $e_{\mathrm{J}}(m,j)=\delta_{m,0}\delta_{j,M}$.

7.1.2 Infinitely small mutation rate

Clearly the limit

$$\lim_{\mu\to 0^+}\boldsymbol{\pi}=\sum_{\mathrm{X=C,D,J}}\alpha_{\mathrm{X}}\,\mathbf{e}_{\mathrm{X}} \tag{7.6}$$

will provide the values of α_{X}, but this limit cannot be obtained directly from equation (7.5). There is an alternative though. It has been proven [129] that the $\mu\to 0^+$ limit of this process is equivalent to another process with three states, C, D, J, in which the transition probability between X and Y is equal to the probability that a single mutant of type Y invades an otherwise homogeneous population of X individuals, thus transforming it into a homogeneous population of Y individuals. Intuitively, this is tantamount to saying that mutations are so rare that the ultimate fate of a mutant is decided before the next mutation occurs. The normalised stationary vector in this space,

$$\boldsymbol{\alpha}=(\alpha_{\mathrm{C}},\alpha_{\mathrm{D}},\alpha_{\mathrm{J}}), \tag{7.7}$$

provides the values of the coefficients α_{X} in equation (7.6). Note that this coefficients represent the fraction of time that the system spends in each homogeneous state, as we will check in section 7.2.

Following [57], let ρ_{YX} denote the probability that a single Y mutant takes over the population made of the mutant and $M-1$ individuals of type X. Then the transition probability of going from state X to a different state Y in the three-states Markov chain defined above will be $r_{\mathrm{YX}}=\rho_{\mathrm{YX}}\mu$. Introducing $\mathbf{R}=(r_{\mathrm{YX}})$ so that the elements in each column add up to one (this fixes the diagonal of the matrix), we can rewrite this matrix as $\mathbf{R}=\mathbf{I}+\mu\mathbf{Q}$, where

$$\mathbf{Q}=\begin{pmatrix}-\rho_{\mathrm{DC}}-\rho_{\mathrm{JC}} & \rho_{\mathrm{CD}} & \rho_{\mathrm{CJ}}\\ \rho_{\mathrm{DC}} & -\rho_{\mathrm{CD}}-\rho_{\mathrm{JD}} & \rho_{\mathrm{DJ}}\\ \rho_{\mathrm{JC}} & \rho_{\mathrm{JD}} & -\rho_{\mathrm{CJ}}-\rho_{\mathrm{DJ}}\end{pmatrix}. \tag{7.8}$$

In the stationary state, the dynamics leads to $\pi = R\pi$. Vector $\boldsymbol{\alpha}$ is then the solution of the linear system $\mathbf{Q}\boldsymbol{\alpha} = \mathbf{0}$. A little bit of algebra leads to the result

$$\alpha_{\mathrm{C}} = (\rho_{\mathrm{CD}}\rho_{\mathrm{CJ}} + \rho_{\mathrm{CD}}\rho_{\mathrm{DJ}} + \rho_{\mathrm{CJ}}\rho_{\mathrm{JD}})/A, \tag{7.9}$$

$$\alpha_{\mathrm{D}} = (\rho_{\mathrm{DC}}\rho_{\mathrm{DJ}} + \rho_{\mathrm{DC}}\rho_{\mathrm{CJ}} + \rho_{\mathrm{DJ}}\rho_{\mathrm{JC}})/A, \tag{7.10}$$

$$\alpha_{\mathrm{J}} = (\rho_{\mathrm{JC}}\rho_{\mathrm{JD}} + \rho_{\mathrm{JC}}\rho_{\mathrm{CD}} + \rho_{\mathrm{JD}}\rho_{\mathrm{DC}})/A, \tag{7.11}$$

with A chosen so as to fulfil

$$\sum_{\mathrm{X=C,D,J}} \alpha_{\mathrm{X}} = 1. \tag{7.12}$$

7.1.3 Finite mutation rates

If the mutation rate is not zero the Markov chain is ergodic and the stationary state can be obtained by solving numerically the master equation (7.5). This is accomplished with better accuracy by splitting

$$\mathbf{T} = \mathbf{T}_0 + \mathbf{T}_1, \tag{7.13}$$

$$\boldsymbol{\pi} = \sum_{\mathrm{X=C,D,J}} \alpha_{\mathrm{X}}\, \mathbf{e}_{\mathrm{X}} + \boldsymbol{\pi}_1, \tag{7.14}$$

with $\mathbf{T}_0$ the transition matrix in the absence of mutations—i.e., with transitions describing only the imitation process. Then $\boldsymbol{\pi}_1$ is the solution of the linear system

$$(\mathbf{I} - \mathbf{T})\boldsymbol{\pi}_1 = \sum_{\mathrm{X=C,D,J}} \alpha_{\mathrm{X}}\, \mathbf{T}_1\mathbf{e}_{\mathrm{X}}. \tag{7.15}$$

7.1.4 Imitation rules

In order to specify the transition matrix $\mathbf{T}$ we need to describe the imitation process. Of the many different rules applied in the literature [98] we have chosen the three most commonly employed: unconditional imitation, proportional update, and a Moran process. In all cases the corresponding matrix $\mathbf{T}$ is obtained in Appendix 7.B.

Under unconditional imitation two players are chosen at random among the population, one as the focal player and the other one as the model to imitate. The focal player compares both payoffs and changes her strategy to that of the model if the latter has a higher payoff. In this case, the strategy with the highest fitness never changes except by mutation, which is the only source of stochasticity in this rule.

Appendix 7.C discusses the value $\boldsymbol{\alpha}$ for this update rule. There are two possibilities:

i $r > 1 + (n - 1)d$. In this cases all three homogeneous states are equally likely [c.f. equation (7.38)].

ii $r < 1+(n-1)d$. In this cases J is the only absorbing state of the process [c.f. equation (7.40)].

Proportional update is entirely similar to unconditional imitation with the exception that imitation occurs with probability proportional to the payoff difference between the model and the focal players. For this reason the values of $\boldsymbol{\alpha}$ for this rule are the same as those for unconditional imitation.

In a Moran process a strategy is chosen to be imitated (or reproduced) with a probability proportional to its population-dependent fitness. The player who imitates (or is replaced by the offspring of) this selected player is randomly chosen from the rest of the population. The only drawback of this rule is that fitnesses must be positive for it to make sense, so they cannot be directly the payoffs of the game, because they can take negative values. A standard mapping between payoff and fitness is obtained by introducing the *selection strength* s [130]. This weights the contribution of the game to the total fitness of the strategy as $F = 1-s+sP$, with P the average payoff. Bounding the value of s we can force F to be positive.

The Moran process thus described defines a birth-death process with two absorbing states, and the corresponding probabilities ρ_{XY} are obtained via standard formulae (see Appendix 7.C).

7.2 Robustness of the cycles using different selection dynamics

In this section we compare the results of agent-based simulations with those obtained by solving numerically the stationary equation (7.5). Simulations implement the following stochastic process. We start with a population of M individuals with equal amounts of C, D and J players. Then:

1. Assuming that every time step each individual plays many rounds of the game with different, randomly gathered groups of n players, the payoffs they obtain

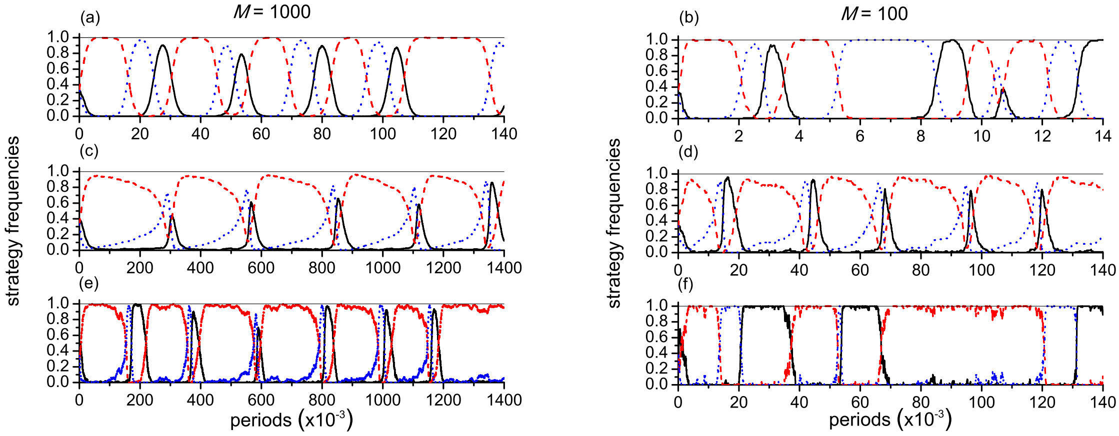


Figure 7.1: *Time evolution of the frequencies of the three strategies in a population of* $M = 1000$ *(left) and* $M = 100$ *(right) individuals playing a PG game with jokers with different update rules: (a), (b) unconditional imitation, (c), (d) proportional update, and (e), (f) a Moran process. The presence of jokers induces a cyclic behaviour irrespective of the update rule and the population size, as long as the mutation rate* $\mu > 0$. *Black solid lines: cooperators, red dashed lines: defectors, and blue dotted lines: jokers. Parameters* $n = 5, r = 3, d = 0.4$, $\mu = 0.001$*; in (a)-(d)* $s = 1$*, in (e),(f)* $s = 0.38$*. One period corresponds to one updating event according to the evolutionary rule used.*

will be proportional to the average payoffs, as calculated in Appendix 7.A. Thus we assume that these expressions provide the payoffs each individual gains every time step.

2. These payoffs are used to update the population according to the corresponding imitation rule. We implement the three rules described in Sec. 7.1.4.

3. With probability μ each newborn mutates to a different strategy (any of the other two with equal probability).

A quite general result is that, irrespective of the population size, at low mutation rates simulations show patterns of cyclic invasions C→D→J→C (see figure 7.1). These patterns resemble the limit cycles observed in the replicator dynamics (see chapter 6), i.e., for infinite populations.

Roughly speaking we can distinguish three regimes of mutations. In the low mutation regime the system spends most of the time in homogeneous states, and the dynamics of the system is well described by the $\mu \to 0$ limit of the stationary probability distribution $\boldsymbol{\pi}$. This can be clearly seen in figure 7.2. The dashed-dotted curves in figures 7.2(a), (c) and (e) represent the fraction of time spent in transients when a homogeneous population is replaced by another one arisen as the result of mutations. This fraction is very small up to $\mu \approx 10^{-5}$–10^{-4}, depending on the imitation rule. For larger mutation rates (μ up to 10^{-3}–10^{-2}) the system spends as much time in homogeneous populations as in mixed transient states. This is the regime displayed in figure 7.1, where cycles are clearly defined even though for some imitation rules (particularly so for proportional update) certain homogeneous populations that are hardly ever reached [figure 7.1(b) shows burst of cooperators which never reach a fraction higher than 80% of the population]. For even higher mutation rates homogeneous populations are very rare and the behaviour of the system is very different, typically dominated by defectors [see figures 7.2(b), (d) and (f)].

Unconditional imitation is practically a deterministic rule in the low mutations regime. For $\mu \lesssim 10^{-4}$ the population is almost always homogeneous, and is made of each of the three strategies with equal probability [see figures 7.1(a), (b) and figures 7.4(a), (b)]. Figure 7.2(a) shows this probability as a function of the joker's inflicted damage d. As long as $d > 0$ and $r > 1 + (n-1)d$ we find each strategy equally likely. For $r < 1 + (n-1)d$ a homogeneous population of jokers cannot be invaded because this is the only absorbing state of the Markov chain for $\mu = 0$. For $d = 0$ jokers do not inflict damage. Then the system spends most of the time in a homogeneous population of defectors. However, random drift allows for occasional invasions by jokers, who are subsequently wiped out by cooperators, who in its turn get replaced again by defectors. Figure 7.3(b) illustrates a typical realisation exhibiting one of these turn-overs.

As of proportional update, its main difference with unconditional imitation is its being a truly probabilistic rule, in which individuals only imitate higher payoffs with a certain probability. Although in the small mutations regime this leads to the same probability of mutual invasion of strategies as for unconditional imitation, the stochastic nature of this rule renders much longer invasion times. This can be clearly appreciated in figure 7.1.

Another effect of stochasticity is that the time spent in transient states is also longer, thus shrinking the low mutations regime by more than one order of magnitude [compare

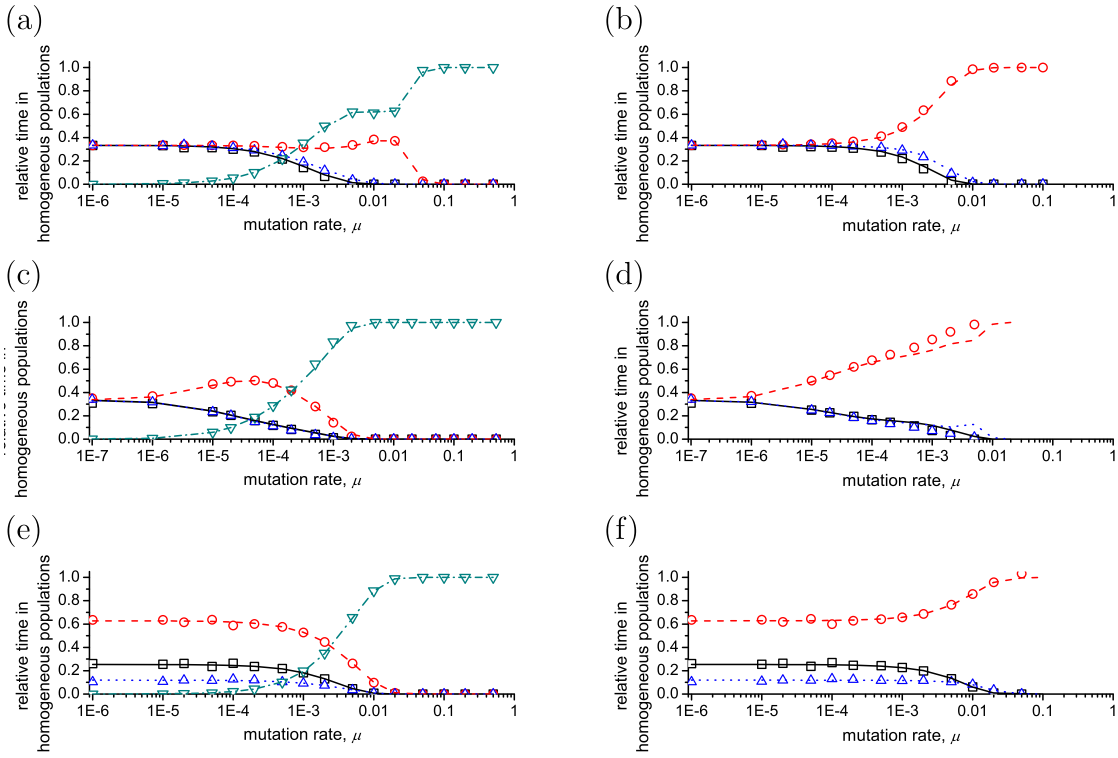


Figure 7.2: *Relative times spent in homogeneous as well as in transient states in a population of* $M = 100$ *individuals. For practical purposes, a state is considered homogeneous if more than 95% of individuals belong to the same strategy. Symbols are the result of agent-based simulations; lines are obtained from the solution of equations* (7.14)–(7.15)*. Results for cooperators are represented with (black) squares and solid lines, those for defectors with (red) circles and dashed lines, and those for jokers with (blue) triangles and dotted lines. Panels (a), (c) and (e) also show (with inverted triangles and dashed-dotted lines) the fraction of time spent in transient states. Panels (b), (d) and (f) show the relative fractions of the time spent in homogeneous states in which we find each of the three strategies. Panels (a) and (b) correspond to unconditional imitation, panels (c) and (d) to proportional update, and panels (e) and (f) to a Moran rule. We can see that high mutation rates promote defection over the other two strategies. Parameters used are* $n = 5, r = 3, d = 0.4$*; selection strength is* $s = 1$ *in (a)–(d) and* $s = 0.38$ *in (e) and (f).*

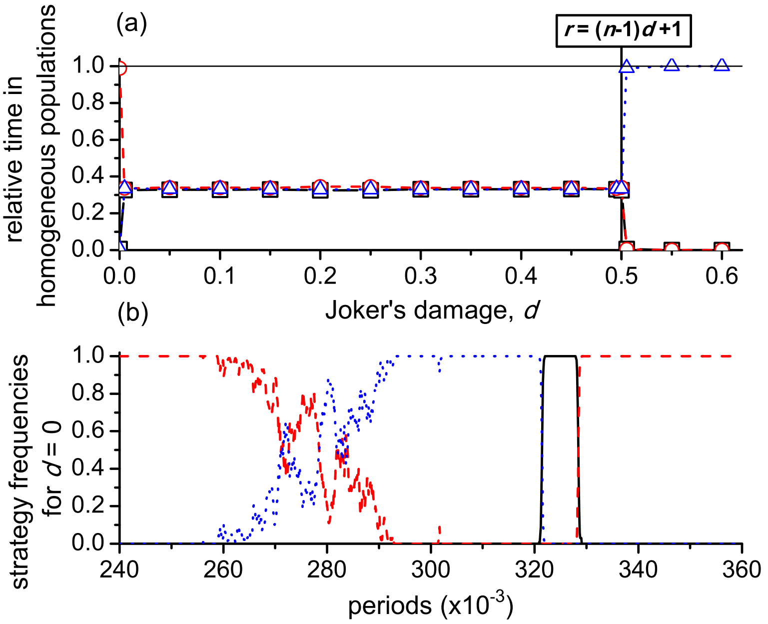


Figure 7.3: *Evolution of a population of $M = 100$ individuals by unconditional imitation. (a) Fraction of time spent in homogeneous populations of cooperators (red squares and solid line), defectors (red circles and dashed line) and jokers (blue triangles and dotted line), as a function of joker's inflicted damage d. Symbols correspond to an agent-based simulation; lines to the results obtained from numerical computation of the stationary probability distribution. (b) A realisation made with $d = 0$ showing an invasion of defectors by jokers through pure drift, and the subsequent burst of cooperators and turn-over by defectors. Parameters: $n = 5, r = 3, s = 1$ and $\mu = 5 \times 10^{-5}$.*

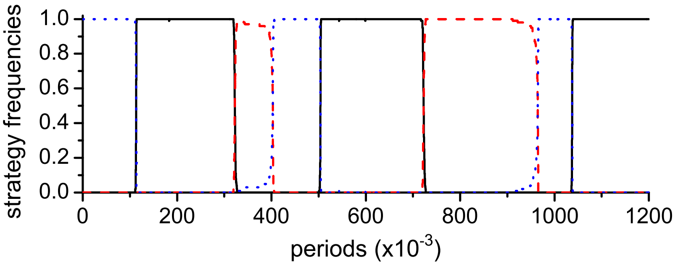


Figure 7.4: *Realisation of an agent-based simulation of a population with $M = 100$ individuals evolving through proportional update. Notation is as in figure 7.3. Parameters: $n = 5, r = 3, d = 0.4, \mu = 5 \times 10^{-6}, s = 1$.*

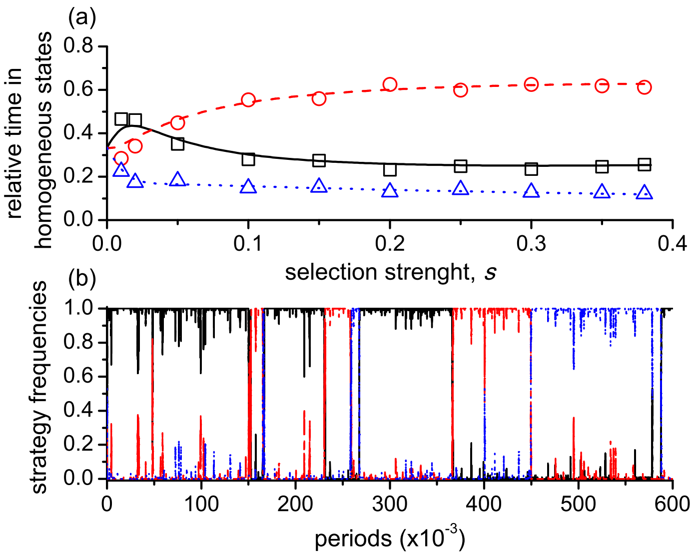


Figure 7.5: *A population of* $M = 100$ *individuals evolving through Moran update. (a) Comparison of the the relative times in which the population is in a homogeneous state vs. the selection strength,* s*, for low mutation rates. Lines represent the analytical estimates obtained in Sec. 7.C.2; symbols represent the results from agent-based simulations. (b) Fractions of each strategy as a function of time as obtained from a realisation of an agent-based simulation. Cooperators are represented with a black solid line and squares, defectors with a red dashed line and circles, and jokers with a blue dotted line and triangles. Parameters are* $n = 5, r = 3, d = 0.4$ *and* $\mu = 5 \times 10^{-5}$*. In (b) the selection strength is* $s = 0.05$.

figures 7.2(a) and (c)]. The effect is particularly notorious for jokers, who take a long time to invade defectors, thus extending the life time of defective populations. This effect is illustrated in figure 7.4, which represents a typical realisation of an agent-based simulation.

The Moran process is the most random of the three evolutionary dynamics because even strategies not performing very well have a chance to get imitated. The effect is more noticeable the smaller the population. This dynamics imposes an upper limit to the selection strength s (see Sec. 7.1.4) and the probabilities to find the population in each of the three homogeneous states depend on the parameters of the game and on s in a nontrivial way (see Sec. 7.C.2). These probabilities are represented in figure 7.5(a) as a function of s. The theoretical predictions of Sec. 7.C.2 agree with the simulations. This figure shows that cooperation is highly promoted for small $s(0.005 < s < 0.05)$. In this limit cooperative populations are found with almost 50% probability. This probability decreases down to around 25% for larger s. Figure 7.5(b) shows a typical realisation of this process, exhibiting a defining feature of this process, namely the frequent failures of attempted invasions.

Whichever the update rule, when mutation rates are not small the system is better characterised by providing the stationary probability distribution π, as obtained from equation (7.15)). The results are plotted in figure 7.6 for all three imitation rules and different mutation rates μ. For low and intermediate values of μ the higher probabilities are found near the border of the simplexes, consistent with the cyclic behaviour of the system. However, for high μ the probability peaks around a point. This point is interior for the most stochastic rules, but corresponds to a defective population for unconditional imitation. figure 7.7 shows the results for the same parameters using the replicator dynamics, so a direct comparison can be made.

7.3 Discussion of the results in finite populations

In this chapter we have expanded the results and have proven that the oscillatory dynamics does not occur only for infinite (or very large) populations evolving under a replicator dynamics, but also in the case of finite populations and for different update rules. The dynamical rules analysed in this chapter are unconditional imitation,

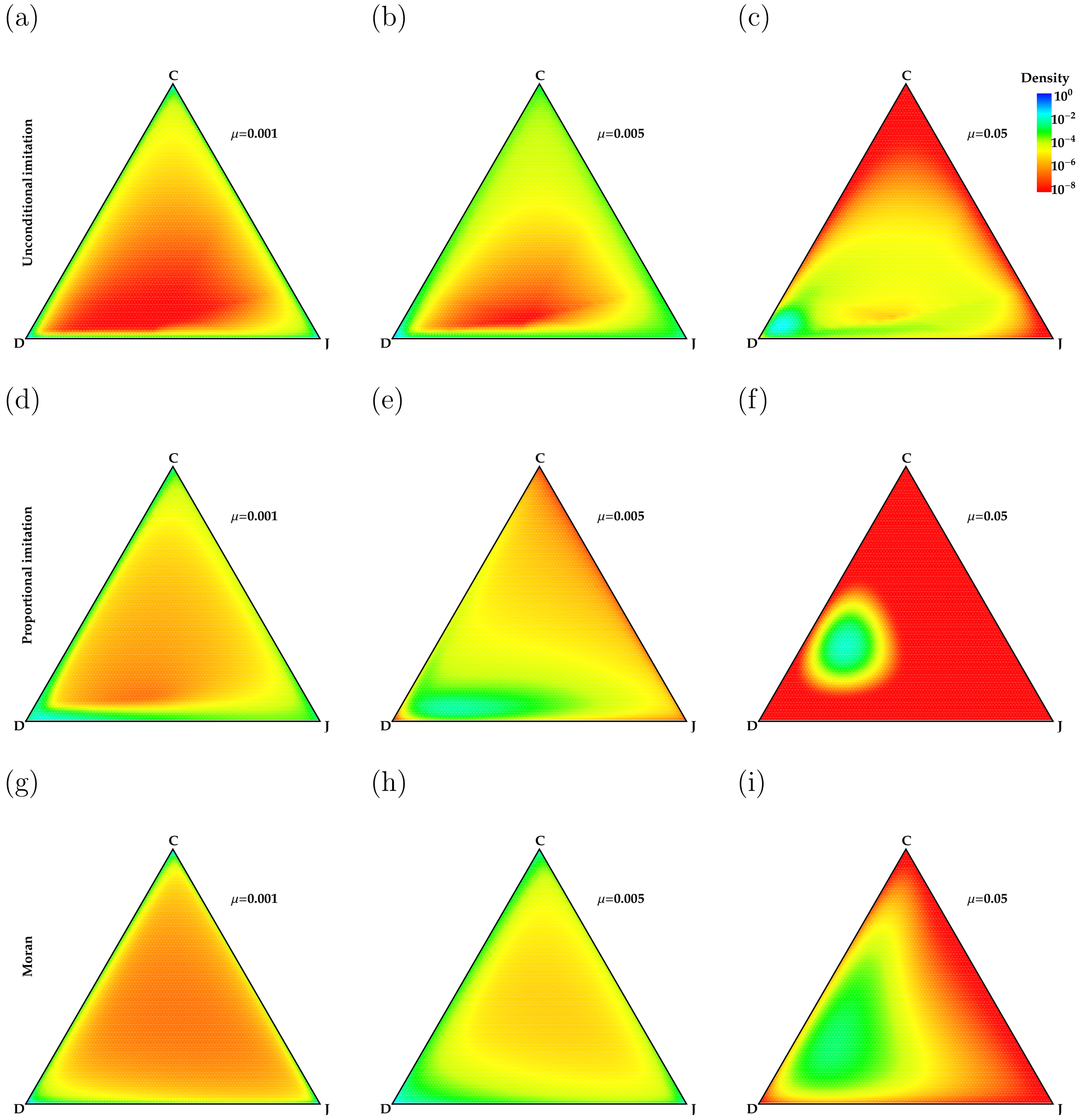


Figure 7.6: *Density plots for the probability of finding the system in each population state as obtained by solving numerically equation* (7.5)*. First row corresponds to unconditional imitation, second row to proportional imitation, third row to a Moran process. In each case mutations increase left to right. In all three cases low mutation rates* (μ) *yield high probabilities near the boundaries of the simplexes, specially near the corners, corresponding to cyclic transitions between homogeneous states. Increasing* μ *increases the probability to find the system near homogeneous defective populations. For high* μ *an attractive point appears close to the D corner which goes away from it upon increasing* μ*. Parameters are* $n = 5, r = 3, d = 0.4$*; the selection strength is* $s = 1$ *in the first and second rows,* $s = 0.38$ *in the third. Mutation rates appear near each simulation. Densities are plotted using a logarithmic scale. figure 7.7 shows the replicator dynamics in infinite populations for the same mutation rates, to allow for a comparison.*

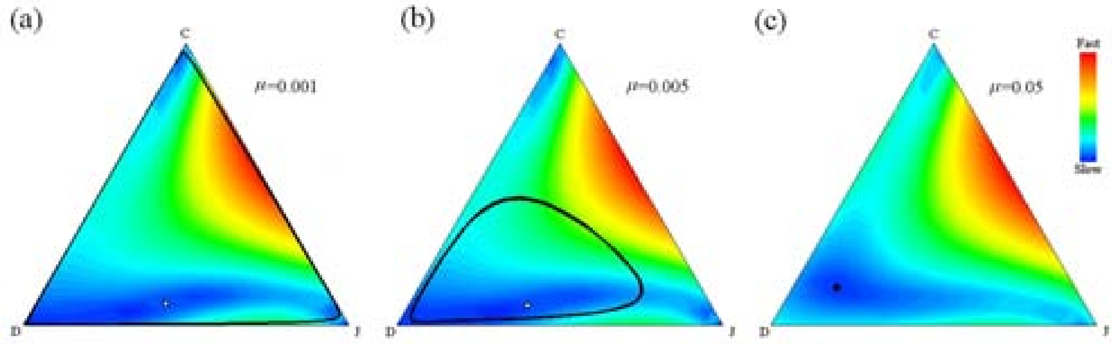


Figure 7.7: *Cycles induced by jokers in infinite populations. This figure allows for a comparison with the results in finite populations of figure 7.6. The simplexes describe the replicator-mutator dynamics for a population of cooperators, defectors, and jokers, with parameter values satisfying* $n > r > 1 + d(n - 1)$*, for which a rock-paper-scissor dynamics is expected. For small mutation rates, the only equilibrium is a repeller (white dot in (a),(b)), and trajectories end up in a stable limit cycle of decreasing amplitude with increasing* μ *(black line); when mutations reach a critical value* μ_c*, the system undergoes a Hopf bifurcation and a stable mixed equilibrium appears (black dot in (c)). Thus the presence of jokers induces periodic bursts of cooperation for low mutation rates, and stable coexistence for high* μ*. Parameters:* $n = 5$*,* $r = 3$*,* $d = 0.4$*,* μ *is (a) 0.001, (b) 0.005, (c) 0.05. (Images generated using a modified version of the Dynamo Package [127]).*

proportional update, and a Moran process. In all cases the system exhibits finite time lapses in which most of the population is composed by cooperative individuals, finding that the Moran process for low (but not extremely low) selection pressures is the most favourable to cooperation—as the system spends 50% of the time in cooperative states. Under unconditional imitation system spends one third of the time in cooperative states, whereas the more stochastic nature of proportional update favours defection due to the slower invasion of jokers, and thus the system stays longer in defective states—especially so for high mutation rates.

In summary, we have proven that the existence of jokers, i.e., individuals whose purely destructive behaviour damages the common enterprises represented by PG games, allows for the emergence of robust evolutionary cycles in finite populations regardless of the updating method chosen. Together with the existence of limit cycles for infinite populations evolving via a replicator-mutator dynamics (section 6.4), the present results show that limit cycles are a generic feature of the dynamics generated by destructive agents, not restricted to a particular selection dynamics. This is a dynamical feature that makes this model different from other three-player games like that of loners [118], for which cycles are structurally unstable and their existence strongly depends on the absence of mutations and other kinds of perturbations, and thus it might be applied to situations observed in nature and history, where periods of destruction, cooperation and defection have been reported to occur cyclically.

Appendices

7.A Average payoffs in a finite population

Let us denote $P_{\mathrm{X}}(m,l)$ the average payoff that a player of type X receives when the population is made of m cooperators, j jokers, and $M-m-j$ defectors. This average payoff is calculated by averaging the corresponding payoff (6.1) with the probability distribution (7.1). For defectors this implies

$$P_{\mathrm{D}}(m,j) = \sum_{\substack{k,l\geq 0\\ k+l<n}} \frac{rk-dl}{n-l} p(k,l|n-1,m,j,M-1). \tag{7.16}$$

To perform this average it will prove convenient to factorise the probability distribution as the product of two standard hyper-geometric distributions, i.e.,

$$p(k,l|n,m,j,M) = p(l|n,j,M)p(k|n-l,m,M-j). \tag{7.17}$$

where

$$p(l|n,j,M) = \frac{\binom{j}{l}\binom{M-j}{n-l}}{\binom{M}{n}}. \tag{7.18}$$

The first term in (7.17) is the probability of selecting l jokers out of the population, and the second term is the conditional probability of subsequently selecting k cooperators, given that we have already selected the l jokers.

A useful identity of the hyper-geometric distribution —consequence of the properties of the binomial coefficients— is

$$k\,p(k|n,m,M) = \frac{nm}{M} p(k-1|n-1,m-1,M-1). \tag{7.19}$$

Substituting factorisation (7.17) into (7.16) and making use of this identity we readily obtain

$$P_{\mathrm{D}}(m,j) = \frac{rm}{M-j-1}\sum_{l=0}^{n-1}\frac{n-l-1}{n-l}\,p(l|n-1,j,M-1) \\ - d\sum_{l=0}^{n-1}\frac{l}{n-l}\,p(l|n-1,j,M-1). \tag{7.20}$$

A new identity, namely

$$\frac{p(l|n-1,j,M-1)}{n-l} = \frac{M}{n(M-j)}p(l|n,j,M), \tag{7.21}$$

allows us to do the sum

$$\sum_{l=0}^{n-1}\frac{p(l|n-1,j,M-1)}{n-l} = \frac{M[1-p(n|n,j,M)]}{n(M-j)}. \tag{7.22}$$

It will prove convenient to introduce the function

$$\Xi(n,j,M) \equiv \frac{j}{M-j}\left[1-\frac{(j-1)\cdots(j-n+1)}{(M-1)\cdots(M-n+1)}\right], \tag{7.23}$$

in terms of which

$$\begin{aligned} 1-p(n|n,j,M) &= 1-\frac{j(j-1)\cdots(j-n+1)}{M(M-1)\cdots(M-n+1)} \\ &= \frac{M-j}{M}\left[1+\Xi(n,j,M)\right]. \end{aligned} \tag{7.24}$$

This allows us to write

$$\sum_{l=0}^{n-1}\frac{p(l|n-1,j,M-1)}{n-l} = \frac{1+\Xi(n,j,M)}{n}, \tag{7.25}$$

and using this in (7.20) obtain

$$P_{\mathrm{D}}(m,j) = \frac{rm[n-1-\Xi(n,j,M)]}{n(M-j-1)} - d\,\Xi(n,j,M). \tag{7.26}$$

As for the average payoff of a cooperator,

$$\begin{aligned} P_{\mathrm{C}}(m,j) = -1 &+ \sum_{\substack{k,l\geq 0\\ k+l<n}}\frac{r(k+1)-dl}{n-l} \\ &\times p(k,l|n-1,m-1,j,M-1) \\ &= r\sum_{l=0}^{n-1}\frac{p(l|n-1,j,M-1)}{n-l} - 1 + P_{\mathrm{D}}(m-1,j) \\ &= \frac{r}{n}[1+\Xi(n,j,M)] - 1 + P_{\mathrm{D}}(m-1,j). \end{aligned} \tag{7.27}$$

Therefore

$$\begin{aligned} P_{\mathrm{C}}(m,j) =& \frac{r}{n}\left(1+\frac{(n-1)(m-1)}{M-j-1}\right)-1 \\ &+\left[\frac{r}{n}\left(1-\frac{m-1}{M-j-1}\right)-d\right]\Xi(n,j,M). \end{aligned} \tag{7.28}$$

Finally, $P_{\mathrm{J}}(n,j)=0$ because jokers get zero regardless of the composition of the population.

7.B Calculation of the transition matrices

Transition probabilities $T(m,j|m',j')$ are obtained according to the specified update rule. We will calculate those corresponding to the rules used in this work. But before we proceed let us introduce some shorthands. We will write $T_{\epsilon_1,\epsilon_2} \equiv T(m,j|m+\epsilon_1,j+\epsilon_2)$, where $\epsilon_1,\epsilon_2 \in \{-1,0,1\}$. Also by $\omega^{\mathrm{XY}}_{\epsilon_1,\epsilon_2}$ we will denote the probability that a player of type Y is chosen to be replaced by a player of type X when the population is made of $m+\epsilon_1$ cooperators, $j+\epsilon_2$ jokers, and $M-m-j-\epsilon_1-\epsilon_2$ defectors. Whether the Y player is finally replaced by an X one depends on mutations, thus

$$\begin{aligned} T_{1,0} =& \omega^{\mathrm{DC}}_{1,0}(1-2\mu)+\left(\omega^{\mathrm{JC}}_{1,0}+\omega^{\mathrm{CC}}_{1,0}\right)\mu, \\ T_{1,-1} =& \omega^{\mathrm{JC}}_{1,-1}(1-2\mu)+\left(\omega^{\mathrm{DC}}_{1,-1}+\omega^{\mathrm{CC}}_{1,-1}\right)\mu, \\ T_{-1,0} =& \omega^{\mathrm{CD}}_{-1,0}(1-2\mu)+\left(\omega^{\mathrm{JD}}_{-1,0}+\omega^{\mathrm{DD}}_{-1,0}\right)\mu, \\ T_{0,-1} =& \omega^{\mathrm{JD}}_{0,-1}(1-2\mu)+\left(\omega^{\mathrm{CD}}_{0,-1}+\omega^{\mathrm{DD}}_{0,-1}\right)\mu, \\ T_{-1,1} =& \omega^{\mathrm{CJ}}_{-1,1}(1-2\mu)+\left(\omega^{\mathrm{DJ}}_{-1,1}+\omega^{\mathrm{JJ}}_{-1,1}\right)\mu, \\ T_{0,1} =& \omega^{\mathrm{DJ}}_{0,1}(1-2\mu)+\left(\omega^{\mathrm{CJ}}_{0,1}+\omega^{\mathrm{JJ}}_{0,1}\right)\mu, \end{aligned} \tag{7.29}$$

In all cases there are two possibilities for a Y individual to become an X one, either a pair XY is selected, the update takes place and no mutation occurs, or another pair ZY is selected (with Z $\neq$ X) but a mutation changes Z into X.

Finally, the probability that no change of strategy occurs $T_{0,0}=T(m,j|m,j)$ is obtained as

$$T_{0,0} = 1-(1-\mu)\sum_{\mathrm{X}\neq\mathrm{Y}}\omega^{\mathrm{XY}}_{0,0}-2\mu\sum_{\mathrm{X}}\omega^{\mathrm{XX}}_{0,0}, \tag{7.30}$$

where the subscript $0,0$ refers to a population made of m cooperators, j jokers, and $M-m-j$ defectors.

Notice that the expansion (7.14) readily follows from expressions (7.29) and (7.30).

7.B.1 Unconditional imitation

This rule prescribes that two players are selected at random from the population and the strategy of the model player (X) replaces that of the focal player (Y) if the latter has a lower payoff. Accordingly, if X $\neq$ Y,

$$\omega^{\mathrm{XY}}_{\epsilon_1,\epsilon_2} = \frac{n^{\mathrm{X}}_{\epsilon_1,\epsilon_2} n^{\mathrm{Y}}_{\epsilon_1,\epsilon_2}}{M(M-1)} \Theta\left(P^{\mathrm{X}}_{\epsilon_1,\epsilon_2} - P^{\mathrm{Y}}_{\epsilon_1,\epsilon_2}\right), \tag{7.31}$$

where $\Theta(x) = 1$ if $x > 0$ and 0 otherwise, and $n^{\mathrm{X}}_{\epsilon_1,\epsilon_2}$ denotes the number of individuals of type X in the population (e.g., $n^{\mathrm{C}}_{1,0} = m+1$, $n^{\mathrm{D}}_{1,0} = M-j-m-1$, $n^{\mathrm{J}}_{1,-1} = j-1$, $n^{\mathrm{D}}_{0,0} = M-j-m$, etc.). On the other hand, in order to account for mutations we must define

$$\omega^{\mathrm{XX}}_{\epsilon_1,\epsilon_2} = \frac{n^{\mathrm{X}}_{\epsilon_1,\epsilon_2}(n^{\mathrm{X}}_{\epsilon_1,\epsilon_2} - 1)}{M(M-1)}. \tag{7.32}$$

7.B.2 Proportional update

Similarly to the previous rule,

$$\omega^{\mathrm{XY}}_{\epsilon_1,\epsilon_2} = \frac{n^{\mathrm{X}}_{\epsilon_1,\epsilon_2} n^{\mathrm{Y}}_{\epsilon_1,\epsilon_2}}{M(M-1)} \Psi\left(P^{\mathrm{X}}_{\epsilon_1,\epsilon_2} - P^{\mathrm{Y}}_{\epsilon_1,\epsilon_2}\right), \tag{7.33}$$

where $\Psi(x) = x/\Omega$ if $x > 0$ and 0 otherwise, Ω being a constant ensuring that $\Psi\left(P^{\mathrm{X}}_{\epsilon_1,\epsilon_2} - P^{\mathrm{Y}}_{\epsilon_1,\epsilon_2}\right) \leq 1$ (typically Ω is chosen as the largest possible payoff difference). As in the previous rule $\omega^{\mathrm{XX}}_{\epsilon_1,\epsilon_2}$ is given by (7.32).

7.B.3 Moran process

In this case payoffs are replaced by fitnesses $F^{\mathrm{X}}_{\epsilon_1,\epsilon_2} = 1 - s + sP^{\mathrm{X}}_{\epsilon_1,\epsilon_2}$ (see Sec. 7.1.4). Let us introduce the total fitness of the population

$$\Phi_{\epsilon_1,\epsilon_2} \equiv \sum_{\mathrm{X}} n^{\mathrm{X}}_{\epsilon_1,\epsilon_2} F^{\mathrm{X}}_{\epsilon_1,\epsilon_2}. \tag{7.34}$$

The Moran rule specifies that a player is chosen for reproduction proportional to its fitness and the offspring replaces another randomly chosen individual from the rest of the population. So if X $\neq$ Y,

$$\omega^{\mathrm{XY}}_{\epsilon_1,\epsilon_2} = \frac{n^{\mathrm{Y}}_{\epsilon_1,\epsilon_2}}{M-1} \frac{n^{\mathrm{X}}_{\epsilon_1,\epsilon_2} F^{\mathrm{X}}_{\epsilon_1,\epsilon_2}}{\Phi_{\epsilon_1,\epsilon_2}}, \tag{7.35}$$

and

$$\omega^{\mathrm{XX}}_{\epsilon_1,\epsilon_2} = \frac{n^{\mathrm{X}}_{\epsilon_1,\epsilon_2} - 1}{M-1} \frac{n^{\mathrm{X}}_{\epsilon_1,\epsilon_2} F^{\mathrm{X}}_{\epsilon_1,\epsilon_2}}{\Phi_{\epsilon_1,\epsilon_2}}, \tag{7.36}$$

7.C Stationary probabilities in the weak mutation limit

7.C.1 Unconditional imitation and proportional update

According to the payoffs obtained in Appendix 7.A:

1. $P_D(m,0) > P_C(m,0)$ for all $0 < m < M$, so D always invades C, but C never invades D.

2. $P_C(m, M-m) > P_J(m, M-m)$ for all $0 < m < M$, provided $r > 1 + (n-1)d$ (the rock-paper-scissors condition), so under this assumption C always invades J, but J never invades C.

3. $P_J(0,j) > P_D(0,j)$ for all $0 < j < M$, so J always invades D, but D never invades J.

Therefore

$$\mathbf{Q} = \begin{pmatrix} -1 & 0 & 1 \\ 1 & -1 & 0 \\ 0 & 1 & -1 \end{pmatrix}. \tag{7.37}$$

This implies

$$\alpha_{\mathrm{C}} = \alpha_{\mathrm{D}} = \alpha_{\mathrm{J}} = \frac{1}{3}. \tag{7.38}$$

On the other hand, if $r < 1 + (n-1)d$ neither C invades J nor vice-versa, so in this case

$$\mathbf{Q} = \begin{pmatrix} -1 & 0 & 0 \\ 1 & -1 & 0 \\ 0 & 1 & 0 \end{pmatrix}, \tag{7.39}$$

which implies

$$\alpha_{\mathrm{C}} = \alpha_{\mathrm{D}} = 0, \quad \alpha_{\mathrm{J}} = 1. \tag{7.40}$$

7.C.2 Moran Process

The Moran process for a population with two strategies defines a birth-death process with two absorbing states. The details of the calculation of ρ_{YX} can be found in [57] and follow standard formulae for this kind of processes [131]. Summarising, if we denote $P_{\mathrm{YX}}(m)$ the payoff received by a type Y individual when the population is made of m Y individuals and $M-m$ X individuals, then

$$\rho_{\mathrm{YX}}^{-1} = \sum_{m=0}^{M-1} q_m, \qquad \rho_{\mathrm{XY}} = q_{M-1}\rho_{\mathrm{YX}}, \tag{7.41}$$

where $q_0 = 1$ and

$$q_m = q_{m-1}\frac{1-s+sP_{\mathrm{XY}}(M-m)}{1-s+sP_{\mathrm{YX}}(m)}, \qquad 0 < m < M. \tag{7.42}$$

Payoffs $P_{\mathrm{XY}}(m)$ and $P_{\mathrm{YX}}(m)$ are obtained from the formulae of Appendix 7.A. The maximum value of the selection strength s is given by

$$s_{\max} = \frac{1}{1-\min\limits_{\mathrm{XY},m} P_{\mathrm{XY}}(m)}. \tag{7.43}$$

Part IV

Conclusions

Chapter 8

Conclusions

1 - Cooperation is promoted in a prisoner's dilemma –the most difficult case for the evolution of cooperation– whenever there are at least three strategies that differ in their cooperative and selfishness levels, and mutations occur

Part I consisted of a general introduction of the concepts. In particular, chapter 2 was devoted to introduce the PD and shown some of its properties. There, I proved that...

- ... if fitness is additive, direct interactions between individuals in which the actor suffers a fitness change in order to produce a fitness change in the recipient only result in prisoner's dilemmas and harmony games. This is important to identify situations in nature in which the prisoner's dilemma is the only mathematical representation, which was recently questioned by some authors.
- ... in the absence of mutations, the most selfish strategy (parasitism) is promoted by natural selection in prisoner's dilemmas whenever the dynamics are ruled by the difference between strategies payoffs, or between strategies payoffs and mean population payoff. This result is not new, but shows the importance of the problem of the evolution of cooperation.
- ... when mutations occur, unexpected high levels of altruism and free-riding are found in well-mixed populations containing altruists, free-riders, and parasites. Therefore the importance of including non-aggressive strategies in the cooperative definition, as the combination of such non-aggressive strategies, as altruists and

free-riders, allows for their survival in much higher levels than expected in the presence of parasites.

2 - The finiteness of resources promotes cooperation in well-mixed populations of unconditional cooperators and defectors playing an a-priori prisoner's dilemma

As it has been proven in part II, the existence of limiting resources generates dynamical payoffs and promotes cooperation in all cases studied, at least for some parameters combination. The main results found are that, in addition to dominance of defection (parasitism) . . .

- . . . whenever the limiting resource constrains reproduction and death of individuals, coexistence and dominance of cooperation are possible with increasing the costs of defection, or the attacking (interacting) rates.
- . . . if the limiting resource constrains only reproduction and deaths occur at random, coexistence is possible for sufficiently large defective costs and attacking rates. This is due to a self-organising process that tunes the payoff matrix to neutral.
- . . . if the population size is kept constant by the action of some limiting factor (e.g. space), and reproduction is ruled by another limiting resource, a phase transition which depends only in the resource influx happens. This phase transition separates defective states for high resource fluxes from coexistence states of cooperation and defection when resources are scarce. This presents a possible scenario for the evolution of multicellular organisms.

3 - Indiscriminate destruction may promote cycles of cooperation, defection and destruction

Part III was devoted to the study of the effect of the inclusion of destructive individuals in public good games. This may represent situations in which destruction refers to resources, or more generally, affecting in some way the fitness of the individuals. The main results found are that. . .

- . . . if destruction is too intense, no cooperative or defective individual survives.
- . . . in the presence of mutations some parameter combinations allow for robust evolutionary cycles of cooperation, defection and destruction, triggered by the decrease in mean population fitness created by the defective individuals. This is the first example of robust limit cycles with unconditional strategies in the public goods game.
- . . . the evolutionary cycles found happen irrespective of population size and evolutionary rule chosen. Therefore limit cycles are a generic feature of the dynamics generated by destructive agents, not restricted to a particular selection dynamics. Furthermore, it is possible to make a precise prediction of the mean time spent in each possible state by means of stochastic calculus.

The results presented here thus shed light on some previously unexplored scenarios which allow for a better understanding of the evolution of cooperation in nature and society, and I hope that they will be useful in the further development not only of our knowledge, but also in the development of experiments which may result in new disease treatments, or the management of common resources.

Publications derived from this work

The development of the present PhD thesis has resulted in the following publications, listed by publication date:

- The evolution of cooperation: history and concepts:
    1. **The tower of babel of cooperation** *Proc. Royal Soc. B* (Submitted). Requejo, R.J.
- Resource constraints in the evolution of cooperation:
    1. **Scarcity may promote cooperation in populations of simple agents** *Phys. Rev. E* (Submitted). Requejo, R.J. & Camacho, J.

2. **Analytical models for well-mixed populations of cooperators and defectors under limiting resources** Phys. Rev. E. (2012) 85, 066112. Requejo, R.J. & Camacho, J.
3. **Coexistence of cooperators and defectors in well mixed populations** *Phys. Rev. Lett.* (2012) 108, 038701. Requejo, R.J. & Camacho, J.
4. **Evolution of cooperation mediated by limiting resources: Connecting resource based models and evolutionary game theory** *J. Theor. Biol.* (2011) 272, 35–41. Requejo, R.J. & Camacho, J.

- Destruction as a source of regeneration:

1. **Stability and robustness analysis of cooperation cycles driven by destructive agents in finite populations** *Phys. Rev. E.*, (Submitted). Requejo, R.J., Camacho, J., Cuesta, J.A. & Arenas, A.
2. **The joker effect: Cooperation driven by destructive agents** *J. Theor. Biol.* (2011) 279, 113–119. Arenas, A., Camacho, J., Cuesta, J.A. & Requejo, R.J.

Chapter 9

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