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Cooperation and psychopathy: A game-theoretic perspective.

by

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ABSTRACT

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In the last century, academics have focussed on understanding how we make decisions and they have proven through lab and web experiments that people do not always follow a purely rational process. Contrariwise, several exogenous and endogenous mechanisms have been found to influence our decision-making patterns, leading us towards cooperative behaviours, even when personal costs are involved. In this thesis, I investigate how a specific aspect of personality, namely psychopathic traits, affects cooperative actions in different scenarios, employing both primary and secondary experimental data. Furthermore, I explore the beneficial and detrimental role of some of the most defining dimensions of psychopathy in the evolution of a population through an individual-based model.

Firstly, I address the topic by analysing the data of two laboratory experiments previously conducted. Both experiments examine the influence of psychopathic traits in an iterated Prisoner's Dilemma game, with the presence of opponents emotional facial feedback. While in the first experiment those feedbacks are purely contextual, in the second one they are manipulated to investigate their effects on cooperation, while controlling for psychopathic traits. Results from the first experiment show a negative marginal effect of a dimension of psychopathy, namely disinhibition, on cooperative actions. In the second experiment, higher levels of fearless dominance have a negative influence on cooperation over time, although the presence of emotional facial feedbacks does not affect the level of cooperation. Moreover, I find a positive correlation between psychopathic measures and the adoption of defective strategies in the game. Thus, this first part of the thesis sheds light on the interaction of psychopathic traits and the presence of emotional stimuli received from the opponent after each decision.

Both these experiments investigate the effects of psychopathic traits on decision-making from an individual point of view. In the second part, I approach the subject from a group level view. I designed and conducted a laboratory experiment examining the influence of the presence of relatively high psychopathic individuals in groups on the level of cooperative actions. The main result is that, independent of individuals own psychopathic measures, belonging to a group with a larger number of high psychopathic people leads group members towards less cooperative behaviours. This second part approaches the study of decision-making and psychopathic traits by investigating group dynamics, providing new interesting results on group composition and cooperation, as well as an innovative experimental design to investigate group decisions.

Lastly, I model the evolution of a population composed by two main agents types, one of which incorporates some of the most characteristic feature of psychopathy (such as selfishness and risk-seeking attitudes). Relying on empirical findings, I developed an individual-based model mimicking the evolution of a population under different environmental conditions. Through this model, I examine the beneficial and detrimental effects of individuals with selfish and risk-seeking over several generations: while they can be harmful in situations of prosperity, they become helpful, if not essential, in periods of hardship.

This thesis inspects the role of psychopathic traits in decision-making processes from a wide range of perspectives. Doing so, it enables the reader to have a comprehensive understanding on how this specific dimension of personality shapes both individual and group cooperation in different scenarios, and how psychopathic individuals can be (or not) evolutionarily adaptive.

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Chapter 1 Introduction

The ambitious project of modelling human behaviour has attracted a great number of researchers from several disciplines over the past decades: understanding what factors affect our decision-making remains a fascinating topic for the research community. Scholars acknowledged the complexity of human behaviour and the difficulty of modelling decision-making processes in a realistic way, and in the last century the use of experimental gaming as a tool to study people's behaviour has become more and more frequent [1]. The study of the factors that push humans towards cooperative instead of competitive behaviours is one of the main open fields in this area and it is what I have focussed on in this thesis.

Over the years, several studies have been conducted to observe how endogenous and exogenous factors affect our decision-making process, and several phenomena, besides pure rationality, have been discovered to influence humans in their decision-making processes. Some early studies were conducted with small groups of participants with different levels of various personality characteristics (e.g. dominance, need for achievement and anxiety) to assess the influence of such traits in social interaction [2, 3]. Bonacich (1972) addressed conflict between individual and collective goals during cooperation in social interactions, proving that an increase in the conflict leads to a rise in group friendliness and, hence, cooperation [4]. Coordination, communication and consensus were also outlined as three main components in decision-making processes [5, 6]. More recent studies examined the impact of other mechanisms on decision-making: reputation [7, 8], punishment [9, 10] and altruism [11, 12] are just some of the aspects that were discovered to influence the individual's behaviour in one-to-one interactions. Studies reveal that people are more keen on helping those who help others [13, 14, 15], and that reputation is a driving force of cooperative behaviours [8]. Additionally, the interpersonal connections in a community and the density of these links are recognised as being among the main aspects of the decision-making processes in both public and private situations [8, 12]. Another innovative point of view is the physiological perspective. By studying brain reactivity, researchers have been able to discover that specific brain responses associated with decision-making vary with personality traits. Increased activation in posterior cingulate cortex and anterior insula was found for offenders with antisocial personality disorder and psychopathy during punishment tasks [16]. Brain lesions have also been found to interfere in the decision-making process, altering decisions and reactions to others' actions [17, 18]. Activity in the anterior cingulate cortex was found to reflect the ability of humans to assess volatility in an optimal manner and adjust decision-making accordingly [19].

In this thesis, I contribute to the understanding of human decision-making processes by examining the role of psychopathic traits on decision-making processes. Adopting psychological experiments and mathematical simulations, I try to disentangle the impact of psychopathic traits on cooperation both at the individual and at the group level in different scenarios. I also investigate whether some aspects of psychopathy could provide an adaptive advantage for the population under certain environmental conditions.

The research questions of this thesis are *"How do some aspects of psychopathy, that are common in the general population, affect the development of cooperative behaviours? Under which circumstances can those traits be beneficial and advantageous for the survival of the community?"*

The rest of this chapter describes the central concepts used in the thesis, summarising previous results relating psychopathy and cooperation.

1.1 Game theory

The increasing interest in human interpersonal behaviour led the research community into a wide range of open questions. As soon as researchers tried to investigate human actions with real-world game theoretic experiments, it became apparent that people behaved differently from what rationality predicted: individuals cooperated much more than expected, breaking the assumption of rationality which was at the base of game theory. This discovery lead to the necessity of including factors other than rationality in modelling human decision-making processes.

The first trace of this discipline was recorded in the eighteenth century [20], although it became a distinct field in the early 1900s with John von Neumann [21]. In all societies, people interact constantly. These interactions might be cooperative, such as a collaboration for a common aim, or competitive, such as between politicians in elections. In both cases, people's behaviour is affected and affects other people's well being. These situations require a complex reflection which allows us to account for several factors and a wide range of circumstances before finally deciding on a behavioural strategy. Game theory approaches the subject by analysing cooperative and competitive behaviours in a wide range of scenarios (games). Games are designed to reproduce everyday situations, either in one-to-one conditions or community interactions. Simulating real-world interactions, researchers explore how different conditions affect human decisions.

This theory aims to elaborate models describing human behaviours in real life situations. Reality is depicted as a game with some formal elements [22]:

1. a list of players,
2. a description of players' possible actions,
3. a detailed illustration of the outcome for each possible action.

Formally, a normal-form game includes [23]:

1. a finite set of players, $N = 1, \dots, n$,

2. a collection of sets of strategies, $S_1, \ldots, S_n$,
3. a set of payoff functions, $u_1, \ldots, u_n$, each assigning a payoff value to each combination of chosen strategies, that is $u_i : S_1 \times \ldots \times S_n \to R$ for each $i \in N$.

One of the most important concepts of game theory was developed by John F. Nash in the 1990s:

"A Nash equilibrium is a vector of actions $\mathbf{a}^*$ with the property that no player i can do better by choosing an action different from a_i^*, given that every other player j adheres to a_j^*" (Osborne 2000, p.20). The vector of actions $\mathbf{a}^*$ is constructed in such a way that the action of player i is a_i^*. Formally, $\mathbf{a}^*$ is a Nash equilibrium if

$$u_i(a_i^*, a_{-i}^*) \geq u_i(a_i, a_{-i}^*) \quad \text{for every action } a_i \text{ of player i, for every player i} \tag{1.1}$$

where u_i is a payoff function that represents player i's preferences given that player i chooses a_i while every other player j chooses a_j^*.

The presence of a Nash equilibrium depends on the game and it is also possible to have multiple equilibria. Considering a small number of options, it is possible to examine each possible decision and control whether it satisfies the equilibrium condition. On the other hand, with more complicated games, this practice becomes too complex, hence the introduction of the *best response functions*:

$$B_i(a_{-i}) = \{a_i \in A_i : u_i(a_i, a_{-i}) \geq u_i(a_i', a_{-i}) \quad \forall \quad a_i' \in A_i\} \tag{1.2}$$

where any action in $B_i(a_{-i})$ is at least as good for player i as every other action of player i when the other players' actions are given by a_{-i}.

Game theory employs several different games to represent real world situations. To describe the games, it is important to know some basic concepts, such as [24]:

- Zero-sum games
- Cooperative & non-cooperative games
- Simultaneous & sequential-move games
- Symmetric games
- Two-person & *n*-person games
- Perfect information game

A game is a *zero-sum* game if the total sum of players' payoffs is equal to zero. In these games, if there are only two players, the amount one player wins is equal to the amount the other player loses.

A game is said to be *non-cooperative* if the players are not able to form binding agreements, although this impairment does not affect the ability of players to cooperate if that is beneficial.

On the other hand, in a *cooperative* game, players can discuss and stipulate agreements before taking a decision, which will be in concordance with the agreement.

In *simultaneous-move* games, all players take a decision at the same time, without knowing what the other players will choose. In contrast, in *sequential-move* games, some players have complete (or partial) information about what other players decided in the previous round.

Symmetric games are defined such that all players have the same set of decisions and outcomes at each stage.

Another important difference between games is the number of players. In a *two-player* game, only two individuals face each other and the outcome of their decision is based on the opponent's strategy. In contrast, an *n-person* game is played by a group of n players, where the outcome depends on each individual's choice.

Independently of the number of participants, a game has *perfect information* if each player has full information about the strategies played by each other player. Hence, recalling the previous definitions, a perfect information game has to be sequential.

My interest focuses on two specific games: the Prisoner's Dilemma (PD) and the Public Goods Game (PGG).

Both games are competitive, simultaneous-move, symmetric, non zero-sum games. The main difference is the number of players: while the PD is a 2-player game, the PGG is played by a community of n members.

1.1.1 Prisoner's Dilemma

The Prisoner's Dilemma is one of the most well-known examples in game theory representing a situation of two individuals who are suspected of a crime. Not having enough evidence to convict them, the police offer them a bargain which is explained in Table 1.1.

Table 1.1: Payoff matrix showing the number of years of imprisonment for each prisoner, given the decision each of them takes.

		Prisoner 1	
		Stay Silent	Confess
Prisoner 2	Stay Silent	2,2	5,1
	Confess	1,5	4,4

In a more formal way, the normal-form representation of this game can be depicted as follows:

Players: $N = 1, 2$.
Actions: $s_i = \{\text{stay silent (C), confess (D)}\}$ for $i \in N$.
Payoff: Let $v_i(s_1, s_2)$ be the payoff to player i if player 1 chooses s_1 and player 2 chooses

s_2:

$$\begin{aligned} u_1(D,D) = u_2(D,D) = 4 = \mathbf{P}\text{unishment} \\ u_1(C,C) = u_2(C,C) = 2 = \mathbf{R}\text{eward} \\ u_1(D,C) = u_2(C,D) = 5 = \mathbf{S}\text{ucker} \\ u_1(C,D) = u_2(D,C) = 1 = \mathbf{T}\text{emptation} \end{aligned} \tag{1.3}$$

The payoff function (also called *utility function*) needs to satisfy the following relations:

$$\begin{aligned} T > R > P > S \\ R > \frac{(S+T)}{2} \end{aligned} \tag{1.4}$$

Recalling the definition, the Nash equilibrium for the two prisoners would be: $\{$*confess, confess*$\}$. This is the only Nash equilibrium for the game and it remains the only one also when considering a repetition of the game over several rounds.

1.1.2 Public Goods Game

On the other hand, the Public Goods Game is used to assess individuals' behaviour with respect to the society they are a member of. Each member of the population has to decide whether to contribute to the public good or not (and, if so, how much of their personal resources to contribute), knowing that the gathered resources will be multiplied by a fixed factor and redistributed to the community's members equally, independent of their initial contribution.
The normal-form representation of the game is:

Players: $N = 1, 2, \dots, n$
Actions: $c_i \in [0\%, 100\%] * r_i$, for $i \in N$, where r_i are the resources of player i
Payoff: Let C be the total contribution of the community, $C = \sum_{i=1}^{n} c_i$, and m be the multiplier:

$$u_i(c_i) = \frac{C * m}{n} - c_i, \quad \forall i \in N \tag{1.5}$$

The Nash equilibrium in a one-shot PGG would be not to invest anything in the public good, which is called the free rider strategy, $c_i = 0\%$.

1.1.3 Iterated Games

Despite what the theory tells us, a large number of empirical experiments have repeatedly found a significant number of cooperative behaviours in both PD and PGG (and their iterative versions). At the same time, several studies have investigated the reasons for such behaviours. In order to describe the dynamics of the strategies, we need to consider several rounds of the games, hence employing iterated games. By repeating the games over multiple rounds, the aim is to capture the pattern of long-term interactions. In this context, the PD is used to investigate how cooperation is achieved and how it persists over time.

Strategies can be of two types: *pure* or *mixed*. The former determines all players' moves during the game as they play a single strategy throughout the rounds, while the latter is a probability distribution over all possible pure strategies. Let's define the pure strategies $R_1, \dots, R_N$. Then a mixed strategy will correspond to a point $\mathbf{p}$ in the set [25]:

$$S_N = \{\mathbf{p} = (p_1, \dots, p_N) \in \mathbb{R}^N : p_i \geq 0 \quad \text{and} \quad \sum_{j=1}^{N} p_i = 1\}. \tag{1.6}$$

Hence, if we first consider a two-player game, the payoff matrix will be:

$$U = (u(R_i, R_j))_{i,j \in \{1,\dots,N\}} = (u_{ij})_{i,j \in \{1,\dots,N\}}, \tag{1.7}$$

where u_{ij} is the payoff for a player adopting the pure strategy R_i and the opponent playing the pure strategy R_j.
The payoff for strategy $\mathbf{p}$ against strategy $\mathbf{q}$ will be

$$\mathbf{p} \cdot U\mathbf{q} = \sum_{ij} u_{ij} p_i q_j \tag{1.8}$$

and, if we want to rewrite the Nash equilibrium condition, we obtain:

$$\mathbf{p} \cdot U\mathbf{q} \leq \mathbf{q} \cdot U\mathbf{q}, \tag{1.9}$$

where $\mathbf{q}$ is the Nash equilibrium and $\mathbf{p} \neq \mathbf{q}$.

When considering stability for iterated games, a natural concept is related to the stability of a strategy over time, which leads to the evolutionarily stable strategy (ESS). An ESS can informally be defined as a strategy S that cannot be invaded over time by any other strategy. Formally, $\hat{\mathbf{p}} \in S_N$ is an evolutionarily stable strategy if the inequality

$$\mathbf{p} \cdot U(\epsilon\mathbf{p} + (1-\epsilon)\hat{\mathbf{p}}) < \hat{\mathbf{p}} \cdot U(\epsilon\mathbf{p} + (1-\epsilon)\hat{\mathbf{p}}) \tag{1.10}$$

holds $\forall \mathbf{p} \in S_N$, with $\mathbf{p} \neq \hat{\mathbf{p}}$ and $\forall \epsilon > 0$ sufficiently small.

Applying this concept to the the PD and the PGG game, it is easy to observe that the ESS and Nash equilibrium coincide in both cases. A purely defective strategy is the only ESS for the PD, while the free-rider strategy is the only ESS for the PGG.

It is indeed possible to prove that an evolutionarily stable strategy satisfies the strict Nash equilibrium condition [25]:

Theorem 1 *The strategy* $\hat{\mathbf{p}} \in S_N$ *is an ESS if and only if*

$$\hat{\mathbf{p}} \cdot U\boldsymbol{q} > \boldsymbol{q} \cdot U\boldsymbol{q} \tag{1.11}$$

$\forall \boldsymbol{q} \neq \hat{\mathbf{p}}$ *in some neighbourhood of* $\hat{\mathbf{p}} in S_N$.

This theorem demonstrates the conceptual similarities between the Nash equilibrium and the evolutionarily stable strategy.

The last thing I introduce is a concept related to the competition of two population types. Let's assume a population is divided into n types $E_1, \ldots, E_n$ with frequencies $x_1, \ldots, x_n$. The fitness of each type i is defined by the ability of that type to survive and reproduce over time [26]. When two or more types compete in the same environment, the fitness determines how well that specific type adapts to the environment and is able to reproduce. If we consider $f_i(\mathbf{x})$ the fitness of type E_i as a function of $\mathbf{x}$ the population evolves according to the replicator equation:

$$\dot{x}_i = x_i(f_i(\mathbf{x}) - \bar{f}(\mathbf{x})), \quad i = 1, \ldots, n \tag{1.12}$$

where $\bar{f}(\mathbf{x}) = \sum x_i f_i(\mathbf{x})$ is the average fitness of the population. This equation describes the evolution of the population composition over time as a function of the fitness. In other words, I can study the competition of multiple species by analysing the proportion of them in the population over time.

1.2 Psychopathy

1.2.1 Definition

Psychopathy was first mentioned by Pinel (1818) as part of his "manie sans delire" concept, which described individuals with undamaged cognitive understanding but impaired affect [27]. Psychopathy is characterised by a wide range of attributes [28]. In his work, Cleckley (1951) described the construct of psychopathy as characterised by a constellation of personality traits including superficial charm, lack of remorse, guilt and fear, poor impulse control, emotional detachment and impairment in building solid relationships, as well as high levels of manipulativeness, dishonesty, low empathy and callousness.

Since then, several conceptualisations have been developed to describe psychopathy in its own completeness. One of the classic conceptualisation of psychopathy distinguishes *primary* and *secondary* psychopathy [29]. Primary psychopathy is connected to callous and manipulative behaviour, and it is also strongly associated with lack of guilt, fear and anxiety. Secondary psychopathy develops from environmental experiences, such as parental abuse or rejection, resulting in emotional problems like impulsivity, neuroticism and aggression [30, 31]. More specifically, according to Karpman (1941) psychopathy can be divided into 2 distinct clinical groups: symptomatic and idiopathic psychopathy [32]. The former includes "all those reactions that on the surface bear close resemblance to what we call psychopathic behaviour, except that in these cases it is not difficult to elicit psychogenesis which is behind the psychopathic indulgence"; while the latter "includes psychopathic reactions for which it is impossible to find any psychogenic factors" (p.113). Hare and Neumann (2008), following the origianl construct of Cleckley (1951), developed another well-known conceptualisation of psychopathy that separates the traits into four main facets [33]: Interpersonal, Affective, Lifestyle, Antisocial (see Table 1.2). They also developed the Hare Psychopathy Checklist-Revised (PLC-R), based on Checkley's work, to assess psychopathic traits in institutionalised populations, and their measure is currently the one most used to assess institutionalised populations. Originally, the measure was formed of two main factors: Factor 1 and 2, [34] and was then separated into 4 other main factors: Interpersonal and Affective (Factor 1), Lifestyle and Antisocial (Factor 2). A total of 18 sub-scales were then defined as shown in Table 1.2.

Table 1.2: Four-factors PCL-R item-based model of psychopathy.

Factors	Sub-scales
Interpersonal	Glibness, superficial charm Grandiose sense of self worth Pathological deception Manipulativeness
Affective	Lack of remorse or guilt Shallow effect Callousness and lack of empathy Failure to accept responsibility for actions
Lifestyle	Need for stimulation, proneness to boredom Parasitic lifestyle Lack of realistic long-term goals Impulsivity Irresponsibility
Antisocial	Poor behaviour control Early behavioural problems Juvenile delinquency Revocation of conditional release Criminal versatility

Psychopathy is also considered as part as the so-called Dark Triad of personality [35]: psychopathy, narcissism and Machiavellianism. A narcissistic person is characterised by a grandiose sense of self-importance, exhibitionism, an inability to tolerate criticism, interpersonal exploitativeness, relationships that alternate from extremes of over-idealisation and devaluation, and lack of empathy [36]. Machiavellianism, on the other hand, is denoted by a relative lack of affect in interpersonal relationships, a lack of concern with conventional morality, manipulativeness and low ideological commitment [37]. Although the three measures cannot collapse to one unifying factor [38], the high correlations amongst them are undeniable.

1.2.2 Measures

Considering the complexity of psychopathic traits and the consequent lack of an exact conceptualisation, developing a single measure to test psychopathy in individuals is a hard task. Several measures have been designed to assess psychopathic traits in institutionalised and non-institutionalised populations. In this section, I present the two measures that I used in my studies.

One of the most widely used measures for non-institutionalised populations was developed by Lilienfeld and colleagues in 1996 [39]: the Psychopathic Personality Inventory (PPI). The Psychopathic Personality Inventory is a 154-item self-report questionnaire that measures the core of the psychopathy dimensions. The measure detects eight main sub-scales that are summarised in three main factors as presented in Table 1.3.

Table 1.3: PPI sub-scales model of psychopathy.

Factors	Scale	Items
Self-centred impulsivity	Machiavellian egocentricity	Narcissism Ruthless attitudes
	Rebellious nonconformity	Recklessness Lack of concern for social norms
	Blame externalisation	Inability to recognise the consequences of one's own actions Tendency to blame others for one's problem Rationalisation of one's misbehaviour
Fearless dominance	Carefree nonplanfulness	Indifference in planning actions
	Social influence	Ability to influence others Manipulativeness
	Fearlessness	Lack of anxiety Risk-seeking attitudes
	Stress immunity	Absence of marked reactions to stress Lack of reaction to provoking events
Coldheartdness		Callousness Lack of guilt and sentimentality

Two main differences between the PLC-R and the PPI are that (1) the former was developed for institutionalized people (either in mental health or penal institutions), while the latter was developed to assess psychopathic traits in the non-criminal population; and (2) the PPI is a self-report questionnaire, accessible to anyone and easy to use, while the PCL-R is a complex test, requiring extensive training, lengthy interviews and most importantly access to criminal records.

Another self-report scale, the Triarchic Model of Psychopathy [40], is the most recently developed test for psychopathic traits. It was initially conceived to solve some of the issues arising from previous measures such as the necessity to test for "successful psychopaths" and the strong correlation between low levels of anxiety and psychopathy. The test is a self-reported questionnaire based on validation in the general population. The construct comprises three main factors: disinhibition, meanness and boldness (see Table 1.4).

Table 1.4: TRIP-M sub-scales model of psychopathy.

Factors	Items
Disinhibition	Impulsiveness Weak restraint Hostility and mistrust Difficulties in regulating emotions
Meanness	Lack of empathy Lack of affiliative capacity Predatory exploitativeness Empowerment through cruelty and destructiveness
Boldness	Social assertiveness Emotional resiliency Risk-seeking attitudes Overconfidence

Thus, different measures have been developed over the years to test psychopathic traits in both institutionalised and non-institutionalised population. Although some researchers are more in favour of one or the other measure, they have all been widely validated over the years and it is not an aim of this thesis to argue the validity of one measure over the others. For my experiment (see chapter 4), I adopted the PPI-R (a revised version of the PPI) measure based on the number of items in the measure, the availability of tests to assess the reliability of the answers, and the possibility to compare my sample with previous studies.

1.2.3 Psychopathic traits and cooperation

When studying how individuals make decisions, one of the main aspects that has been analysed is how personality traits impact the process. A large branch of research has been devoted to shedding light on the impact of psychopathic traits on decision-making, especially in relation to cooperative behaviours. To do so, several studies have employed games to investigate psychopathy and cooperation and, interestingly, results have not all been consistent. One of the first studies on psychopathic traits and cooperation dates back to 1976 [41]. In this study, psychopathy was tested in an experiment investigating interpersonal behaviour in 32 male psychopaths using the Prisoner's Dilemma game. Results suggested that psychopaths may be capable of co-operating and predicting somebody else's behaviour in certain situations. However, secondary psychopaths seemed less able to behave efficiently in the game. A following study analysed psychopathic attributes in a non-institutionalised population which showed a strong correlation between antisocial actions and both primary and secondary psychopathy [42]. Primary psychopathy was correlated with disinhibition and boredom susceptibility while secondary psychopathy was significantly less associated with these two measures.

More recent studies directly examined cooperation and psychopathic traits both in the general population and in offender samples. Curry et al. (2011) tested the correlation between psychopathic traits and cooperation in one-shot Prisoner's Dilemma and bargaining games, showing that cooperative behaviours (in the two games) are associated with different aspects of self-reported psychopathic personality traits [43]. Although overall it showed that psychopathic personality traits lead to lower levels of cooperation, the effects were diverse in the bargaining. Psychopathy was also found to be significantly correlated with negative behaviours (defection), although only for male participants. The authors tested 30 participants using functional brain imaging scan and self-reported psychopathy measures (PPI and Levenson) [44]. Participants were asked to play a Prisoner's Dilemma game in different groups, controlling for gender effect. Results were analysed looking particularly at the outcome of the game, showing that male players with high levels in the Levenson psychopathy scores were significantly more likely to defect overall and also more likely to defect after a previous mutual cooperation. Interestingly, results from the functional brain imaging showed that high-psychopathic subjects found the CD outcome (cooperate while opponent defects) less aversive than low-psychopathic players. Berg, Lilienfeld and Waldman (2013) found that different aspects of psychopathy predicted different behaviours when playing several economic games (economic tasks, Ultimatum game, Dictator game and Prisoner's Dilemma game). Psychopathic traits were assessed with the PPI self-reported questionnaire. While in general high levels of psychopathy predicted low cooperation in the games, coldheartedness and self-centred impulsivity emerged as major predictors of participants' behaviours in the games [45]. Psychopathy is known to predict competitive goals, leading to selfishness and manipulative behaviours. Thus, high psychopathic traits have been found to predict greater monetary gains in competitive interactions, but not in cooperative tasks [46]. Furthermore, psychopathic traits have also been associated with rational choices. Using the Ultimatum game with college students, Osumi and Ohira (2010) tested the conflict between fairness and decision-making, when mediated by psychopathic traits. In their study, individuals with high levels of psychopathy were keener to accept the offer, despite its unfairness. By doing so, they avoid punishment and they choose the most rational option [47]. A similar experiment was implemented with offenders with and without psychopathy. Evidence presented a different result from the previous study: offenders with psychopathic traits showed a similar rejection pattern to healthy individuals. Furthermore, offenders without psychopathy were the only group not adjusting their responses to the alternatives, showing a stronger impairment in social decision-making than prisoners with psychopathy [48]. Looking further at institutionalised populations, Mokros et al. (2008) found that criminal psychopaths demonstrated a significantly higher proneness to competitive behaviour in a Prisoner's Dilemma game than a general healthy adult population. Psychopathic subjects accumulated a higher gain and they exploited their counterpart more strongly than healthy subjects.

Several other studies have investigated how contextual factors and other mechanisms moderated the impact of psychopathic traits on cooperative behaviours. Evidence showed that primary psychopathy predicts defection in low-value relationships [49]: allowing for conversational interaction among participants before the game, the researchers created a sort of low-value social relationship between the individuals. Results showed that higher scores in primary psychopathy were related to lower levels of cooperation with opponents who had interrupted them more frequently, and with whom they did not have common ground. In this sense, the low-value social relationship captured the quality and the duration of a prospective social relationship. Another aspect that has been deeply investigated is the correlation between cooperative decisions and punishment, in relation to psychopathic traits. Individuals with high levels of psychopathy showed significant impairment when choosing between options associated with different levels of reward and punishment, as presented in Blair et al. (2006) [50]. In another study, 19 psychopaths and 21 healthy participants took part in a passive avoidance task. While healthy individuals responded to all levels of reward and punishment, psychopathic participants adjusted their decisions only when a low level of reward and punishment was presented [51]. The presence of a reward and a punishment increased the inhibition of healthy individuals, compared to the absence of both. On the other hand, high psychopathic individuals did not show an increase of inhibition in any of the conditions where reward and punishment were introduced [52]. Therefore, it has been argued that punishment is not an effective tool in the detention of offenders with psychopathic traits [53]. Interestingly, Deutchman and Sullivan (2018) looked at how the contextual framework affected cooperation while looking at participants' Dark Triad traits (psychopathy, narcissism and Machiavellianism) [54]. They tested 1604 participants playing a one-shot Prisoner's Dilemma game in either a social vs non-social context or a gain vs loss context. Participants' personality traits were assessed by a short Dark Triad self-report questionnaire at the end of the game. Individuals high in the Dark Triad scale cooperated significantly less in the PD game, especially when the game was presented as a non-social one. Dark Triad was further examined by Malesza (2018). She sampled 280 individuals playing a repeated version of the Prisoner's Dilemma game. Results reported that the both Machiavellianism and psychopathy were highly predictive of defective strategies over time [55].

Thus, several studies have analysed the impact of psychopathic traits on cooperative behaviours using economic games. Nevertheless, no previous work has considered the relationship between group behaviours and psychopathic traits at the individual level, which is one of the aims of this thesis.

1.3 Individual-Based Modelling

Individual-based models have been widely used by biologists, ecologists, economists and sociologists to describe evolutionary processes. Used to address both applied and theoretical questions, they have become more and more important in the research process in various disciplines. These models, also called agent-based models, aim to simulate populations composed of discrete individuals, each of them with their own set of properties [56]. A simple description of an individual-based model is provided by Railsback (2001) (p.48) [57]: "build a model of an individual organism, build a model of the environment, and let a computer create multiple individual organisms and simulate the interactions of the individuals with each other and the environment". Individuals are described by a simple set of rules and they usually interact with the surrounding environment, learning from their own experiences throughout time. These models allow the formalisation of complex social systems in which individuals interact with each other, learn from their own previous experiences and adapt to a mutable environment, allowing researchers to investigate a broad set of problems. By building models from the bottom up, it is also possible to observe global self-organising effects on the population, without directly manipulating the population. Moreover, even though these models usually describe natural complex systems, through this approach it is possible to manipulate aspects that are not manipulable in lab experiments, providing the opportunity to address aspects that are otherwise hard to handle, because they are too costly or unethical. By exploring new areas, researchers have discovered innovative hypotheses and useful guidance for experimental procedures. Thus, individual-based modelling can bring a notable contribution to the research community, from the postulation of new theories to the verification of them.

1.3.1 Definitions

To have a more formal definition of an individual-based mode (IBM), I refer to Macal and North (2010), who define the three major components of an IBM:

1. a set of agents with their attributes and rules;
2. a set of relationships that define the interactions between individuals, and the topology of connections defining how and with whom they interact;
3. the environment in which individuals interact.

(1) Individuals are described as agents reacting autonomously, depending on the environmental condition. By modelling each individual separately, it is possible to include different sources of variation at the individual level. In doing so, differences that are often hard to control for in experiments can be easily manipulated, allowing for a more detailed model of reality. Such variations are well explained by De Angelis and Mooij (2005) (p.149) [58]:

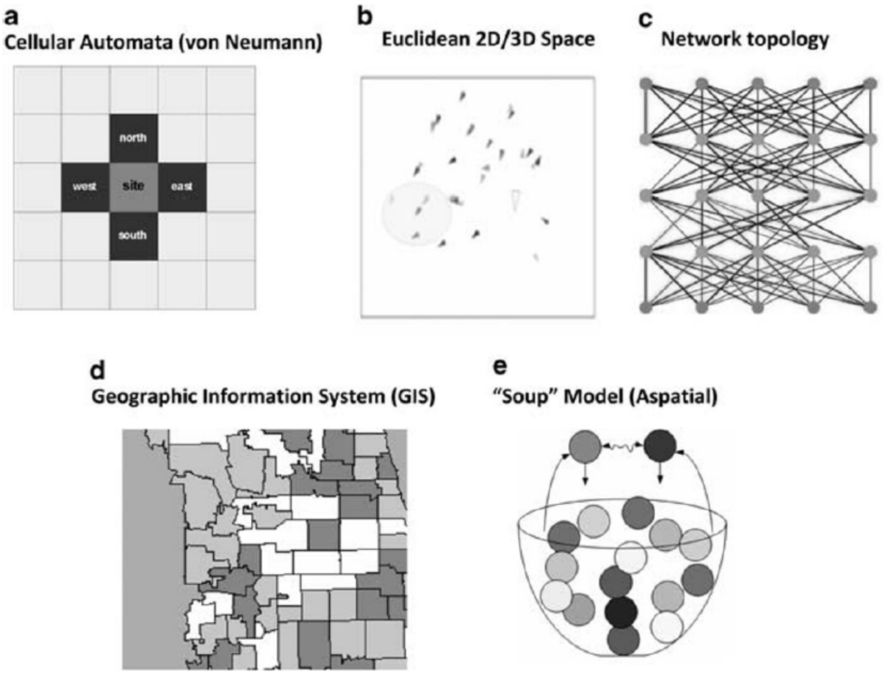
- i) spatial variability, local interactions, and movement;
- ii) life cycles and ontogenetic development;
- iii) phenotypic variability, plasticity and behaviour;
- iv) differences in experience and learning;
- v) genetic variability and evolution.

(i) Although previous models have taken into account spatial distribution (e.g. classical predator-prey models), they did not describe agents as individuals. IBMs take into account populations where individuals carry their singularity, allowing investigation of the effects of non-uniform populations on evolutionary dynamics. (ii) Another innovative feature is the modelling of age-structured populations, in which individuals are defined at different stages of their life. Furthermore, (iii) one of the main aspects of IBMs is the ability to describe each individual separately, allowing a broad variation of traits to emerge in the population. Such variations are achieved by introducing both genetic differences, which are experienced from the beginning of the life cycle, and phenotypic differences, that are developed through the life time of the individual. (iv) Such phenotypic differences evolve as a product of the individual own experiences, which lead each agent to gather information from the environment, and act independently from the group. Lastly, (v) the core of IBMs is the ability to adapt to the circumstances experienced, leading populations to become better and better fit to the environment. This aspect of the models is particularly interesting for studying genetic changes, and it is mostly used by biologists and ecologists.

(2) The second aspect defining an IBM is the set of relationships. This set does not only define how agents are connected to each other, but also what kind of interactions they can have with each other. It is possible to define long-range connections that operate differently from a local network, creating also different layers of connections (e.g. multi-level networks). Different examples of connectedness between agents are shown in Figure 1.1.

Lastly, (3) the environment can be interpreted as the location of agents with respect to each other, as well as a more complex system providing resources and information to each individual. Geographic tools such as GIS make it possible to implement the evolution of the model in a specific and real geographic area of the world, for example in models tracking animal migration.

Figure 1.1: Examples of topologies for individual-based models.



from DeAngelis, D.L. and Mooij, W.M. (2005)

1.3.2 Psychopathic traits and evolutionary fitness

Individual based models have been widely used in ecology [56] and biology [59], and recently also sociologists have adopted simulation models in their research [60].

However, the use of simulation models is barely used in psychology, although the potential benefit of such methodologies is well recognised [61]: a recent study highlights the need for communication between fields, integrating concepts from behavioural ecology to human personality psychology [62].

Nevertheless, researchers have been examining the adaptive fitness of humans considering personality traits. An evolutionary perspective has been adopted to examine whether some dimensions of personality (such as psychopathy) could be adaptive and how those traits were inherited over generations.

Glenn, Kurzban and Raine (2011) shed light on the positive and evolutionary perspective of psychopathic traits [63]. They described the different dimensions of psychopathy, considering the benefits and the costs for each one of them. They then compared two main visions of psychopathy: (1) the adaptive perspective, in which psychopathic traits are considered an adaptive strategy developed over generations as a response to environmental stimuli; and (2) the pathology perspective, in which psychopathy is seen as a dysfunctional pathology deriving from a series of mutations over time. Providing evidence supporting and weakening each of the two theories, the author concluded that both visions could be sustained, and further research should go in that direction.

Moreover, previous research has argued that differences arising from psychopathy can be evolutionarily advantageous [64]. In their work, Krupp et al. sustain that psychopathy is not a disorder but it is an "evolved life history strategy". Although they recognise the physiological differences between psychopaths and non-psychopaths, they assert that such differences are an evolutionary advantage. Because of the main traits of psychopathy (e.g. manipulativeness, exploitativeness, deceiving attitudes, lack of fear and empathy, and superficial charm), psychopathy has been considered to be an "adaptation for social predation" [65]. This line of research is in compliance with the concept of successful psychopathy. Previous studies looked at successful psychopathy as a form of adaptation to the environment. The succesful psychopath is defined as "one who embodies the essential personality characteristics of psychopathy but who refrains from serious antisocial behaviours" [66] (p.459). Manipulative interpersonal attitudes, as well as lack of guilt-aversion, can be interpreted as positive and adaptive behaviours when environmental conditions are harsh, as they lead individuals to gather more resources and therefore be more likely to procreate [67]. In their study, Međedović examined the relationship between psychopathy and fitness, considering the moderating role of the environment, where fitness is represented as the ability to reproduce. Data showed that some aspects of psychopathy (interpersonal and affective sphere) correlate positively with individuals' fitness, leading towards more offspring in the future. At the same time, other aspects such as impulsivity and recklessness are negatively correlated to reproduction success. Moreover, studies looking at the correlation between professional success and psychopathy dimensions found that fearless dominance was positively correlated with success, whereas self-centred impulsivity was negatively linked to professional success [68].

Finally, there has been research focused on the heritability of psychopathic traits and how they affected both reproduction rates and offspring life-style. Hyde et al. (2016) looked at the heritable pathways to early callous-unemotional behaviours, which are at the base of psychopathy [69]. They sampled 561 families that adopted children with biological mothers with severe antisocial behaviours. Their aim was to investigate the heritability of such traits despite the rare contact with the biological mothers. Results showed that children inherited callous and unemotional behaviours from their biological mothers, but the positive reinforcement of the adoptive mothers buffered such behaviours. These results are in line with previous findings that 69% of the variance in latent psychopathic traits are explained by genetic factors, while 31% of it is driven by environmental conditions [70].

Thus, although previous research has investigated the beneficial and adaptive aspects of psychopathy, and the heritability of such behaviours over generations, no previous work has adopted individual-based modelling to investigate the evolution of specific aspects of psychopathy in different environmental scenarios.

1.4 Thesis structure

The thesis consists of three main parts: the analysis of existing experimental data, the discussion of an original experiment of my own, and an individual-based model. In the first two chapters, I analyse data from two experiments conducted by Dr. H. Eisenbarth and collaborators. Chapter 2 examines how psychopathic traits affect cooperation in an environment which provides emotional feedback after decisions. I also present a section highlighting the importance of appropriate statistical analysis when analysing experimental data, providing an example of how incorrect selection of statistical models can provide misleading results. Chapter 3 investigates, through the use of an iterated Prisoner's Dilemma game, the effect of emotional facial feedback on cooperative behaviours when controlling for different levels of psychopathic traits. Both chapters investigate the impact of psychopathic traits on cooperative actions when emotional feedback is presented. While the first article uses the presence of emotional feedback as a purely contextual factor, the second manipulates the emotional feedback participants received during the game. My contribution to both studies relates to the statistical analysis implemented: I organised the dataset and decided how to analyse the data, choosing the most appropriate statistical techniques given the data structure. The analyses were implemented using R and MATLAB. I was the first and corresponding author for both articles. They have been published in *Journal of Individual Difference* and *Scientific Reports* respectively. Both Chapters 2 and 3 present the two articles in their published form, following the classical journal structure of Introduction, Methods and Materials, Statistical Analysis, Results and Discussion, followed by Supplementary Material.

Secondly, I discuss the effects of psychopathic traits on group cooperative behaviours, reporting an experiment I designed and ran at the University of Southampton. I am the first and corresponding author of the article that is published in *Royal Society Open Science*. Chapter 4 reports the study in the article format.

Thirdly, I describe an individual-based model investigating the impact of specific aspects of psychopathic traits on the evolution of a population. Chapter 5 first provides an introduction to the theoretical construction of the model, and it then describes the general model following the ODD protocol [71]. Results are then presented separately in Chapters 6 to 10. Chapter 6 presents a model which does not allow for mutation over generations, to illustrate the basic dynamics of the model. Successively, Chapters 7 to 10 present models where mutation is implemented. Each model presents a new aspect compared to the previous one. In this way, I disentangle the effect of each single component on the results. Moreover, each new aspect included in the model allow me to have a more realistic and complete representation of the real-world interactions and dynamics.

Finally, chapter 11 sets out the conclusions of this thesis, presenting a discussion connecting all three parts of the thesis and future directions of research.

Chapter 2 When do psychopathic traits affect cooperative behaviour? An iterated Prisoner's Dilemma experimental study.

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M.K. and E.H contributed to study conceptualization and data collection; M.T. contributed to data preparation while M.T., R.H. and H.E. contributed to data analysis; all authors contributed to report writing.

Abstract

Personality traits have been long recognised to have a strong impact on human decision-making. In this study, a sample of 314 participants took part in an online game to investigate the impact of psychopathic traits on cooperative behaviour in an iterated Prisoner's dilemma game. We found that disinhibition decreased the maintenance of cooperation in successive plays but had no effect on moving towards cooperation after a previous defection or on the overall level of cooperation over rounds. Furthermore, our results underline the crucial importance of a good model selection procedure, showing how a poor choice of statistical model can provide misleading results.

Keywords
Iterated Prisoner's Dilemma game; Cooperation; Psychopathy; Model Selection.

2.1 Introduction

Exogenous factors, such as economic conditions, utility outcome and equality have long been considered the principal drivers of human decision-making [8, 11]. However, endogenous elements, such as individual propensities, personality traits and emotional conditions have also been recognised to have a strong impact [43, 72, 73]. To assess decision-making, several studies adopted some form of economic game, such as the Prisoner's Dilemma (PD). The PD is a two-person non-zero-sum game, usually adopted in the non-cooperative form, meaning that players have no opportunity to interact with each other besides playing the game [74]. In the PD, two persons each have to decide between two possible actions, giving four possible outcomes (see Table 2.1). Although the optimal play from a purely economic point of view would be to defect[1], several studies have recorded cooperative behaviour of the players. Thus, as purely utilitarian considerations did not sufficiently explain players' behaviour [11, 75], other factors such as reputation [8], punishment and altruism [11] have been discovered to influence individuals' behaviour in economic games.

Table 2.1: Payoff structure of each move in a typical Prisoner's Dilemma game.

	Cooperate	Defect
Cooperate	R = 3, R = 3	S = 0, T = 5
Defect	T = 5, S = 0	P=1, P=1

$T > R > P > S, R > (S + T)/2$

Emotional states and personality measures have been incorporated into economic models and experiments to reflect the fact that participants in economic games are social human agents [73]. Several studies have been carried out regarding the influence of personality on decision-making [72]. As Ibáñez at al (2016) (p.1) states: "personality characteristics would play a significant role in different behaviour underlying cooperation". In this work we focus on a specific aspect of human personality, namely psychopathy. Psychopaths are described as dominant, superficial, manipulative, affective shallow individuals, unable to form strong emotional bonds with others, and lacking in empathy [28]. The experimental findings relating such traits to decision-making so far are not entirely clear and sometimes also contradictory. One of the first studies adopting the PD to assess psychopaths' decisions was [41]: he examined 32 male psychopaths playing 60 trials of the game under two different conditions (communication and non-communication). Unexpectedly, he concluded that psychopaths are capable of cooperating and predicting another person's behaviour. Since then several studies have been conducted to investigate the correlations between psychopathic traits and cooperative behaviours. Criminal psychopaths from a high security psychiatric hospital displayed significantly higher proneness to competitive behaviour in an iterated PD [77], choosing selfish instead of cooperative strategies more often

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[1] In a one-shot PD, the Nash equilibrium states that the optimal choice is to defect, since no matter what the opponent plays, defection yields a higher payoff than cooperation [76].

that healthy adults. Furthermore, a negative correlation between cooperation and psychopathic traits was found in male (but not female) participants in a general population sample [78]. Results suggested that some aspects of psychopathic traits were specifically predictive: primary psychopathy (low-anxious, usually viewed as a direct consequence of some intrinsic deficit), Rebellious Nonconformity (e.g. the propensity to do something others might judge as inappropriate) and Machiavellian Egocentricity (e.g. the willingness to trick someone for one's own sake). Furthermore, results have suggested that different aspects of psychopathy affect cooperation differently, when looking at PD and bargaining games [43]. Primary, but not secondary, psychopathy was found to predict lower acceptance rate of unfair ultimatum game offers, and lower offers in a dictator game in a sample of 47 prisoners [79]. Moreover, psychopathic, high disinhibited and impulsive personality traits are predictive of a lack of reciprocity in a trust game [80]. These dissociative effects of psychopathic traits could be reflected better in a model that directly differentiates disinhibition, meanness (lack of care about other individuals) and boldness (risk-seeking and fearlessness), as the Triarchic Model of Psychopathy does [40].

According to these results, people scoring high in psychopathic measures (primary and/or secondary) are expected to adopt less generous and more selfish behaviours, to aim to maximise their own profit, and not to care about the opponent compared to healthy individuals. In this study, we use an iterated version of the game (IPD) to investigate the effect of personality traits emerging over time. We chose to adopt an iterated version rather than a one-shot PD because: (1) the effect of personality becomes more evident in repeated games [72] and individuals cannot be fully analysed in one-shot games [76]; (2) we investigate how cooperative behaviour changes from one trial to the next.

In the current study, facial expressions of the opponents are presented to the player after each round. The purpose is to create an environment in which players have some sort of connection with their opponent, as opponent characteristics were discovered to have a strong effect on a player's behaviour. However, there is no manipulation of those facial expressions, and we are not testing the effect of those feedbacks on players' decisions. Thus, with this experiment we aim to capture the effect of psychopathic traits on decision-making processes in the presence of facial feedback. Our hypothesis is that players showing lower levels of psychopathy will adopt more cooperative behaviours, compared to players scoring high in the psychopathic measures.

2.2 Methods and Materials

2.2.1 Sample

A total of 398 participants were recruited through social media, email lists and adverts on a University campus.

The experiment was conducted on an online platform, and complete data were available for 378 participants. Participants gave informed consent for participating in an online game. They received a small compensation based on their achieved sum from the game, with each point they accumulated being awarded €0.10 by means of an Amazon voucher.

Participants who took too short or too long time (Mean ± 3*SD) to complete the task were excluded from the study, leading to the exclusion of 4 participants. Moreover, 60 participants did not compile the personality questionnaire in a consistent way and were excluded by the analysis. The final sample was composed of 314 participants (180 females, mean age=27.41). See Table 2.3 for sample descriptive statistics.

Informed consent was obtained from all participants prior to starting the game and participants were debriefed after the game regarding the opponent being PC-based rather than a real other participant. We obtained ethical approval for the study from the German Psychology Association ethics board.

2.2.2 Experiment procedure

After having filled in a short questionnaire on socio-demographic data, the participants were informed about the structure of the game. Each participant played a 15 trial Iterated Prisoner's Dilemma game. The game was presented as a commercial game in which players were the owner of a shop situated next to another store, selling various technical goods. Although participants played against a computer throughout the whole game, they were told they were playing against a human opponent. The opponent was represented by a video clip of a person, taken from the Denver Intensity and Spontaneous Facial Action (DISFA) Database [81]. The opponent was introduced at the beginning of the game showing a 300ms video of a person with a neutral expression, after showing a "wait until we connect you to another player" instruction. In each trial, the participant was asked to decide whether she wanted to sell the good at the standard price (cooperation) or at a sale price (defection). They were encouraged to maximise their own profit, in order to achieve the most points at the end of the game. Four different outcomes were possible, according to the players' decisions: percentages in Table 2.2 show the profit and 4, 3, 2 or 1 points were awarded according to the profit earned in each trial.

Table 2.2: Payoff matrix showing the percentage profit earned during the game by each participant according to both players' decisions.

		Participant	
		Standard Price	Sale Price
Opponent	Standard Price	(30% , 30%)	(10% , 40%)
	Sale Price	(40% , 10%)	(20% , 20%)

The computer was programmed to play a tit-for-two-tats strategy, meaning that it cooperates until the opponent defects twice in a row, then it defects until the player cooperates again. In the last two rounds however, the computer was programmed to defect, as an attempt to simulate human behaviour. A page with the two decisions made and the consequent payoff was shown after each round. In addition to the payoff, participants were shown a short video of facial feedback, supposedly from the webcam of the opponent. Videos were taken from the Denver

Intensity and Spontaneous Facial Action (DISFA) Database [81]. Two individuals were selected (one female and one male) to represent the opponents and 10 different 300ms snips were created for each of the female and the male persons and for each of the happy and sad expressions. For each cooperation, the participant was presented with a happy facial expression video of their opponent, while they were presented with a sad facial expression video of their opponent after each defection.

2.2.3 Questionnaires

At the end of the game, a questionnaire was presented to the participants asking whether they believed in the setting of the game and which strategy they adopted. Participants were asked to state how much they believed they were playing against a real person, choosing a state in a scale from 1 to 5 (1 not at all, 5 completely). Participants were also asked whether they were trying, on a scale from 1 to 5, to maximise their own profit. Lastly, they were asked to fill in the Triarchic Model of Psychopathy questionnaire (TriPM) [82].

In order to control for potential confounders related to anxiety, aggression and depression, we included the Buss Perry Aggression Questionnaire [83], the Penn State Worry Questionnaire [84], the Mood and Anxiety Symptom Questionnaire [85] as well as the Brief Depression Severity Questionnaire [86]. Measures of the PD were not related to any of these variables; therefore we did not include them in further analyses.

2.2.4 Psychopathy measures

Psychopathy was assessed through the Triarchic Model of Psychopathy questionnaire (TriPM). A reliability test (Cronbach's alpha) in the current sample shows acceptable internal consistencies (Table 2.3). Developed by Patrick, Fowles, & Krueger (2009), the questionnaire is based on three factors: *disinhibition, boldness*, and *meanness.*

Disinhibition describes a general propensity toward impulse control problems, involving a lack of self-control, weak restraint and difficulties in regulating emotion (Patrick, Drislane, & Strickland, 2012; Patrick & Drislane, 2015). High level of disinhibition-related behaviour includes irresponsibility, impatience, impulsive actions leading to negative consequences, alienation and distrust, untrustworthiness, proneness to drug and alcohol problems, and engagement in illicit or other norm-violating activities.

Boldness suggests a capacity to remain calm and focus in situations involving pressure and threat. It can be associated with social dominance, low stress reactivity and thrill-adventure seeking [87], and it can be recognised in manifestations of imperturbability, assertiveness, persuasiveness, and social poise.

Meanness entails deficient empathy, lack of close social attachment towards others, rebelliousness and empowerment through cruelty. Individuals with high meanness scores usually show callousness, cold-heartedness and apathy towards others (Patrick, Drislane, & Strickland, 2012). The notion of meanness is central to conceptions of psychopathy in criminal and delinquent samples (Patrick, Fowles, & Krueger, 2009).

Table 2.3: Descriptive statistics for the participant sample.

Variables	Min	Mean	Standard Deviation	Max	Cronbach's α
age	18	27.26	8.92	65	-
gender	1	1.43	0.50	2	-
ethnicity	1	1.02	0.14	2	-
nationality	1	1.05	0.22	2	-
education	2	4.69	0.70	5	-
job	1	3.57	1.47	6	-
degree	1	2.83	1.74	8	-
believe	1	2.06	1.31	5	-
maximise	1	3.73	1.20	5	-
meanness	19	30.99	7.95	67	0.87
boldness	30	50.01	7.50	72	0.81
disinhibition	21	33.58	7.93	62	0.87

Gender: 1 = Female, 2= Male
Ethnicity: 1 = European, 2 = other;
Nationality: 1 = German, 2 = other;
Education: 1 = Primary school, 2 = Secondary school, 3 = Gymnasium, 4 = High school, 5 = Higher school
Degree: 1 = Still in education, 2 = No education completed, 3 = Apprenticeship, 4 = Bachelor, 5 = Master, 6 = Doctoral student, 7 = Doctor, 8 = other
Job sector: 1 = Technical, 2 = Research, 3 = Art and music, 4 = Social, 5 = Economic, 6 = Administrative

2.3 Statistical Analysis

The variables under investigation were the total percentage of cooperation, the percentage of cooperation after a previous cooperation (CaC), and after a previous defection (CaD). The total percentage of cooperation was calculated as the mean percentage of cooperative decisions over the 15 trials; while CaC (CaD) was the percentage of times a participant cooperated immediately following a previous cooperation (defection). The same analyses were implemented on the three dependent variables in parallel. The explained variables were regressed against a fixed set of explanatory variables which included: *gender* (1=female, 2=male) as it has been found to be correlated with psychopathic traits [88, 89]; *age* to control for age effects; the *believe* variable which accounted for the participants' level, on a scale from 1 to 5 (1=not at all, 5=completely), of belief that they were playing against a fellow human; and the *maximise* variable that expresses the extent to which participants were trying to maximise their own profit during the game (1=not at all, 5=completely). The three dimensions of psychopathic personality, *meanness, boldness and disinhibition* were included as dimensional scores. The mean and variance of these measures in our sample are similar to other samples previously collected [90]. Summary statistics for the predictor variables and a correlation matrix amongst dependent and independent variables are provided in Tables 2.3 and 2.4.

The analysis of the data can be divided into three phases. First, candidate models were fit to half of the data in order to identify suitable models for the dataset. Since all three DVs were produced from a series of zeros and ones, we considered a Generalised Linear Model (GLM), a Logistic (LM) and a Beta-Binomial (BBM) regression models as candidate and compared their fits to data. Secondly, repeated k-fold cross-validation was implemented to select the best predictive models from among these candidates. Finally, the selected model was fitted on the complete dataset. All the analyses were implemented in R. More information are provided in the Supplementary Material.

2.4 Results

We first analysed the total rate of cooperation over the fifteen rounds as dependent variable (Table 2.5).

Table 2.5: GLM results for participants' cooperation as a function of their age, gender, level of belief and personality traits.

DV:	overall cooperation	CaC	CaD
intercept	0.69***	0.58***	0.66 ***
	(0.10)	(0.12)	(0.11)
age	-0.003	-0.00	0.00
	(0.02)	(0.00)	(0.00)
gender	0.04	0.07	0.03
	(0.04)	(0.04)	(0.01)
believe	-0.02.	-0.01	-0.03*
	(0.01)	(0.01)	(0.01)
maximise	-0.03*	-0.04.	-0.02
	(0.01)	(0.02)	(0.01)
meanness	-0.08	-0.01	-0.02
	(0.02)	(0.03)	(0.02)
boldness	-0.02	0.01	-0.01
	(0.02)	(0.02)	(0.02)
disinhibition	-0.04 .	-0.06 *	0.00
	(0.02)	(0.03)	(0.02)

Standard errors for coefficients shown in parenthesis;
Significance level: ‘***’ <0.001 ‘**’ <0.01 ‘*’ <0.05 ‘.’ <0.1;
CaC = cooperation after previous cooperation, CaD = cooperation after previous defection

The only variable with a statistically significant impact at the 5% level on predicting the overall cooperation is *maximise*. Participants who aimed to get the highest score possible for themselves were less cooperative than people who were not focused on their gain. In this

Table 2.4: Correlation matrix between dependent and independent variables.

	age	gender	believe	maximise	meanness	boldness	disinhibition	cooperation	CaC	CaD
age	1									
gender	0.22***	1								
believe	-0.17**	-0.03	1							
maximise	-0.20***	0.06	0.07	1						
meanness	-0.01	0.39***	0.04	0.08	1					
boldness	0.01	0.16**	-0.02	0.02	0.10	1				
disinhibition	-0.03	0.25***	-0.05	0.08	0.66***	-0.13*	1			
cooperation	-0.02	0.00	-0.09	-0.14*	-0.11*	0.02	-0.15**	1		
CaC	-0.05	0.01	-0.01	-0.12*	-0.13*	0.00	-0.19**	0.87***	1	
CaD	0.04	0.03	-0.16**	-0.10.	-0.07	-0.03	-0.04	0.82***	0.37***	1.00

Standard errors for coefficients shown in parenthesis; Significance level: ‘***’ <0.001 ‘**’ <0.01 ‘*’ <0.05 ‘.’ <0.1;
CaC = cooperation after previous cooperation, CaD = cooperation after previous defection

sense, their behaviour could be considered rational although it has been proven that cooperative behaviour leads to higher rewards than a negative strategy in an iterated game [91]. Personality traits are not a significant predictor (at the 5% level) when looking at the overall cooperation.

Disinhibition is the only significant personality aspect when considering the maintenance of cooperative behaviours between trials (CaC) (Table 2.5). The less inhibited players were, the more they switched strategy from cooperation to defection. In this sense, more disinhibited players tend to be less consistent in cooperative strategies.

There is no effect of personality traits on the rate of cooperation after a previous defection (Table 2.5), though belief increases cooperation. Players tend to switch from defection to cooperation more often when they believed in the experimental set up, thinking they were playing against another fellow human being.

Furthermore, through the analysis of the dataset we observed the importance of selecting the model with the best fit to the data. The necessity of such a procedure is highlighted by the fact that results from the poorly fit binomial regression would have been very misleading for our dataset: it shows several predictors as being statistically significant and with greater significance levels than for the best fit models (see Appendix).

2.5 Discussion

Our results seem to partially contradict our initial hypothesis that cooperation might be dependent on the player's psychopathic traits. The only impact of psychopathic traits on player's behaviour was found with regard to the maintenance of cooperative behaviour, but not on the overall tendency of players to cooperate, which is inconsistent with previous findings using a similar setup [43, 44].

In our study, more disinhibited individuals engaged in a less continuously cooperative strategy, switching to defection more often than participants with lower disinhibition levels. As disinhibition is conceptualized as irresponsible, impatient and impulsive tendencies, related to antisocial behaviour, these results match previous findings that point to a relationship between rebellious nonconformity and defection [77]. Furthermore, a recent study found a positive association between disinhibition and risk-taking in a loss context [92]. Contrary to our expectations, meanness was not a significant predictor in our models, indicating a lower behavioral relevance of that aspect as previously found [93]. On the other hand, personality traits do not show any effect on the decision to switch to cooperation after a previous defection or on the overall cooperation.

A possible explanation for the lack of an effect of psychopathic traits on cooperation in our experiment is that the majority of the participants (165 out of 314) strongly believed they were playing against a computer (scoring 1 out of 5 for belief) and only 11 participants completely believed they were playing against a real person (scoring 5 out of 5 for belief). Personality traits may not play as much of a role when playing against a computer as they do when interacting with a person. This problem is due to the limitation of the study using an online data collection approach. Thus, design improvements will be necessary to create an environment in which participants can have a more realistic interaction with the opponent. This will make it possible for the participants to totally engage in the game and higher variations could be observed between high and low psychopathic subjects. Moreover, it would be useful to control for other personality dimensions in future works, such as the big five personality traits.

An interesting outcome of our experiment is the correlation between the willingness to maximise the outcome and the strategy adopted: participants defected more overall if they were trying to maximise their own payoff, compared to less profit-oriented players. However, as we measured the motivation to maximise profit only with one item in the questionnaire, this result needs further investigation with more detailed evaluation of the strategic goals of individuals in the game.

Furthermore, we want to emphasise the importance of an appropriate model selection technique. In the appendix we report a very interesting finding: fitting a binomial model would have suggested that several predictors were indeed statistically significant for overall cooperation and with greater significance levels than we observed with our best fit models. Since the binomial model was initially considered the most appropriate regression, but revealed through repeated k-fold cross-validation to be a poor fit to data, this highlights the importance of a rigorous model selection procedure to avoid overstating outcomes and provide a reliable interpretation of experimental results.

Our findings show not only the crucial impact of model selection on the analyses, but also the impact of general game behaviour and belief on the outcome in a game theory paradigm of cooperation. Therefore, future research should not only investigate specific game behaviour but also take into account participants' belief about the experiment [94]. Other confounding variables in such a task could be cognitive and motivational factors, which we were not able to control for. Future investigations should include pre- and post-measurement of such factors, e.g. related to state stress.

Our study adds to the discussion on the use of deception in economic game research [95] and highlights the relevance of further investigation of such effects.

Despite these limitations our study shows evidence for a relationship between psychopathic personality traits, specifically disinhibition, with a switch to defection instead of towards cooperation, but no overall relevance of psychopathic traits for cooperation behaviour in the game. Furthermore, the change of results based on statistical model selection show that findings from such experimental designs including dimensional scores of personality measures can be unstable and models should be carefully selected.

2.6 Appendix

2.6.1 Binomial Regression analysis

An important observation that arose from this analysis is how a model, which sometimes seems the perfect choice, can be in reality extremely far from a good representation of the dataset. A clear example for our dataset is the binomial regression. We expected this model to give the best interpretation of the dataset, as our dependent variable is a binary choice repeated over rounds, and so a binomial distribution might be expected to be the optimal choice to describe our dataset [96]. See supplementary material for more extensive discussion. Nevertheless, we proved that such a model was the worst performing one out of the four analysed. Additionally, it is worth reporting that if we had used the binomial regression model, several of the predictor variables would have appeared to have a statistically significant effect on the level of cooperation as shown in Table 2.6.

Looking at these results, it might have been tempting to select the binomial regression model as the preferred regression and not take into account the analysis implemented for model selection. However, our results highlight the importance of a correct model selection procedure for data analysis and show how easy it is to misinterpret the results of a regression.

Table 2.6: Binomial regression results for participants' cooperation as a function of their age, gender, level of belief and personality traits.

DV:	Overall Cooperation
intercept	0.82 ***
	(0.19)
age	-0.01 **
	(0.00)
gender	0.18 *
	(0.07)
believe	-0.09 ***
	(0.02)
maximise	-0.14 ***
	(0.03)
meanness	-0.04
	(0.04)
boldness	-0.01
	(0.03)
disinhibition	-0.18 ***
	(0.04)

Standard errors for coefficients shown in parenthesis;
Significance level: ‘***’ <0.001 ‘**’ <0.01 ‘*’ <0.05 ‘.’ <0.1;
BIN = binomial generalised linear model

2.7 Supplementary Material

2.7.1 Candidate models

Initially several candidate models were identified, and the best model was subsequently selected from among them. Four models were considered to describe and predict the dataset: Generalised Linear Model (GLM), Logistic Regression (LR), Binomial Generalised Linear Model (BIN) and Beta Regression (BR). The selection of these four specific models was based on the characteristics of the dataset, such as the distribution of the variables, the kind of relationship which was supposed to hold between dependent and predictor variables and the type of variables themselves (i.e. continuous, ordinal or dichotomous).

The GLM has become "psychology's data analytic workhorse" [97]. Used mostly for continuous variables, the GLM offers a flexible interpretation of a wide range of relationships between the independent variables and continuous or dichotomous outcome variables. It can be expressed as follows:

$$g(E[\mathbf{Y}]) = b_0 + b_1\boldsymbol{x}_1 + \ldots + b_k\boldsymbol{x}_k, \tag{2.1}$$

where $E[\mathbf{Y}]$ is the expected value of the dependent variable, in this case the frequency of cooperation for each participant; $g(\cdot)$ is a link function connecting the dependent variable and the predictors $\boldsymbol{x}_1, \ldots, \boldsymbol{x}_k$; while $b_1, \ldots, b_k$ are the estimated coefficients and b_0 is the intercept.

The LR is part of the GLM family and it differs from the previous regression because of the link function. In the LR, the logit function, rather than the identity function, links the mean of cooperation to the predictors. The model is defined as:

$$logit(E[\mathbf{Y}]) = \boldsymbol{\eta} = ln\left(\frac{\hat{\boldsymbol{\pi}}}{1-\hat{\boldsymbol{\pi}}}\right) = b_0 + b_1\boldsymbol{x}_1 + \ldots + b_k\boldsymbol{x}_k \tag{2.2}$$

where $\hat{\boldsymbol{\pi}}$ is the vector of probabilities of $\mathbf{Y}$ taking certain values.

Although the LR is commonly used with categorical dependent variables, it can also be used to estimate probabilities of frequencies. In this case, the logit regression provides an efficient method which tends to provide a useful probabilistic derivation and interpretation [98]. Hence, the overall level of cooperation is defined as the frequency of cooperation of the participants over the fifteen trials. CaC is defined as the percentage of times a player cooperated after a previous cooperation, and CaD as the percentage of times a player cooperated after a previous defection.

A different method to interpret the overall cooperation is by considering the exact number of cooperations and defections for each participant. In this way, the additional information of the number of trials played by each participant can be provided to the model. A straightforward choice is suggested by this description of the data: the binomial regression model. This model belongs to the GLM family and it is closely connected to the LR model. Indeed, it can be expressed as:

$$\eta_i = logit(p_i) = ln\left(\frac{p_i}{1-p_i}\right) = \beta_0 + \beta_1 x_{i1} + ... + \beta_q x_{iq}, \tag{2.3}$$

where p_i is the probability for participant i to cooperate and the response variable $\mathbf{Y} = (y_1, \ldots, y_n)$ is distributed as $y_i \sim B(n_i, p_i)$ where n_i is the number of trials for participant i. However, there are two key differences from the LR model. Firstly, the variable p_i (instead of $\hat{\pi}_i$) is now calculated over the exact number of trials, potentially providing a more accurate approximation of the level of cooperation for each participant. Secondly, while for the LR model the log-likelihood function could be expressed as

$$ln\mathcal{L}(\eta_i; y_i) = \sum_{i=1}^{n} y_i\eta_i - log(1 + e^{\eta_i}), \tag{2.4}$$

for the BIN model, the log-likelihood function includes the additional information of the number of trials:

$$ln\mathcal{L}(\eta_i; y_i) = \sum_{i=1}^{n} y_i\eta_i - n_i log\left(1 + e^{\eta_i} + log\binom{n_i}{y_i}\right) \tag{2.5}$$

Yet another different approach is provided by the beta regression (BR). This model has been proposed as an alternative to linear regression to model clustered binary data, such as in the case of the proportion of successes and failures over a finite number of trials (where success, in this experiment, is defined as cooperation and failure as defection) [96]. Although the model can be expressed as the GLM in Eq(2.1), the central assumption of the regression is that the dependent variable follows a beta distribution [99]. It is characterised by two parameters which allow for modelling a wide range of distribution shapes:

$$f(\mathbf{Y}|\alpha, \gamma) = \frac{\mathit{\Gamma}(\alpha + \gamma)}{\mathit{\Gamma}(\alpha)\mathit{\Gamma}(\gamma)}\mathbf{Y}^{\alpha-1}(1 - \mathbf{Y})^{\gamma-1} \tag{2.6}$$

where $0 \leq \mathbf{Y} \leq 1$, $\alpha, \gamma > 0$ and $\mathit{\Gamma}(\cdot)$ denotes the gamma function [100].

An additional reason to consider the BR regression model is its adaptability to model data concentrated towards the limits of a finite range, as is the case of our data when looking at people who always cooperated and always defected. Despite the good approximation that this distribution provides, the use of the beta regression in behavioural and psychology research has been for some time outside of most experimentalists' reach because of the lack of software implementation [96]. This problem has been solved by a package in R, developed specifically for beta regressions [101].

All the presented models were tested on one half of the data to check that a reasonable fit was possible.

2.7.2 Validation and Model Selection

The second phase of the analysis consisted of cross-validation of the models. Cross-validation has been used to select a model through fitting one half of the data and then predicting the remaining data. Two different techniques were initially considered in this study: holdout and repeated k-fold cross-validation [102]. The results of holdout validation can be highly dependent on the choice of the fitting and testing subsets, and so we implemented repeated k-fold cross-validation on the dataset.

The technique was implemented with the package "cvTools" in R. With this procedure, the complete dataset is first partitioned into k folds, usually of the same size. Subsequently, k iterations of fitting and validation are performed such that at each iteration, the k^{th} fold is held out from the fitting phase and is used for the validation phase instead. The selection of 10 folds is suggested by the literature in which k is usually equal to 5 or 10, according to the sample size. The model selection is automatically done by the function "cvSelect" which compares the prediction errors in each iteration and computes an overall error at the end of the iterations. This procedure is then repeated a certain number of time (5 in this experiment) in order to reduce the bias which could arise from the selection of the k folds. A negative aspect is that the training and testing sets are not independent but overlap and this could lead to an underestimation of the variance [102]. However, it is considered one of the best model selection methods, as it tends to provide a less biased estimate of the prediction accuracy [102]. Additionally, the repetition of the procedure makes the model selection more robust and reduces the possibility of underestimating the variance.

2.7.3 Model Fitting

In this last phase, the selected models were fitted on the complete dataset.

In order to make a comparison between the effects of the personality measure predictors, a normalisation of the variables is necessary. Since the range of the various variables is different, the estimated coefficients cannot be directly compared. Standardizing the predictors is useful not only for the interpretation of the main effects of the regression, but it also helps with the scaling problem [103]. In complicated regressions with many predictors, the most common technique to deal with this problem is to subtract the mean of the variable and divide by the standard deviation. In this way, the variables have roughly the same scale and it is possible to compare their effects on the dependent variable.

This procedure was implemented for the three variables describing the personality traits (meanness, boldness and disinhibition). The results were then analysed to make inferences about the initial hypothesis.

2.7.4 Repeated k-fold cross-validation and Model Selection Results

According to the repeated k-fold cross-validation procedure, GLM was found as the best performing model for CaC and CaD, although the predicted error between GLM and BR are very close. While GLM and BR provided very similar error terms for all three dependent variables, the LR and the BIN scored higher error measures, highlighting that these regression models are not adequate in the prediction of the dependent variable in this experiment (Table 2.7). Despite the initial assumption that the BIN should have performed better (as it includes more information than the other models), it can be seen that the error made in the prediction is instead the highest registered. On the other hand, the difference between GLM and BR performances is slight, but it confirmed the theory behind the regression models. According to the results of the validation procedure, for the overall cooperation, the beta regression model was implemented over the complete dataset. The GLM was implemented for the other two dependent variables.

Table 2.7: Estimated prediction errors for the repeated 10-fold cross validation procedure for all three dependent variables.

DV:	overall cooperation	CaC	CaD
GLM	0.28	0.26 *	0.23 *
BR	0.28 *	0.27	0.23
LR	0.77	0.75	0.63
BIN	1.18	-	-

* selected model;
GLM = generalised linear model,
BR = beta regression,
LR = logistic regression,
BIN = binomial generalised linear model

Chapter 3 The effect of psychopathy on cooperative strategies in an iterated Prisoner's Dilemma experiment with emotional feedback.

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Abstract

As decision-making research becomes more popular, the inclusion of personality traits has emerged as a focal point for an exhaustive analysis of human behaviour. In this study, we investigate the impact of psychopathic traits on cooperation in an iterated Prisoner's Dilemma game with emotional facial feedback. Firstly, we observed how receiving a facial feedback after each decision affected players with different psychopathic trait scores, and how being informed about the opponent's identity influenced cooperative behaviour. Secondly, we analysed the strategies adopted by each player, and how these choices were correlated with their psychopathic traits. Although our results showed no effect of different emotional content in the feedback on cooperation, we observed more cooperative behaviours in those players who were told their opponent was another fellow human, compared to those who were told it was a computer. Moreover, fearless dominance had a very small but consistent negative effect on overall cooperation and on the tendency to maintain cooperative behaviours. We also found that players' personality scores affected the strategies they chose to play throughout the game. Hence, our experiment adds complexity to the body of work investigating psychopathic traits and social interactions, considering not only the environment of facial feedback but also the role of deception in experimental games.

3.1 Introduction

Significant dysfunction in interpersonal relations is a hallmark of psychopathy. It includes traits of callousness, guiltlessness, dishonesty and egocentricity [104]. These self-focused characteristics lend themselves to the significant behavioural differences seen in those high in psychopathic traits, especially in social situations.

The Prisoner's Dilemma game (PD), and its variations, is a commonly used framework for researching personality traits within a social context. Several key studies have employed this game to investigate how psychopathic traits influence cooperation and defection. Interestingly, results have not all been consistent. One of the first studies to use the PD to investigate psychopathic traits surprisingly found that males high in primary and secondary psychopathic traits were not more likely to defect than those low in psychopathy [41]. A later study, however, found a significant negative correlation between psychopathic traits and cooperation, only in male participants [44]. Male prison samples showed a decreased cooperativeness among those high in psychopathy [105], and high levels of impulsivity were also found to be strongly predictive of defective behaviours in the general population [55]. Specifically, two characteristics of psychopathy correlated negatively with cooperation as determined by the Psychopathic Personality Inventory Revised (PPI-R) [106]: Impulsive Nonconformity and Machiavellian Egocentricity. High levels of impulsivity were predictive of repeated defection, while machiavellianism was linked to higher overall defection. At the same time, Narcissistic personality traits have been found to differentially impact on cooperative behaviour and overall outcome [107].

An important aspect to consider in social interactions is individuals' emotional response, especially in relation with personality traits. However, previous research on cooperation in the context of emotional feedback has not considered personality features. In psychopathy, emotional dysfunction has long been a defining characteristic [104], and while there is some debate as to whether there is any dysfunction of emotional recognition [108], the literature is fairly conclusive on a dysfunction in emotional reaction [109, 110]. What remains to be seen is whether this emotional dysfunction affects cooperation in social interaction. One key study attempted to investigate a possible interaction of affective feedback and psychopathic traits in an iterated PD [111]. Participants performed two versions of the game, one with and one without verbal affective feedback. Results showed that psychopathy was significantly associated with reduced cooperation in the affective feedback version of the game, and positively associated with "CD" outcomes in both games (CD = player cooperates while the opponent defects).

Our study aims to build on these findings by implementing an experimental design which includes two different facial feedbacks (smiling and frowning faces) in four separate combinations (see Table 3.1).

Table 3.1: Emotional facial feedback in the four between-subjects conditions.

Player's decision	Opponent's emotional facial feedback			
	Condition 1	Condition 2	Condition 3	Condition 4
Cooperation	neutral	neutral	happy	happy
Defection	neutral	sad	neutral	sad

Given the evidence of the use of facial expression in determining partners' trustworthiness [112], and the association of happy faces with cooperation and sad faces with defection [113], we hypothesise participants to be more likely to cooperate in the presence of happy facial feedback. As such, our first hypothesis is the following: highly psychopathic players will be less cooperative overall, especially in the presence of happy facial feedback, compared to low psychopathic participants.

In addition, we aim to investigate the effect of the opponent's identity on cooperative behaviours. We implemented two game versions, a deception and a non-deception one, to observe differences in participants' behaviour when the opponent is a fellow human or a computer. Playing versus a human opponent has been proven to elicit higher engagement and more positive emotional responses, when compared to computer opponents [94, 114]. Thus, our second hypothesis states that: deceived players will show more cooperative behaviour compared to non-deceived ones.

Lastly, we are interested in estimating the strategies played throughout the game. A pioneer of IPD strategy analysis is Axelrod (1981) [115]. His main interest was to discover "how to play the game (IPD) well". For this purpose, he invited professional game theorists from diverse disciplines to send him strategies that they considered successful. These strategies were then entered in a computer tournament in which each of them played against all the others for 200 rounds. As a result, he obtained a ranking of the most successful strategies devised up to that moment. Since then, strategies have been investigated in depth, however mainly to assess which was the most successful one. In our paper, on the other hand, we aim to identify which are the most used strategies, without focussing on how successful they are. Previous works focused on identifying players' strategies through different techniques. Wedekind and Milinski (1996) [116] were amongst the first to observed subjects' strategies in both a simultaneous and an alternating Prisoner's Dilemma game. Thereafter, various estimation techniques have been used to assess which strategy each subject was playing in different games, analysing players' decisions directly [117, 118, 119, 120]. In this experiment, we implemented the technique first presented by Dal Bó and Fréchette (2011) [117] and we employed the same set of strategies considered in Fundenberg, Rand and Dreber (2012) [121]. We examined players' strategies by comparing each player's decisions throughout the game with some of the best known strategies in game theory [115]. We then analysed whether psychopathy scores correlate with the strategies adopted by the players. Under the assumption that highly psychopathic individuals are less prone to cooperate compared to low psychopathic individuals, we suppose that as psychopathic measures increase, the percentage of participants using defective strategies will increase. Therefore, our third hypothesis claims that high psychopathic individuals will adopt less cooperative strategies, compared to low psychopathic players.

3.2 Methods

3.2.1 Personality measures

The PPI is a 154-item self-report questionnaire [106] on psychopathic traits with 8 sub-scales, and seven of the eight subscales can be grouped into two main factors: Fearless Dominance and Self-centred Impulsivity, while Coldheartedness is considered as an additional factor. In this study, we implemented a 40-item version of the PPI-R [122] (see Supplementary Material for sample questions). Additionally, a recently developed method, the IRS-10, allowed us to test the response reliability of participants in the PPI-R [123]. Participants with IRS-10 scores above the cut-off were deemed to have completed the PPI-R in an inconsistent and therefore unreliable manner and were eliminated from analysis, leading to the exclusion of 14 participants. The cut-off score was set at an IRS-10 at the 95th percentile or higher ($\geqslant 13$).

In addition to the PPI-R, participants also completed the Narcissistic Personality Inventory-16 (NPI-16) [124]. The NPI-16 is a 16-question short-form version of the original NPI-40 [36]. The NPI-16 has shown a high correlation with the original NPI-40 ($r = .90$, $p < 0.001$) and, in addition, it has been shown to possess sufficient internal, discriminant and predictive validity.

3.2.2 Data collection

A total of 233 participants were initially recruited via an online platform, Prolific Academic `https://www.prolific.ac`. Complete data were available for 206 participants; 14 participants were excluded due to inconsistencies in their responses [106]. The final sample was composed of 192 participants (112 female, age: *M=34.5, SD=11.6*). Participants received a small compensation of £2, independent of their achievement in the game.

3.2.3 Procedure

After an introduction page explaining the structure of the game, participants were introduced to a presumed opponent, showing a picture of one of the two individuals (from DISFA [81]). Participants were instructed to play so as to achieve the highest score possible. At the end of the 30 rounds, participants completed the PPI-R, and the NPI-16, followed by a feedback page which included yes/no questions such as "Did you believe you were playing against a real person?" and "Did you try to maximise your own profit?". Participants were then debriefed about the nature of the game and the computer based opponent.

3.3 Material

3.3.1 Experimental Design

Ethical approval was obtained from the Faculty of Medicine Ethics Committee and Research Governance Office at the University of Southampton, all experimental and survey procedures followed ethical guidelines from the declaration of Helsinki as well as guidelines of the institutional review board. All participants gave informed consent for participating in an online game. The experiment was constructed with four different conditions and two game versions. Firstly, we divided the complete sample equally into two groups: the Deceived and the Non-Deceived subgroups. Although in reality all participants played against a computer, deceived participants were told they were playing against a human opponent. Participants in the non-deception version were informed they were playing against a computer, however they were instructed to consider the stimuli they were going to see during the game (emotional feedback) as if they were received from real human opponents.

Secondly, we implemented four conditions symmetrically on the two subgroups divided according to the emotional content (happy, neutral and sad) of the facial feedback participants received after each round (Table 3.1). Videos for the facial feedbacks were taken from the Denver Intensity and Spontaneous Facial Action (DISFA) Database [81]. Two individuals were selected (one female, one male) and 10 different 300 ms snips were created for each of the female and the male actors and for each of the happy, neutral and sad expressions. Participants in each group, deceived and non-deceived, were randomly assigned to one of the four conditions. The game was programmed to give equal numbers of male and female opponents and equal numbers of participants in each of the four conditions.

Participants were instructed to imagine a scenario in which they were the owner of an electronics shop, competing against another electronics store. In each of the 30 rounds, they were asked to assign to individual products either standard price (cooperation) or sale price (defection), knowing that their opponent was asked the same question. According to the decisions made by the player and the computer, four outcomes were possible (Table 3.2).

Table 3.2: Payoff matrix showing the percentage profit earned according to both players' pricing decisions.

		Participant	
		Standard Price	Sale Price
Opponent	Standard Price	(30% , 30%)	(10% , 40%)
	Sale Price	(40% , 10%)	(20% , 20%)

The computer was programmed to play a tit-for-two-tats strategy, meaning that it cooperates until the opponent defects twice in a row, then it defects until the opponent cooperates again. In the last two rounds however, the computer was programmed to defect, as an attempt to simulate human behaviour. A page with the two decisions made and the consequent payoff was shown after each round. In addition to the payoff, participants were able to see a short video representing the presumed opponent's face.

3.4 Statistical Analysis

Three main questions were explored:

1. which factors affected the overall rate of cooperation during the game?
2. what persuaded players to continue cooperating?
3. can we approximate players' behaviour with well known strategies?

To investigate the first two points, analyses were implemented on two different dependent variables: the overall percentage of cooperation for each participant over the 30 trials, and the number of times a participant cooperated immediately following a previous cooperation ("cooperation after cooperation" - CaC). The number of cooperations immediately following a defection was also regressed without reporting any significant effect (marginal effect of fearless dominance at the .05 level of significance, see Supplementary Material). The same analyses were implemented on the two dependent variables in parallel. The two explained variables were regressed against a fixed set of explanatory variables (see descriptive statistics in Table 3.3) which included *gender* (1=female, 2=male), as it has been found to be correlated with psychopathic traits, the four personality factors (*fearless dominance, self-centred impulsivity, coldheartedness* as dimensional scores, and *narcissism*), and the *maximise* variable describing, on a scale from 1 to 5, how much the players tried to maximise their own profit. To account for the effect of the two game versions, we included as fixed effect the *game version* variable (1=deception, 2=non-deception) which controlled the effect of the deception/non-deception games participants played. For the four conditions implemented in the game, we modelled them as a 2x2 factorial design, as explained in Table 3.4. Descriptive statistics of the variables are presented in Table 3.3, and the correlation coefficients can be found in Table 3.5.

Table 3.3: Descriptive statistics for the participant sample.

Variables	Min	Mean	Standard Deviation	Max	Cronbach's α
gender	1	1.58	0.49	2	-
maximise	1	4.26	0.90	5	-
fearless dominance	17	34.67	7.51	56	0.83
self-centred impulsivity	16	30.91	5.89	49	0.73
coldheartedness	5	10.78	2.97	20	0.75
narcissism	0	0.08	0.09	0.33	0.54

Table 3.4: Two-by-two factorial analysis of the four conditions implemented.

positive feedback	negative feedback	
	absence of negative feedback (0)	presence of negative feedback (1)
absence of positive feedback (0)	condition 1	condition 2
presence of positive feedback (1)	condition 3	condition 4

The regression analysis consisted of two phases: model selection and model interpretation. Three models were considered, according to the structure of the dependent variables. Since both variables were produced from a series of zeros and ones, we considered a Generalised Linear Model (GLM), a Logistic (LM) and a Beta-Binomial (BBM) regression models as candidate and compared their fits to data. To select the best fitting model for our data, a repeated k-fold cross-validation was implemented. Finally, the best fitting model was implemented on the data and the results were interpreted.

A different approach was used for the analysis of the strategies adopted. In this case we followed the technique presented in Dal Bó and Fréchette (2011) [117]. Detail of the technique can be found in the Supplementary Material. In order to be able to infer the players' strategies, we focused our attention on a sub-set of the multitude of existing games strategies (see more details in the Supplementary Material). Amongst them, we then repeated the analysis for those strategies which were most chosen and had a stronger correlation with the participants' personality traits (Table 3.6).

Table 3.5: Bivariate correlation matrix among variables.

	cooper-ation	CaC	sum psychopathic traits	self-centred impulsivity	fearless dominance	coldhearted-ness	narcis-sism	max-imise
cooperation	1	-	-	-	-	-	-	-
CaC	0.90***	1	-	-	-	-	-	-
sum psychopathic traits	-0.15*	-0.12	1	-	-	-	-	-
self-centred impulsivity	-0.02	0.00	0.59***	1	-	-	-	-
fearless dominance	-0.17*	-0.18 *	0.71***	-0.07	1	-	-	-
coldheartedness	-0.14 .	-0.06	0.48***	0.28 ***	0.13 .	1	-	-
narcissism	-0.03	-0.04	0.47***	0.25 ***	0.40 ***	0.27 ***	1	-
maximise	-0.17*	-0.15 *	0.03	-0.01	0.01	0.18 *	-0.01	1

Significance level: ‘***’ <0.001 ‘**’ <0.01 ‘*’ <0.05 ‘.’ <0.1; *sum psychopathic traits* is an aggregate measure of the PPI-R questionnaire.

Table 3.6: Description of the main four strategies considered.

Strategy	Abbreviation	Description
Tit for three tat	TF3T	Cooperate until the opponent defects three times in a row, then defect till the opponent cooperates again
Two tit for two tat	2TF2T	Cooperate until the opponent defects twice in a row, then defect till the opponent cooperates twice in a row
Grim	Grim	Cooperate until the opponent defects, then defect forever
Always defect	ALLD	Defect at each round

Interestingly, these strategies capture the most important aspects of IPD strategies [115]: punishment (Grim, TF3T), forgiveness and niceness (TF3T, 2TF2T). At the same time, ALLD represents a purely defective strategy, which is known to be the optimal strategy in an IPD and one of the most used one. The complete results for this pre-analysis can be found in the Supplementary Material. All data and code can be found on the osf platform.

3.5 Results

3.5.1 Cooperation analysis

The GLM was selected as the best model for both dependent variables using 5-fold cross-validation (see Supplementary Material).

To address the partialling issue [125], we first regressed the dependent variables over the four personality trait variables (Table 3.7). The findings from this initial basic analysis were corroborated by the complete regressions subsequently conducted. Fearless dominance emerged as the only consistently statistically significant predictor: the lower people's score in this factor of psychopathy, the more they cooperated over the 30 rounds and the more they persisted in cooperative strategies. As we hypothesised at the beginning, players who scored high in this psychopathy measure tended to cooperate less than low-psychopathic individuals. However, the analysis also shows that the different feedback conditions did not affect the rate of cooperation: receiving different types of emotional feedback did not affect individuals' strategy, neither for the overall cooperation nor for CaC.

To investigate whether participants showing different levels of psychopathy were differentially influenced by the facial feedbacks, we included the interaction terms between the cumulative score of psychopathy and the four conditions (Table 3.8). Results show a very small and marginally significant effect of two interaction terms (positive * negative * psychopathy and positive * psychopathy). Due to the small effect size and the marginal level of statistical significance (< 0.1), the terms do not add any crucial contribution to the results previously found in Table 3.7. Hence, although we found that psychopathic traits do affect cooperation, we did not find any correlation with the facial feedback they were receiving during the game.

At the same time, playing the deception/non-deception version had a slight effect on the overall cooperation, but it had a strong and statistically significant effect on CaC: participants playing the deception version of the game were more inclined to maintain cooperative behaviour compared to participants who were informed about the real identity of their opponent. However, there are no differences between low and high psychopathic players when looking at the game version (Table 3.8). In this sense, these results confirm our second hypotheses, proving that the opponent's identity affects individual's decisions.

Table 3.7: GLM coefficients for participants' overall cooperation and cooperation after cooperation.

DV:	overall cooperation	CaC	overall cooperation	CaC
intercept	0.42 ***	0.412***	0.66 ***	0.71 ***
	(0.02)	(0.02)	(0.12)	(0.13)
gender			-0.08 .	-0.12 *
			(0.04)	(0.05)
maximise			-0.05 .	-0.05 .
			(0.02)	(0.03)
fearless dominance	-0.01 *	-0.01 *	-0.01 **	-0.01 **
	(-003)	(0.00)	(0.00)	(0.00)
self-centred impulsivity	-0.00	-0.00	-0.00	-0.00
	(0.00)	(0.00)	(0.00)	(0.00)
coldheartedness	-0.01 .	-0.01	-0.01	-0.00
	(0.01)	(0.01)	(0.01)	(0.01)
narcissism	0.28	0.23	0.21	0.16
	(0.28)	(0.33)	(0.27)	(0.32)
positive feedback			0.05	0.07
			(0.06)	(0.07)
negative feedback			0.04	0.09
			(0.07)	(0.07)
positive*negative feedback			-0.03	-0.10
			(0.09)	(0.10)
game version			-0.07 .	-0.14**
			(0.04)	(0.05)

Standard errors for coefficients shown in parenthesis.
Significance level: ‘***’ <0.001 ‘**’ <0.01 ‘*’ <0.05 ‘.’ <0.1

Table 3.8: Interaction terms in GLM models for participants' overall cooperation and cooperation after cooperation, considering participants' cumulative measure of psychopathy.

DV :	overall cooperation	cooperation after cooperation (CaC)
game version*sum psychopathic measures	0.00	0.00
	(0.00)	(0.00)
positive*negative feedback*sum psychopathic measures	0.01 .	0.01
	(0.00)	(0.01)
positive feedback*sum psychopathic measures	-0.01 .	-0.01
	(0.00)	(0.01)
negative feedback*sum psychopathic measures	-0.01	-0.00
	(0.13)	(0.01)

The interaction terms are regressed separately, controlling for gender, game version, maximise, narcissism and conditions.

Standard errors for coefficients shown in parenthesis. Significance level: ‘***’ <0.001 ‘**’ <0.01 ‘*’ <0.05 ‘.’ <0.1

Two other factors appeared to influence players' cooperative behaviours: *gender* and *maximise*. As reported in the literature [126], females show more cooperative behaviour than males, and this situation was confirmed by our experiment; in addition the effect was stronger when looking at the inclination of participants to maintain cooperative behaviour.

The maximise variable expressed the participants' willingness to maximise their own profit during the game. As shown in the correlation matrix (Table 3.5), maximise is positively correlated with coldheartedness, a factor of psychopathy: the more players were goal oriented (goal=maximise their own profit), the higher their score in the subscale of psychopathy. Furthermore, though the impact was very small, we found that the more the participants aimed to achieve a high score, the less they cooperated with their partners.

Overall, our results record a main effect of fearless dominance on both overall cooperation and CaC and a main effect of the game version in the maintenance of cooperative strategies. In addition, we observed two other main effects: gender and maximise both had a negative effect on cooperation and cooperation over time.

3.5.2 Strategies

The second main objective of this study was to identify players' strategies. Here we report only the four most significant strategies (Table 3.9), while the complete results can be found in the Supplementary Material. The four strategies were selected to represent the main categories of strategies, given the results reported in the Supplementary Material. 2TF2T was the most frequently chosen strategy amongst the forgiving strategies, TF3T amongst the cooperative ones, and Grim amongst the unforgiving ones, while ALLD is the representative for defective strategies.

Table 3.9: Percentages of individuals adopting each one of the four strategies. Statistical significance describes how significantly different from zero are the percentages estimated through MLE. We also show the correlation matrix between the strategies adopted by each participant and their psychopathic traits.

Percentage of participants adopting the selected strategies.

Gamma	TF3T	2TF2T	Grim	ALLD
0.88**	0.15	0.22	0.07	0.55**
(0.13)	(0.10)	(0.11)	(0.05)	(0.08)

Bootstrapped standard errors (shown in parentheses) used to calculate p-values.

Correlation matrix between strategies adopted and psychopathic traits.

	TF3T	2TF2T	Grim	ALLD
Fearless Dominance	-0.03	0.01	-0.01	0.01
Self-centred impulsivity	0.14*	-0.08	0.07	-0.06
Coldheartedness	0.20**	-0.19**	0.05	0.12.

Significance level: '***' <0.001 '**' <0.01 '*' <0.05 '.' <0.1

Table 3.9 reports the percentages of players adopting such strategies, where the statistical significance depends on how different those percentages are from zero. The estimates are obtained via maximum likelihood estimation for each subject separately, and the results reported are the average over the 192 participants of the experiment. In other words, we calculated the probability of each participant to adopt each one of the selected strategies, maximising the estimations in such a way to minimise the error individually for each subject. Gamma represents the averaged error in the estimation of such probabilities, with $\gamma < 1$ representing a good approximation.

More than half of the participants adopted a strategy that was approximated as the purely defective ALLD. This is in line with the high level of defection recorded during the experiment. The rest of the players divided between unforgiving strategies such as Grim (7%) and forgiving strategies such as TF3T and 2TF2T (37%).

Coldheartedness strongly influenced the use of both TF3T and 2TF2T, and self-centred impulsivity had also an impact on the adoption of TF3T. It is interesting to notice the contradictory correlations of coldheartedness: while higher levels of this sub-scale are positively correlated with TF3T, it is negatively correlated with 2TF2T. Both strategies are considered forgiving and nice, nevertheless, they have opposite correlations with this sub-scale of psychopathy. Furthermore, both self-centred impulsivity and coldheartedness are positively correlated with TF3T, suggesting that the higher participants were in two of the three sub-scales of psychopathy, the more they adopted such a strategy. It is interesting the absence of effect of fearless dominance on strategy selection despite its effect on overall cooperation and cooperation after cooperation. Considering such contradictory results, it would be interesting to observe a longer game, to study the effect on psychopathic traits of strategy selection in greater depth, untangling these correlations.

3.6 Discussion

This study focuses on the interaction between personality traits and cooperation in the framework of an iterated Prisoner's Dilemma in the presence of emotional facial feedback. Our finding of a significant negative correlation between the fearless dominance score and cooperation is surprising. Previous studies typically found significant relationships between self-centred impulsivity [105] and cooperation, with a particular correlation between Impulsive Nonconformity and Machiavellian Egocentricity, two sub-scales that partially contribute to the self-centred impulsivity scale. Based on our findings, we suggest that the fearlessness and stress immunity sub-scales buffered the threat of retaliatory defection, urging participants to risk continued defection in pursuit of higher gains. This is supported by assumptions suggesting that high fearless dominance traits may provide an adaptive advantage to the individual [106]. An increase in boldness and a decrease in fear would allow the individual to take calculated risks to obtain greater rewards [92, 127].

Although a marginal interaction effect between the treatments and psychopathic traits was recorded, the absence of significance of the facial feedback conditions on the player's cooperation is puzzling. A possible interpretation is that the participants may have interpreted seeing the emotional reactions of their opponent as an attempt at manipulation towards a cooperative goal, resulting in a retaliatory defection. Moreover, they could have interpreted the computer feedback as unrealistic, thus, they might not have taken that factor into consideration in the decision-making process. This is a limitation of our study and the only real solution would be to remove the computer component of the game and use a real-life opponent. Another explanation, and potential confounder, were the experiment instructions. They emphasised the game-like nature of the PD, specifically encouraging participants to earn the most points. These directions may have created an atmosphere of competition, where it is socially acceptable to maximise your own benefits, even at a cost to your opponent, instead of a social exchange scenario. This would explain why defection levels were so high and also why negative emotional feedback was not effective in deterring defection.

Our study also adds interesting findings to the literature investigating the relationship between the opponent's identity and participants' performance. Comparing the strategies of players in the deception version with those who were aware they were playing against a computer, we can see that dealing with a human opponent drives participants towards a more consistent cooperative behaviour.

Moreover, this study adopted an important line of inquiry which looked directly at participants' sequence of decisions throughout the entire game, estimating which strategies were more likely to be adopted. Although the estimated coefficients describing the percentages of players adopting each specific strategy are not significantly different from zero (apart from the completely defective strategy ALLD), it is interesting to observe some significant correlations between the probability of adopting a particular strategy and the participants' psychopathic traits. It would be interesting to investigate this point further, allowing for a longer game, as having a longer pattern of decisions will allow for a better estimation of the strategies used.

Despite the limitations encountered, our work adds complexity and insight to the body of work investigating psychopathic traits and social interactions within an affective feedback environment. Future research should take into consideration the potential of face-to-face interactions to investigate psychopathy effects on decision-making in a more realistic scenario, and a more thorough analysis of player's strategies to identify patterns typical for specific personality traits.

3.7 Supplementary Material

3.7.1 Regression analysis

K-fold cross-validation procedure

To select the best fitting model for our dataset, a 5-fold cross-validation procedure was implemented. As stated in the main body, three regression models were considered for all three dependent variables, namely the Generalised Linear Model (GLM), the Beta-Binomial Model (BBM) and the Logistic Model (LM). The technique was implemented with the package "cvTools" in R.

GLM and BBM's performances were remarkably close for all three dependent variables, while LM showed a bad fit in all three cases, see Table 3.10.

More information about the procedure adopted can be found in Sections 2.7.1, 2.7.2.

Table 3.10: Repeated 5-fold cross-validation results: estimated prediction errors.

DV:	overall cooperation	cooperation after cooperation	cooperation after defection
GLM	0.196 *	0.257 *	0.234 *
BBM	0.199	0.257	0.239
LM	0.646	0.734	0.777

* selected model

Additional results

For completeness, we report the results for the variable CaD: cooperation after a previous defection. As for CaC, this is calculated as the number of times a participant cooperated immediately following a previous defection. The same analyses reported in the main manuscript were implemented on CaD. Table 3.11 reports the results of the regression analysis, while Table 3.12 reports the interaction terms. None of the variables under observation had a significant impact on the participants' tendency to move towards a more cooperative strategy after a previous defection. Similarly, the interaction terms between the conditions implemented in the experiment and the psychopathic traits had no effect on the individuals' tendency to move towards cooperative behaviours.

Table 3.11: GLM results for participants' cooperation after a previous defection CaD Basic regressions without covariates and complete regressions with covariates for all three dependent variables.

DV	CaD	CaD
intercept	0.40 ***	0.49 ***
	(0.02)	(0.13)
gender		-0.03
		(0.05)
maximise		-0.01
		(0.02)
fearless dominance	-0.01	-0.01 .
	(0.00)	(0.001)
self-centred impulsivity	0.00	0.00
	(0.00)	(0.00)
coldheartedness	-0.01	-0.01
	(0.01)	(0.01)
narcissism	0.29	0.26
	(0.28)	(0.29)
positive feedback		-0.10
		(0.07)
negative feedback		-0.04
		(0.07)
positive *negative feedback		0.02
		(0.09)
game version		-0.01
		(0.05)

Standard errors for coefficients shown in parenthesis. Significance level: '***' <0.001 '**' <0.01 '*' <0.05 '.' <0.1

Table 3.12: Interaction terms in GLM models for participants' cooperation after defection, considering participants' cumulative measure of psychopathy.

DV :	cooperation after defection (CaD)
game version*sum psychopathic measures	0.01
	(0.00)
positive*negative feedback*sum psychopathic measures	0.01
	(0.00)
positive feedback*sum psychopathic measures	-0.01
	(0.00)
negative feedback*sum psychopathic measures	-0.01
	(0.01)

The interaction terms are regressed separately, controlling for gender, game version, maximise, narcissism and conditions.

Standard errors for coefficients shown in parenthesis. Significance level: '***' <0.001 '**' <0.01 '*' <0.05 '.' <0.1

3.7.2 Strategy analysis

Strategies selection

In an infinite Iterated Prisoner's Dilemma there are an infinite number of strategies to choose from. For this reason, when trying to identify which strategy a participant is playing, it is important to restrict the infinite set to a finite, but still representative, sub-set of strategies.

In this analysis, we adopted the strategies selected by Fundenberg, Rand and Dreber (2012) [121]. Starting from the most known strategies analysed in the literature (Always cooperative/defective, Tit for Tat, Win-Stay, Lose-Shift), they included several variations (see Table 3.13). These strategies capture the principal features considered in strategies: niceness, fairness, punishment, forgiveness, leniency and exploitation [115, 121]. Strategies considered nice are for example ALLC, TFT, where the latter has been highly discussed to be one of the most successful strategy for the IPD. TFT and its variations are also considered to be fair strategies, giving the benefit of the doubt to the opponent before punishing him for his defective behaviour. On this point, forgiveness is another aspect often discussed when looking at strategies. T2 (formulated by Bó and Fréchette (2011) [117]) is an example of a forgiving strategy, as well as TFT and its modifications (2TFT, 2TF2T) . In contrast, Grim is considered an unforgiving strategy, as well as its lenient variations (Grim2, Grim3). Lastly, they considered those strategies which tried to exploit the opponent, by defecting most of the time (ALLD), although sometimes showing a cooperative behaviour at the beginning (CALLD). For a more detailed explanation of the strategies please see Fundenberg, Rand and Dreber (2012) online Appendix.

Furthermore, it is important to consider that completely random strategies cannot be approximated. In this sense, they included the alternating strategy, which can be seen as a random strategy, as it is not based on the opponent's decisions, but only on the individual's previous choice.

Table 3.13: Description of the twenty strategies initially considered.

Strategy	Abbreviation	Description
Always cooperate	ALLC	Cooperate in each round.
Tit for tat	TFT	Cooperate until the opponent defects, then defect till the opponent cooperates again.
Tit for two tat	TF2T	Cooperate until the opponent defects twice in a row, then defect till the opponent cooperates again.
Tit for three tat	TF3T	Cooperate until the opponent defects three times in a row, then defect till the opponent cooperates again.
Two tit for tat	2TFT	Cooperate until the opponent defects, then defect till the opponent cooperates twice in a row.
Two tit for two tat	2TF2T	Cooperate until the opponent defects twice in a row, then defect till the opponent cooperates twice in a row.
T2	T2	Cooperate until the opponent defects, then defects twice and return to cooperate (regardless the opponent's decisions).
Grim	Grim	Cooperate until the opponent defects, then defect till the end of the game.
Lenient Grim 2	Grim2	Cooperate until the opponent defects twice in a row, then defect till the end of the game.
Lenient Grim 3	Grim3	Cooperate until the opponent defect three times in a row, then defect till the end of the game.
Win-Stay, Lose-Shift	WNLS	Cooperate if in the previous round both players made the same decision, defect otherwise.
Win-Stay, Lose-Shift with 2 rounds of punishment	2PTFT	Cooperate if both players made the same decisions in the previous two rounds. Defect otherwise.
Always defect	ALLD	Defect in each round.
False cooperator	C-ALLD	Cooperate in the first round then defect till the end of the game.
Exploitative Tit for tat	DTFT	Defect in the first round, then play TFT.
Exploitative Tit for two tat	DTF2T	Defect in the first round, then play TF2T.
Exploitative Tit for three tat	DTF3T	Defect in the first round, then play TF3T.
Exploitative Grim2	DGrim2	Defect in the first round, then play Grim2.
Exploitative Grim3	DGrim3	Defect in the first round, then play Grim3.
Alternator	DC-Alt	Defect in the first round, then alternate cooperation and defection.

Maximum Likelihood Estimation for participants' strategies

As stated in the main manuscript, the procedure follows the one presented in Bó and Fréchette (2011) [117]. Supposing that each participant starts with a fixed strategy, this technique allows for errors in the pattern of decisions over the rounds. The likelihood of adopting a specific strategy s^k is calculated by allowing a deviation between the decision expected by s^k and the actual decision taken by the player at each round. Knowing the history of each participant, it is possible to deduce the next move for each of the selected strategies and calculate the difference between that decision and the one made by the participant. In a more formal way, this is translated with a function:

$$1\{s_{ir}(s^k) + \gamma\epsilon_{ir} \geq 0\} = \begin{cases} 1 \text{ (cooperate)} & \text{if } s_{ir}(s^k) + \gamma\epsilon_{ir} \geq 0 \\ 0 \text{ (defect)} & \text{if } s_{ir}(s^k) + \gamma\epsilon_{ir} < 0 \end{cases} \tag{3.1}$$

where $1\{\cdot\}$ is an indicator function (meaning it can only take 0 and 1 as values), ir stands for subject i and round r; s^k is a specific strategy k, $s_{ir}(s^k)$ is the action implied by the strategy s^k given the history recorded (1=cooperation, -1=defection)[1], ϵ is the error term and γ is the variance of the error. The error term is independent across subjects, rounds, interactions and histories, and γ can be interpreted as the probability of making a mistake, supposing the strategy decision is the correct one. Moreover, the density of the error is assumed to be such that the likelihood that, over all rounds, subject i uses strategy s^k is:

$$p_i(s^k) = \prod_{R\in\mathbb{R}} \left(\frac{1}{1+exp(-s_{ir}(s^k)/\gamma)}\right)^{y_{ir}} \left(\frac{1}{1+exp(s_{ir}(s^k)/\gamma)}\right)^{1-y_{ir}}, \tag{3.2}$$

where y_{ir} is player's i decision at round r.
Hence, the probability of an error in the implementation of a strategy is equal to $\frac{1}{1+exp(\frac{1}{\gamma})}$. Thus, for example, if player i cooperates in round r and the expected decision, according to s^k, is to defect (-1), the internal term of Equation (3.2) would be equal to $\frac{1}{1+exp(\frac{1}{\gamma})}$ which tends to 0 as $\gamma \to 0$. On the contrary, if the expected decision for the strategy is cooperation, the internal term of Equation (3.2) would be equal to $\frac{1}{1+exp(\frac{-1}{\gamma})}$ which tends to 1 as $\gamma \to 0$.

Considering now the set of strategies $K = \{s^1, \ldots, s^k\}$ under analysis, and the complete dataset collected, the log-likelihood function for the entire sample is:

$$\mathcal{L} = \sum_I ln\left(\sum_K p(s^k)p_i(s^k)\right). \tag{3.3}$$

Here, $p(s^k)$ represents the proportion of data which is attributed to strategy s^k. More properly, p stands for the distribution of the strategies over the dataset. If we had an infinite population, p would express the exact fraction of individuals playing s^k. As in our experiment we have a finite number of subjects, we would have a certain variance, different from zero, in

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[1] The different codification for cooperation and defection is based on equation (3.2), as one of the two members has to be equal to 1 at each round. Any codification that satisfies that condition could be used.

the population shares.

The next step is to implement Maximum Likelihood Estimation (MLE) to estimate the γ parameter and the fractions $\{p(s^1), \ldots, p(s^k)\}$ of individuals adopting the strategies we hypothesised. The MLE process is implemented in MATLAB using the *fmincon* function which is a non-linear programming solver. The function calculates the values of γ and $p(s^i)$, where $i \in \{1, \ldots, k\}$, and maximises the log likelihood function, under the constraint that they belong to $[0, 1]$.

The final step is to generate the standard errors for the estimated frequencies by constructing 100 bootstrap samples for the complete dataset, and then performing the MLE for γ and $p(s^i)$ on the bootstrapped samples. The standard errors are calculated by taking the standard deviation of the estimates calculated, and the t-test p-values are generated using the *normcdf* function.

Complete results

Table 3.14 reports the complete results for the 20 strategies considered. The results include both the estimation of the strategies across the population and the correlation between the strategies and the personality traits of the participants. The results reported for the percentages of participants adopting each one of the selected strategies are calculated as the mean over each participant. We run the estimation for each player individually and we then reported the average percentages for each of the strategies. In the same way, the error Gamma is the average of the errors calculated for each player.

Table 3.14: Percentages of individuals adopting each one of the twenty strategies. Statistical significance describes how significantly different from zero are the percentages estimated through MLE. We also show the correlation matrix between the strategies adopted by each participant and their psychopathic traits.

Percentage of participants adopting the selected strategies.										
ALLC	TFT	TF2T	TF3T	2TFT	2TF2T	Grim	Grim2	Grim3	T2	
0.009 (0.016)	0.010 (0.027)	0.002 (0.045)	0.099 (0.054)	0.032 (0.054)	0.111 (0.084)	0.037 (0.028)	0.027 (0.030)	0.002 (0.019)	0.038 (0.027)	
WSLS	2PTFT	ALLD	CALLD	DTFT	DTF2T	DTF3T	DGrim2	DGrim3	DC-alt	Gamma
0.006 (0.007)	0.000 (0.005)	0.471** (0.074)	0.025 (0.026)	0.076 (0.036)	0.042 (0.052)	0.000 (0.020)	0.000 (0.004)	0.001 (0.015)	0.012 (0.018)	0.823 *** (0.100)

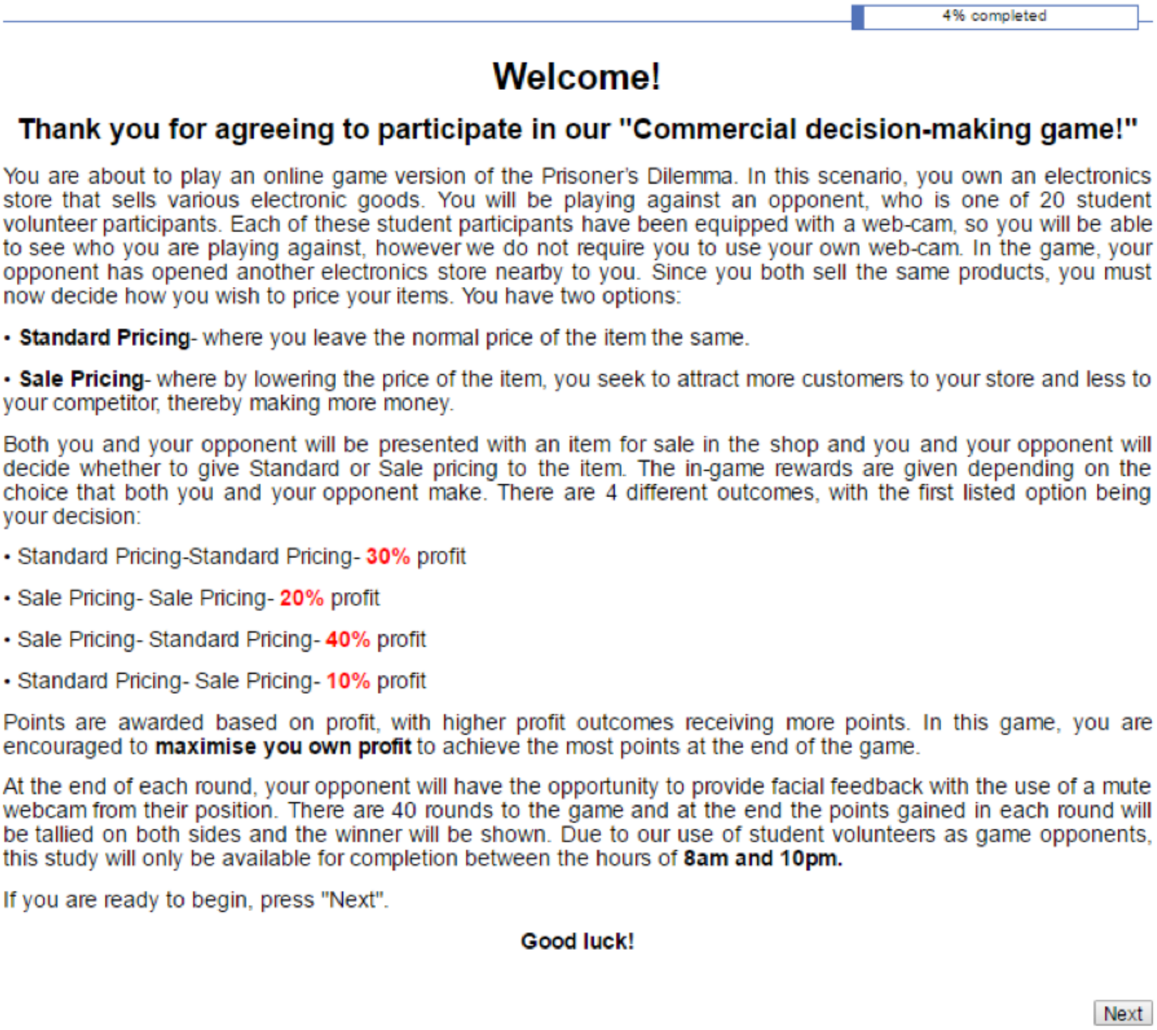
Correlation matrix between strategies adopted and psychopathic traits.										
	ALLC	TFT	TF2T	TF3T	2TFT	2TF2T	Grim	Grim2	Grim3	T2
Fearless Dominance	0.028	0.019	-0.055	-0.040	0.017	0.037	0.002	0.028	- 0.041	-0.075
Self-centred implusivity	0.054	-0.092	0.085	0.174*	0.121.	-0.116	0.148*	-0.160*	0.031	-0.041
Coldhearted-ness	0.052	-0.120.	-0.033	0.174*	-0.031	-0.137 .	0.074	0.080	-0.006	0.049
	WSLS	2PTFT	ALLD	CALLD	DTFT	DTF2T	DTF3T	DGrim2	DGrim3	DC-alt
Fearless Dominance	0.057	-0.008	0.020	-0.023	-0.018	-0.034	-0.056	-0.013	0.020	-0.013
Self-centred implusivity	0.002	-0.023	-0.044	-0.011	0.054	-0.015	0.099	-0.023	0.039	-0.132.
Coldhearted-ness	-0.008	0.042	0.105	-0.031	0.055	-0.128.	-0.035	0.032	0.0126	-0.134.

Bootstrapped standard errors (shown in parentheses) used to calculate p-values.

*** Significant at the 1 percent level. ** Significant at the 5 percent level. * Significant at the 10 percent level.

3.7.3 Instructions and screenshots

Instructions



Welcome!

Thank you for agreeing to participate in our "Commercial decision-making game!"

You are about to play an online game version of the Prisoner's Dilemma. In this scenario, you own an electronics store that sells various electronic goods. You will be playing against an opponent, who is one of 20 student volunteer participants. Each of these student participants have been equipped with a web-cam, so you will be able to see who you are playing against, however we do not require you to use your own web-cam. In the game, your opponent has opened another electronics store nearby to you. Since you both sell the same products, you must now decide how you wish to price your items. You have two options:

- **Standard Pricing**- where you leave the normal price of the item the same.

- **Sale Pricing**- where by lowering the price of the item, you seek to attract more customers to your store and less to your competitor, thereby making more money.

Both you and your opponent will be presented with an item for sale in the shop and you and your opponent will decide whether to give Standard or Sale pricing to the item. The in-game rewards are given depending on the choice that both you and your opponent make. There are 4 different outcomes, with the first listed option being your decision:

- Standard Pricing-Standard Pricing- **30%** profit

- Sale Pricing- Sale Pricing- **20%** profit

- Sale Pricing- Standard Pricing- **40%** profit

- Standard Pricing- Sale Pricing- **10%** profit

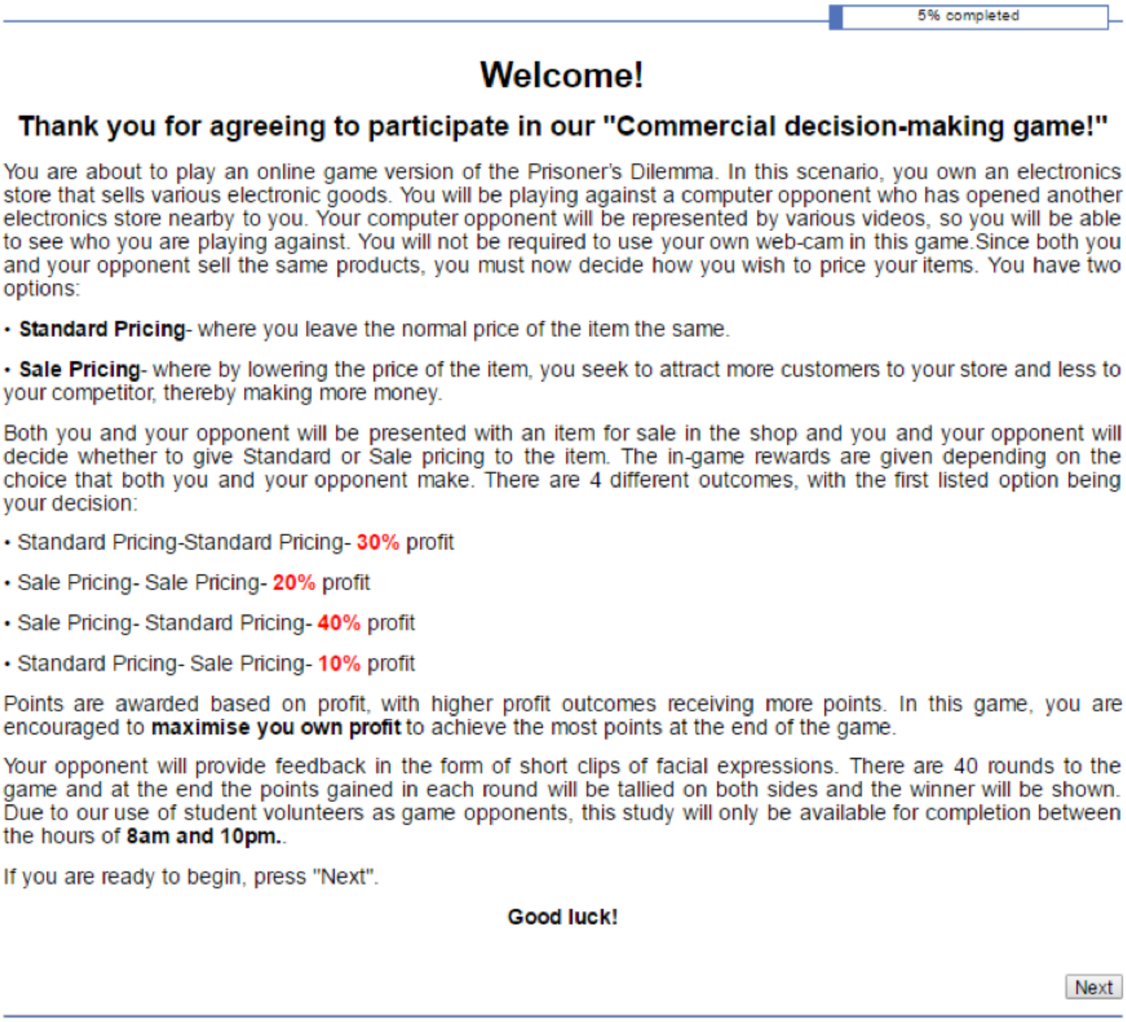
Points are awarded based on profit, with higher profit outcomes receiving more points. In this game, you are encouraged to **maximise you own profit** to achieve the most points at the end of the game.

At the end of each round, your opponent will have the opportunity to provide facial feedback with the use of a mute webcam from their position. There are 40 rounds to the game and at the end the points gained in each round will be tallied on both sides and the winner will be shown. Due to our use of student volunteers as game opponents, this study will only be available for completion between the hours of **8am and 10pm.**

If you are ready to begin, press "Next".

Good luck!

Figure 3.1: Deception version



Welcome!

Thank you for agreeing to participate in our "Commercial decision-making game!"

You are about to play an online game version of the Prisoner's Dilemma. In this scenario, you own an electronics store that sells various electronic goods. You will be playing against a computer opponent who has opened another electronics store nearby to you. Your computer opponent will be represented by various videos, so you will be able to see who you are playing against. You will not be required to use your own web-cam in this game.Since both you and your opponent sell the same products, you must now decide how you wish to price your items. You have two options:

- **Standard Pricing**- where you leave the normal price of the item the same.
- **Sale Pricing**- where by lowering the price of the item, you seek to attract more customers to your store and less to your competitor, thereby making more money.

Both you and your opponent will be presented with an item for sale in the shop and you and your opponent will decide whether to give Standard or Sale pricing to the item. The in-game rewards are given depending on the choice that both you and your opponent make. There are 4 different outcomes, with the first listed option being your decision:

- Standard Pricing-Standard Pricing- **30%** profit
- Sale Pricing- Sale Pricing- **20%** profit
- Sale Pricing- Standard Pricing- **40%** profit
- Standard Pricing- Sale Pricing- **10%** profit

Points are awarded based on profit, with higher profit outcomes receiving more points. In this game, you are encouraged to **maximise you own profit** to achieve the most points at the end of the game.

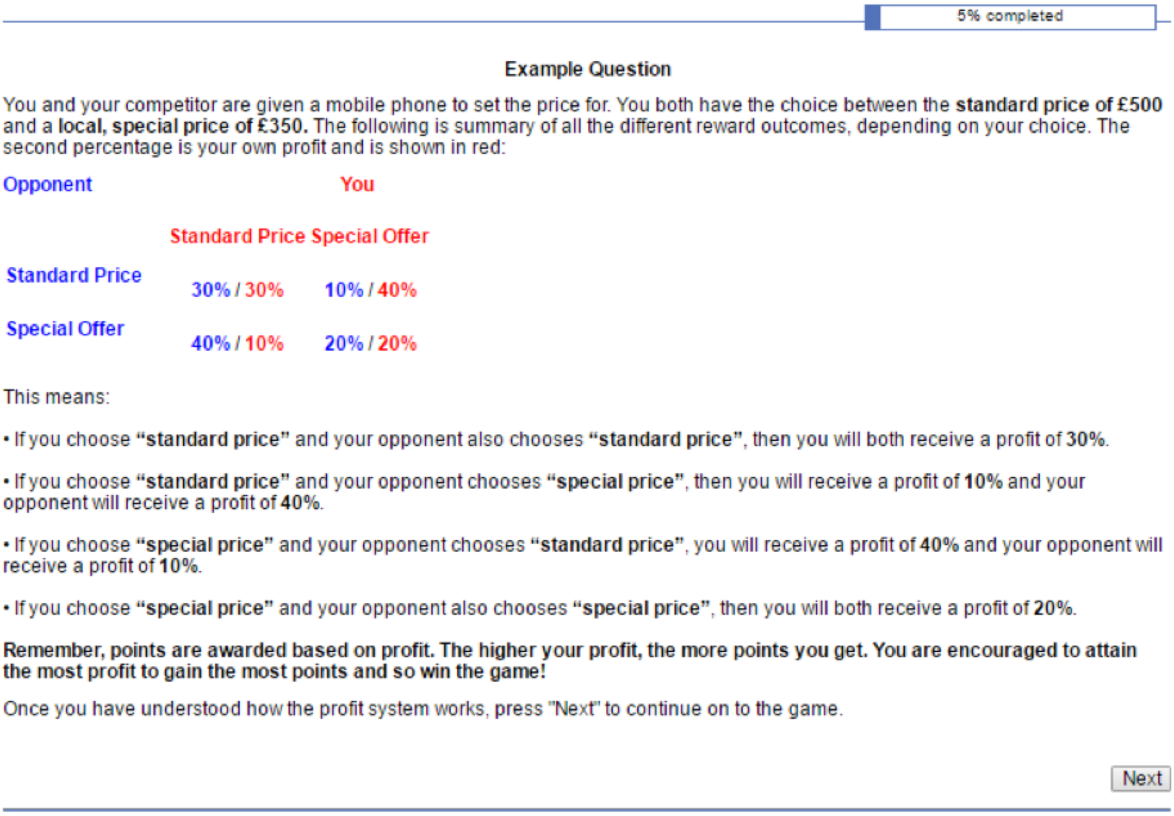
Your opponent will provide feedback in the form of short clips of facial expressions. There are 40 rounds to the game and at the end the points gained in each round will be tallied on both sides and the winner will be shown. Due to our use of student volunteers as game opponents, this study will only be available for completion between the hours of **8am and 10pm.**.

If you are ready to begin, press "Next".

Good luck!

Figure 3.2: Non-deception version

Experiment scenario and decision page



Example Question

You and your competitor are given a mobile phone to set the price for. You both have the choice between the **standard price of £500** and a **local, special price of £350.** The following is summary of all the different reward outcomes, depending on your choice. The second percentage is your own profit and is shown in red:

Opponent

You

	Standard Price	Special Offer
Standard Price	30% / 30%	10% / 40%
Special Offer	40% / 10%	20% / 20%

This means:

- If you choose **"standard price"** and your opponent also chooses **"standard price"**, then you will both receive a profit of **30%**.
- If you choose **"standard price"** and your opponent chooses **"special price"**, then you will receive a profit of **10%** and your opponent will receive a profit of **40%**.
- If you choose **"special price"** and your opponent chooses **"standard price"**, you will receive a profit of **40%** and your opponent will receive a profit of **10%**.
- If you choose **"special price"** and your opponent also chooses **"special price"**, then you will both receive a profit of **20%**.

Remember, points are awarded based on profit. The higher your profit, the more points you get. You are encouraged to attain the most profit to gain the most points and so win the game!

Once you have understood how the profit system works, press "Next" to continue on to the game.

Figure 3.3: Experiment scenario

You and your competitor are given the coffee machine to set the price for. You both have the choice between the **standard price of £1200** and a local **special price of £1000**.

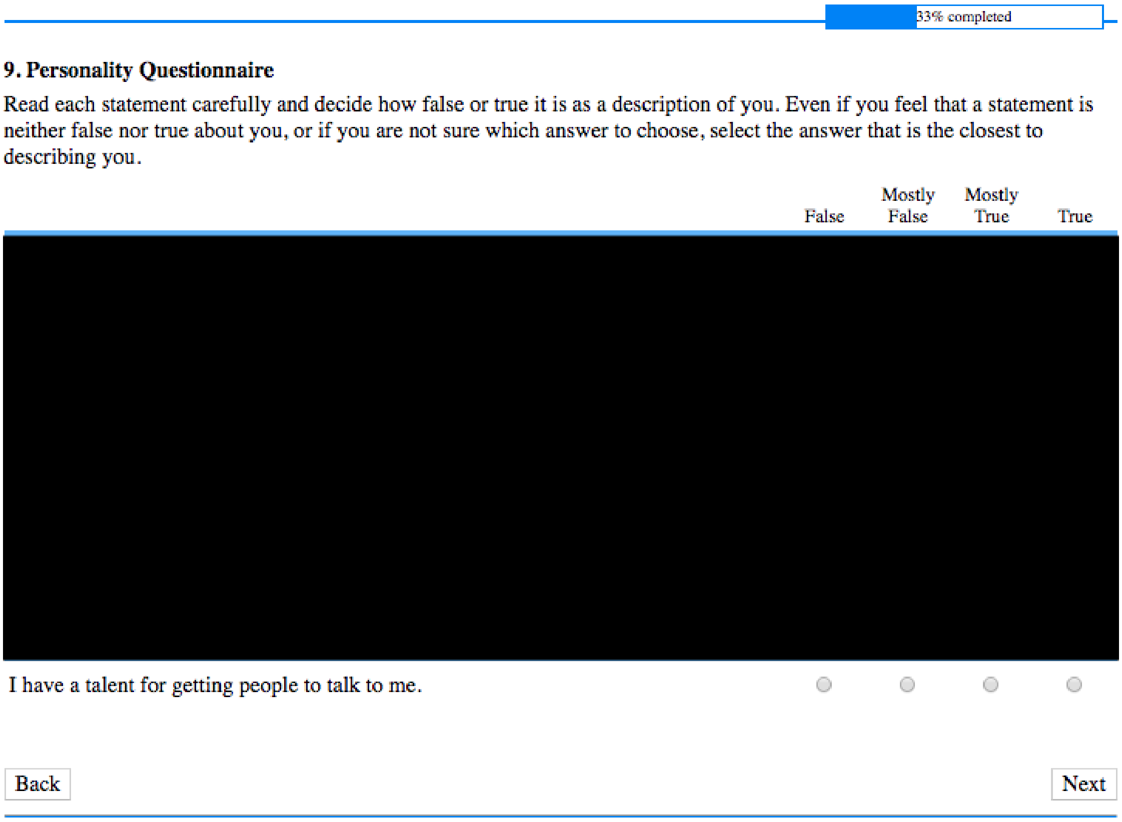
The following is summary of all the different reward outcomes, depending on your choice.The second percentage is your own profit and is shown in red:

Opponent	**You**	
	Standard Price	**Special Offer**
Standard Price	**30% / 30%**	**10% / 40%**
Special Offer	**40% / 10%**	**20% / 20%**

○ Standard Price ○ Special Offer

Figure 3.4: Decision page

Personality questionnaire



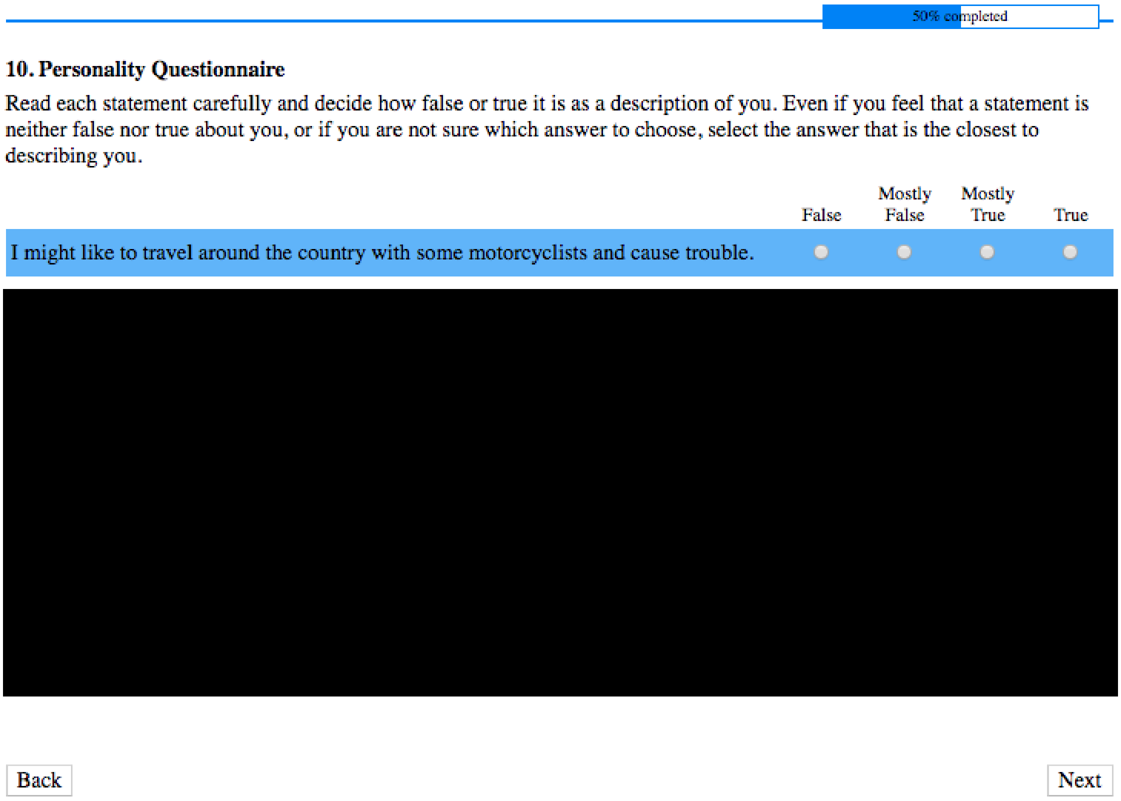
9. Personality Questionnaire

Read each statement carefully and decide how false or true it is as a description of you. Even if you feel that a statement is neither false nor true about you, or if you are not sure which answer to choose, select the answer that is the closest to describing you.

[redacted]

	False	Mostly False	Mostly True	True
I have a talent for getting people to talk to me.	○	○	○	○

Figure 3.5: Personality test-sample 1



10. Personality Questionnaire

Read each statement carefully and decide how false or true it is as a description of you. Even if you feel that a statement is neither false nor true about you, or if you are not sure which answer to choose, select the answer that is the closest to describing you.

	False	Mostly False	Mostly True	True
I might like to travel around the country with some motorcyclists and cause trouble.	○	○	○	○

[redacted]

Figure 3.6: Personality test-sample 2

Follow-up questionnaire

Thank you for taking part in this study. We hope you enjoyed playing the game! Before you go, we have a few more questions we would like to about your experience. Please take time to answer these questions as they will provide us with valuable feedback.

	Strongly Disagree				Strongly Agree
During the game, I tried as hard as possible to maximize my profits.	○	○	○	○	○

1. I believed that I was playing against a real player

[Please choose] ▾

	Strongly Agree				Strongly Disagree
My game play was affected by whether I believed I was playing against a real computer or not.	○	○	○	○	○

2. How did this belief affect you?

	Strongly Disagree				Strongly Agree
It made me more likely to defect	○	○	○	○	○
It made me more likely to cooperate	○	○	○	○	○
It did not affect me	○	○	○	○	○

3. How did you hear about this site?

[Please choose] ▾

4. How did you find the number of trials in the Prisoner's Dilemma Game

[Please choose] ▾

Feedback:

Figure 3.7: Follow-up questionnaire

Chapter 4 How group composition affects cooperation in fixed networks: can psychopathic traits influence group dynamics?

The following article is now published:
Testori, M., Hoyle, R. B., & Eisenbarth, H. (2019). How group composition affects cooperation in fixed networks: can psychopathic traits influence group dynamics?. *Royal Society open science*, 6(3), 181329. doi: http:10.1098/rsos.181329

Authors' contributions:
M.T. contributed to study conceptualization, experimental design, data collection and data preparation. All authors contributed to data analysis and report writing and gave final approval for publication.

Abstract

Static networks have been shown to foster cooperation for specific cost-benefit ratios and numbers of connections across a series of interactions. At the same time, psychopathic traits have been discovered to predict defective behaviours in game theory scenarios. This experiment combines these two aspects to investigate how group cooperation can emerge when changing group compositions based on psychopathic traits. We implemented a modified version of the Prisoner's Dilemma game which has been demonstrated theoretically and empirically to sustain a constant level of cooperation over rounds. A sample of 190 undergraduate students played in small groups where the percentage of psychopathic traits in each group was manipulated. Groups entirely composed of low psychopathic individuals were compared to communities with 50% high and 50% low psychopathic players, to observe the behavioural differences at the group level. Results showed a significant divergence of the mean cooperation of the two conditions, regardless of the small range of participants' psychopathy scores. Groups with a large density of high psychopathic subjects cooperated significantly less than groups entirely composed of low psychopathic players, confirming our hypothesis that psychopathic traits affect not only individuals' decisions but also the group behaviour. This experiment highlights how differences in group composition with respect to psychopathic traits can have a significant impact on group dynamics, and it emphasizes the importance of individual characteristics when investigating group behaviours.

Keywords
Prisoner's Dilemma, Evolutionary Game Theory, Psychopathy, Group Differences.

4.1 Introduction

Human interactions are characterised by complex networks of individuals and relationships. Cooperation is one of the basic interactions amongst them, and for decades researchers have tried to explain how it evolves and which circumstances can boost cooperative behaviours. Evolutionary game theory offers numerous examples of how to foster cooperation by modelling human actions in various situations. Mechanisms such as the evolution of communities in networks, reputation systems, both altruistic and institutional punishments, iteration of games over time have all been proven to sustain cooperation, both theoretically and experimentally [11, 115, 128, 129, 130, 131]. A recent experiment [132] confirmed an important theoretical argument claiming that : "natural selection favours cooperation, if the benefit of the altruistic act, b, divided by the cost, c, exceeds the average number of neighbours, k, which means $\frac{b}{c} > k$" ([133], p. 502). In their experiment, Rand and co-workers proved that, satisfying the benefit-cost condition and adopting a static instead of a well-mixed network, cooperation was not only fostered but also maintained over time. All the above mentioned works address the study of cooperation by looking at how external factors influence and promote collaborative behaviours. In the current study, however, we are interested in exploring how individual characteristics interact with these exogenous mechanisms, when considering group dynamics.

Human personality traits and group dynamics have been analysed in the study of teamwork and effectiveness, especially in the workplace. Existing research has clearly established that group personality composition affects group performance [134, 135, 136, 137]. Teams with higher extraversion and emotional stability were found to enhance productivity and team viability [135]. Conscientiousness, agreeableness, and openness to experience at the group level were positively correlated with team performance, as were the differences in extraversion and emotional stability amongst group members [136]. In small groups, extraversion, both at the individual and at the group level, predicted task focus and group performance [134].

Thus, numerous analyses have been implemented to disentangle possible connections among cooperation, group performance and personality traits. However, no previous contribution has looked at the relationship between psychopathic traits and group dynamics, which is the focus of our study.

In his work, Cleckley (1951) [28] described the construct of psychopathy as characterised by a constellation of personality traits including superficial charm, lack of remorse, guilt and fear, poor impulse control, emotional detachment and impairment in building solid relationships, as well as high levels of manipulativeness, dishonesty, low empathy and callousness. Several studies have examined the effect of psychopathy on cooperation, especially using game theory. One of the first studies using game theory to investigate psychopathic traits adopted the Prisoner's

Dilemma game, and surprisingly it found that males high in primary and secondary psychopathy were not more likely to defect than those low in such traits [41]. Nevertheless, later studies reported significant negative correlation between psychopathic traits and cooperation [44], and male prison samples showed a decreased cooperativeness among those high in psychopathy [105]. High levels of impulsivity were also found to be strongly predictive of defective behaviours in the general population [55]. Although prior research has looked at the relationship between psychopathic traits and cooperation, no study has yet examined how psychopathy affects group cooperation.

To address this gap, we conducted a laboratory experiment using the experimental design proposed by Rand et al. (2014) [132], including participants' psychopathic traits. We were interested in how the introduction of high psychopathic individuals would affect cooperation at the group level, in an environment that has been proven to foster and maintain cooperation. Participants' psychopathic traits were assessed before the lab experiment, and groups were formed in such a way as to have either $0\%, 20\%$ or 50% of high psychopathic people in each group. Our goal was to find an answer to the research question: *"Do high psychopathic people in the general population affect group dynamics?"*.

While several studies have looked at the general population when investigating psychopathy [44, 55], in this experiment we used a sub-sample of the general population, composed of undergraduate students, in which the variation of psychopathic traits was quite small. In this way, we observed whether even small changes in psychopathic traits can have an impact not only on individuals' strategy but also on group dynamics. Based on previous findings and on the depiction of psychopathic traits, our hypothesis is that groups with a greater density of high psychopathic individuals will show less cooperative behaviours, when compared to groups with low or zero density of high psychopathic participants.

4.2 Methods

4.2.1 Sample

Participants were recruited amongst Southampton University students. A total of 305 participants filled in the online PPI-R questionnaire [122]. Amongst them, 201 participants took part in the lab experiment after being invited by the researcher. This selection was due to their availability to take part in the lab experiment and on their consistency in filling the online questionnaire. The first two sessions were pilot versions (used to check the functionality of the experiment) and were not included in the final sample, which was composed of 190 participants (115 female, age: *M=23.31, SD=4.68*). Each participant took part to the experiment only once. Participants gave informed consent for participating in a laboratory game and ethical approval was obtained from the Faculty of Mathematical Sciences at the University of Southampton. Our data are deposited at Dryad: https://datadryad.org/review?doi=doi:10.5061/dryad.ms57853

Table 4.1: Descriptive statistics for the participants sample.

	Min	Max	Mean	Standard Deviation	Cohen's d study 1	Cohen's d study 2
Age	19	52	23.32	4.66	-	-
Gender	1	2	1.60	0.49	-	-
Nationality	1	2	1.40	0.49	-	-
Cumulative psychopathy measure	85	111	98.15	5.05	-2.11	-2.28
Fearless dominance	29	46	36.66	2.55	-2.19	-2.90
Self-centred impulsivity	27	45	37.16	3.20	-2.83	-2.34
Coldheartdness	7	16	11.82	1.98	-1.43	-1.11
Maximise.yourself	0	1	0.75	0.43	-	-
Maximise.links	0	1	0.59	0.49	-	-
Behaviour.neighbours	0	1	0.86	0.35	-	-

Gender: 1=male, 2=female; Nationality: 1=UK, 2=Other;
Maximise.yourself ,Maximise.links,Behaviour.neighbours: 0=no, 1=yes.

4.2.2 Personality Measures

The PPI is a 154-item self-report questionnaire [106] on psychopathic traits with 8 sub-scales: Machiavellian Egocentricity, Social Potency, Coldheartedness, Carefree Nonplanfulness, Fearlessness, Blame Externalisation, Impulsive Nonconformity and Stress Immunity. Seven of the eight subscales can be grouped into two main factors: Fearless Dominance and Self-centred Impulsivity, while Coldheartedness is considered as an additional factor. Eisenbarth et al. (2015) [122] proposed a 40-item version of the PPI, which was used in this study. A recently developed method, the IRS-10, allowed us to test the response reliability of participants in the PPI-R [123]. Participants with IRS-10 scores above the cut-off (99th percentile) were deemed to have completed the PPI-R in an inconsistent and therefore unreliable manner and were eliminated from analysis, leading to the exclusion of 2 participants.

To compare the psychopathic traits of our sample with data from previous studies ([138]-study 1- and [139]-study 2-), we calculated Cohen's (1988) [140] approximate metrics for group differences, where d = 0.2 is considered a weak difference, d = 0.5 is medium, and d = 0.8 or higher is large. We compared the cumulative measure of psychopathy PPI-R-SUM, and the three sub-categories of Fearless Dominance, Self-Centred Impulsivity and Coldheartdness (see Table 4.1 for results). Our sample reports smaller values compared to the two reference studies (thus the negative sign of the Cohen's d) considered and such differences are all large (d>0.8).

4.2.3 Experimental Design

In this experiment, we used the design implemented by Rand et al. (2014) [132]. Participants were arranged on a ring connected to one neighbour on each side, for a total of k=2 links per player. They had an initial endowment of 100 points, and they played a repeated cooperation game over 50 rounds. In each round, they had to choose whether to defect, by doing nothing, or to cooperate, by paying a cost of $c = 10$ points per neighbour to give each of them a benefit of $b = 60$ points ($\frac{b}{c} = 6 > k = 2$). This setting was chosen according to the Rand et al. (2014) [132] findings, where this ratio showed a more constant maintenance of cooperation over rounds. Each player made a single decision in each round, meaning that they could not cooperate with one neighbour and defect with the other. At the end of each round, participants were shown their neighbours' decisions, as well as the cumulative and the round payoff earned by themselves and by each neighbour. Participants were assigned to a position on the network and they did not change neighbours throughout the entire game. The number of rounds was not shown during the game in order to simulate an infinite game and to avoid an end-of-game effect, although they were initially informed of the duration of the game (roughly 40 minutes) and the total number of rounds.

4.2.4 Experimental Manipulation

High psychopathic individuals were defined as those participants scoring in the top quartile of the PPI-R total score for our sample (PPI-R total score > 101), while all other players were considered low psychopathic. The percentage of highly psychopathic individuals per session was manipulated in order to obtain three conditions: *high*, *low* and *zero* density (Table 4.2). High and low psychopathic participants were arranged on the ring in such a way as to avoid clusters of high or low psychopathic players, i.e. high psychopathic individuals were evenly distributed around the ring in each session. The difference in groups' size did not affect the cooperation evolution over the fifty rounds in any of the three conditions (Pearson's correlation p-value = $\{0.67, 0.50, 0.29\}$ respectively for the three conditions).

Table 4.2: Descriptive statistics for the three conditions.

Conditions	% of high psychopathic individuals	Sessions	Partici-pants	Participants per session
High	M=50.75%, SD=5.75	8	73	Median=9, Range=$\{8, 11\}$
Low	M=20%, SD=9.82	6	55	Median=9, Range=$\{7, 11\}$
Zero (Baseline)	M=0%, SD=0	9	62	Median=7, Range=$\{5, 9\}$

4.2.5 Experimental Procedure

First, participants filled in an online questionnaire to assess their psychopathic traits and gave their consent to be contacted for a lab experiment. Participants were told the questionnaire was a personality test and no specific instructions were released regarding the effect of the questionnaire on the invitation to the lab experiment. Participants were then invited by the researcher to attend a lab session, according to their personality score. Each participant was randomly assigned to a computer station according to their psychopathic scores, and they were not able to see each others' screens. Participants received a £10 fixed rate for completing the experiment, plus an additional £1 for every 1000 points earned during the game (*M=£2.75, SD=1.13*). Players read the instructions on the screen and they then played one practice round, which was not included in the final payoff. After having completed the game, they filled in a short questionnaire to assess their understanding of the game and to describe their strategy and predispositions during the game. Three main questions were asked during this follow up questionnaire: *"Did you try to achieve the highest score for yourself?"*, (variable: Maximise.yourself), *"Did you try to obtain the highest score for yourself AND your links?"*, (variable: Maximise.links) and *"Did you adjust your strategy according to your neighbours' previous actions?"*, (variable: Behaviour.neighbours). Participants' answers were then used in the analysis to observe which motivations were more influential in the strategies adopted.

4.3 Results

Since the aim of the experiment was to investigate group variations in the three conditions, the analysis adopted the average of cooperative decisions per group (0=defect, 1=cooperate). Figure 4.1 illustrates the groups cooperation throughout the fifty rounds for the high and zero density conditions. It is evident, by looking at the overall level of cooperation, that groups composed by 50% of high psychopathic people cooperated significantly less than groups entirely composed by low psychopathic people (significance level in Table 4.4). This result corroborated our theoretical prediction, proving the influence of psychopathic traits not only on individuals' decisions, but also on group behaviours.

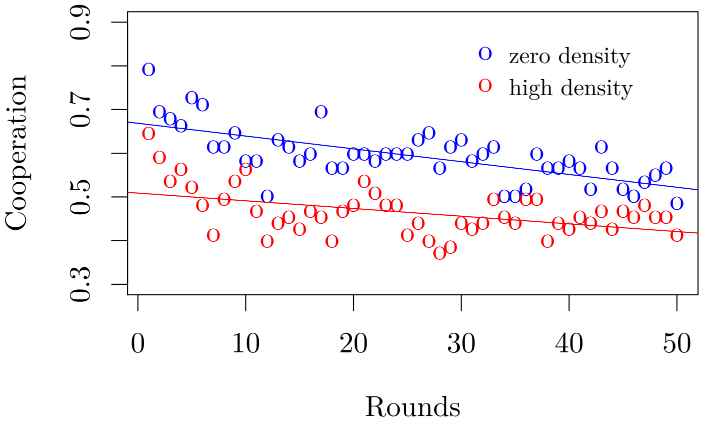


Figure 4.1: Cooperation variable calculated as the average cooperation per group per round. Zero density condition promotes cooperation compared to high density groups. The fraction of subjects cooperating in each round is shown averaged over groups, for the zero (blue circles) and high (red circles) density conditions.

On the other hand, Figure 4.2 compares the evolution of cooperation throughout the game between the zero and the low density conditions. Although the overall cooperation between the two conditions is not largely different, the trend confirms what reported in Figure 4.1: groups having some high psychopathic players exhibited a consistently lower level of cooperation compared to groups entirely composed of low psychopathic individuals. Hence, both Figures 4.1 and 4.2 corroborate our initial hypothesis that having high psychopathic players alters the group dynamics toward less cooperative behaviours.

To observe whether this behaviour is actually caused by the presence of high psychopathic individuals in the group, we looked at the correlation between psychopathic traits and cooperation. As Table 4.3 reports, having higher scores in the fearless dominance sub-scale of psychopathy is correlated with less cooperative behaviours. This supports the claim that high psychopathic individuals show less cooperative behaviour compared to low psychopathic individuals. In particular, our results suggest that the fearless dominance component of psychopathy is the driving

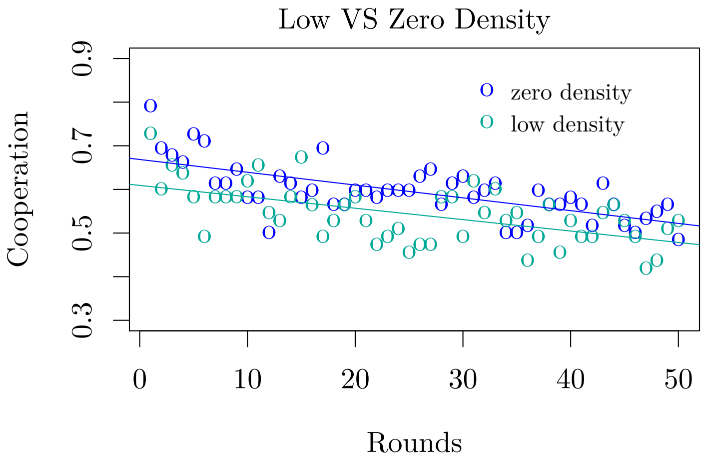


Figure 4.2: Cooperation variable calculated as the average cooperation per group per round. Cooperation in the zero and low density conditions is not significantly different, but we can observe an overall lower level of cooperation in the low density groups, compared to the zero density one. The fraction of subjects cooperating in each round is shown averaged over groups, for the zero (blue circles) and low (red circles) density conditions.

factor of such divergence in behaviours.

This difference in results between conditions is confirmed when analysing the data in more detail (using logistic linear mixed models, with random effects at the subjects level). We included demographic characteristics (*age, gender* and *nationality*) to adjust for possible disparities across condition samples, and possible motivation variables (*maximise.links, maximise.yourself* and *behaviour.neighbours*) to have a more detailed representation of the dynamics. Demographics statistics of the sample are reported in Table 4.1. The effect of the high condition (reference category: zero condition) is statistically significant (Table 4.4 model 1), even without adjusting for possible divergences in the conditions' sample. This means that groups composed of 50% of high psychopathic subjects cooperated significantly less than groups composed only of low psychopathic people. Including the interaction terms between the conditions and the rounds, we observe an increase in the significance level of the high density condition. The interaction terms disentangle the overall effect of the conditions on cooperation from the evolution of cooperation over rounds (adjusting for the slope of cooperation). Thereby, we can see that the overall level of cooperation in the high condition is significantly lower than the one in the zero condition, but the level of cooperation is maintained more constant over time in the high density condition, compared to the zero density case. Hence, the positive sign of the interaction coefficient explains this difference in the maintenance of cooperation over time. This difference in the evolution of cooperation was evident from Figure 4.1, and it is further analysed later in the results.

Furthermore, it is interesting to observe some other significant correlations relating participants' motivations to their strategies (Table 4.4 model 3). Trying to maximise both the neighbours' payoff and their own (*maximise.links*) led participants to cooperate significantly more, compared to players who did not try to achieve the best for both themselves and their

Table 4.3: Bivariate correlation matrix among cooperation, personality traits and social demographics.

	Fearless Dominance	Self-Centred Impulsivity	Coldheartdness	age	gender	nationality	Maximise links	Maximise yourself	Behaviour neighbours
Fearless Dominance	1	-	-	-	-	-	-	-	-
Self-Centred Impulsivity	0.01	1	-	-	-	-	-	-	-
Coldheartdness	0.10	-0.08	1	-	-	-	-	-	-
age	0.04	-0.04	-0.09	1	-	-	-	-	-
gender	0.13*	0.19**	0.10	0.04	1	-	-	-	-
nationality	0.15*	0.01	0.05	-0.26***	0.07	1	-	-	-
Maximise links	-0.02	0.17	-0.06	-0.09	-0.01	-0.03	1	-	-
Maximise yourself	0.03	0.00	-0.01	0.20**	0.05	0.03	-0.33***	1	-
Behaviour neighbours	-0.05	0.04	-0.05	0.12	-0.05	-0.01	-0.03	0.25***	1
cooperation	-0.16*	0.06	0.05	-0.11	-0.11	-0.17*	0.37***	-0.24***	-0.31***

Significance level: ‘***’ <0.001 ‘**’ <0.01 ‘*’ <0.05 ‘.’ <0.1
Gender: 1=male, 2=female; Nationality: 1=UK, 2=Other

links. In contrast, players who tried to maximise only their own profit (*maximise.yourself*) had a tendency to cooperate less than others, although not to a significant extent. An interesting finding arose from the *behaviour.neighbours* variable: when participants reported being influenced by their links' actions, they cooperated significantly less compared to players who were not influenced by their neighbours' decisions. Notice that neither of those variables are correlated with the individuals' personality measures (Table 4.3). Finally, the data show a significantly higher cooperation of UK citizens, compared to others (Nationality: 1=UK, 2=Others).

Moreover, by including the individual personality measures in the regression model (Table 4.4 model 5), we noticed that the individual differences do not have a statistically significant effect on cooperation. In other words, despite the individual psychopathic measures, players adopted more defective behaviours when they were part of a group half composed of high psychopathic people (i.e. high density condition). Such a result corroborates our initial hypothesis: when composed by both high and low psychopathic members, groups cooperate less regardless of members' individual psychopathic traits.

Table 4.4: Cooperation as a function of descriptive characteristics and motivations. Logistic linear mixed models, with random effect at the subjects level.

	model 1	model 2	model 3	model 4	model 5
Age	-	0.04	0.04	0.04	0.03
	-	(0.03)	(0.03)	(0.03)	(0.03)
Gender	-	-0.32	-0.32	-0.32	-0.38
	-	(0.27)	(0.27)	(0.27)	(0.28)
Nationality	-	-0.77**	-0.68*	-0.68*	-0.60*
	-	(0.29)	(0.29)	(0.29)	(0.29)
Maximise.links	-	1.33***	1.34***	1.34***	1.30***
	-	(0.29)	(0.28)	(0.28)	(0.28)
Maximise.yourself	-	-0.20	-0.23	-0.23	-0.24
	-	(0.34)	(0.34)	(0.34)	(0.34)
Behaviour.neighbours	-	-2.40***	-2.35***	-2.36***	-2.37***
	-	(0.43)	(0.43)	(0.43)	(0.43)
Condition *low*	-0.37	-	-0.42	-0.45	-0.40
	(0.40)	-	(0.34)	(0.36)	(0.36)
Condition *high*	-0.92*	-	-0.80*	-1.01**	-1.06**
	(0.37)	-	(0.32)	(0.33)	(0.35)
Fearless Dominance	-	-	-	-	-0.08
	-	-	-	-	(0.05)
Self-Centred Impulsivity	-	-	-	-	0.06
	-	-	-	-	(0.04)
Coldheartdness	-	-	-	-	0.09
	-	-	-	-	(0.07)
Round	-	-	-0.01***	-0.01***	-0.02***
	-	-	(0.00)	(0.00)	(0.00)
Condition *low* * Round	-	-	-	0.00	0.00
	-	-	-	(0.00)	(0.00)
Condition *high* * Round	-	-	-	0.01*	0.01*
	-	-	-	(0.00)	(0.00)
Intercept	0.86**	1.53	2.21***	2.31*	2.26
	(0.27)	(0.94)	(0.95)	(0.96)	(2.79)

Standard errors in parenthesis. Significance level: ‘***’ <0.001 ‘**’ <0.01 ‘*’ <0.05 ‘.’ <0.1

The focus of this experiment was to observe the main effect on group dynamics, when changing the group composition. As visible in Figure 4.1 and from the results in Table 4.4, psychopathic traits not only influenced individuals’ behaviour, but they also had a strong impact on the groups' cooperation, as initially hypothesised. In order to have a better understanding of how groups acted throughout the fifty rounds, we divided the game into four consecutive subsets and observed how the high and low density groups behaved (Table 4.5), compared to the zero density (logistic linear mixed model, random effect at subjects level).

As remarked above, the level of cooperation in the high density condition was overall significantly lower than the one in the zero density condition, and this trend was consistent over all fifty rounds. In contrast, the behavioural pattern in the low condition did not diverge significantly from the zero density condition, except from the third quarter of the game. In rounds 26-37 both high and low density groups cooperated significantly less than the zero density groups. However, looking at the interaction term between conditions and rounds, we can see that it is positive for both conditions. Since the interaction term describes the differences in the slopes of the two cooperation lines (high and low conditions compared to the zero density one), the positivity of the coefficient indicates a significantly less steep decrease in cooperation in both high and low groups compared to the zero density condition in rounds 26-37.

Table 4.5: Cooperation as a function of rounds and conditions. Logistic multilevel regression with random effect for subjects.

	(1)	(2)	(3)	(4)
	Round 1-12	Round 13-25	Round 26-37	Round 37-50
Condition *low*	-0.76	0.31	-3.46*	-1.17
	(0.49)	(0.81)	(1.36)	(1.49)
Condition *high*	-1.12*	-1.77*	-4.57***	-2.27.
	(0.46)	(0.74)	(1.22)	(1.35)
Round	-0.13***	-0.02	-0.07**	-0.04
	(0.03)	(0.03)	(0.03)	(0.02)
Condition *low* * Round	0.08.	-0.03	0.10*	0.02
	(0.04)	(0.04)	(0.04)	(0.03)
Condition *high* * Round	0.05	0.05	0.12**	0.04
	(0.04)	(0.04)	(0.04)	(0.03)
Intercept	1.81***	0.98.	2.96**	1.94
	(0.34)	(0.55)	(0.94)	(1.01)

Standard errors in parenthesis. Significance level: '***' <0.001 '**' <0.01 '*' <0.05 '.' <0.1

Lastly, since the experiment adopted the experimental design proposed by Rand and collegues (2014)[132], we were interested in observing whether our results could replicate their findings. In Table 4.6, we considered the last half (rounds 26-50), the last third (34-50) and last quarter (38-50) of the game as analysed in Rand et al. (2014)[132]. Our results showed no correlation between the level of cooperation and the rounds for both low and high conditions. On the other hand, it seems that participants in the zero density condition suffered the end-of-game effect [141, 142]: players show a significant decrease in cooperation towards the end of the game.

Table 4.6: Pearson's correlation coefficients between rounds and overall cooperation in the three conditions. Cooperation varies only in the zero density condition.

	Round 26-50	Round 34-50	Round 38-50
Condition zero	-3.50 **	-0.25	-1.92 .
Condition low	-1.53	-0.61	-0.87
Condition high	1.71	-0.43	1.20

Significance level: ‘***’ <0.001 ‘**’ <0.01 ‘*’ <0.05 ‘.’ <0.1

4.4 Discussion

We investigated the effect of different group composition on cooperative behaviours, looking at different density of psychopathic traits within the group members. Manipulating the group configuration, we looked at how groups with a low/high density of highly psychopathic people (20/50%) behaved, compared to groups with no highly psychopathic players (0 %). We adopted the experimental design developed by Rand et al. (2014), setting the ratio between cost and benefit of cooperation greater than the number of links each participant had ($\frac{b}{c} = 6 > k = 2$). We implemented this design to analyse how the introduction of high psychopathic people would affect the group behaviour, in an environment that has been shown to maintain cooperation over rounds.

Our results show that *people with higher levels of psychopathic traits do affect group dynamics*. We found a significant divergence of cooperation in those groups having a high density of high psychopathic participants compared to the zero density groups. Our findings were also robust when controlling for individuals' personality measures: belonging to a group composed by both high and low psychopathic individuals led players towards more defective strategy, regardless their personal level of psychopathy. This has relevant implications for group settings, e.g. team work in companies or educational environments. On an individual level, psychopathy has been found to be related to counterproductive work behaviour [143] and negative impact on employees (e.g. [144]). Our results therefore align with negative effects of psychopathic personality traits on individuals in the work context but extend those findings to less cooperative behaviour in team settings. This could have implications for building and managing teams, especially when cooperative behaviour is crucial for successful team work. This result is additionally striking, considering the sample of the experiment: in contrast to previous studies on psychopathy [105], we considered psychopathic traits in a subset of the general population (undergraduate students), rather than in criminal psychopaths. Furthermore, as our sample was composed of university students, the range of psychopathy measures was very restricted, even compared to the general population [138, 139]. Nevertheless, the effect of the high density condition is evident and strongly significant.

This study also highlighted that a substantial proportion of individuals high on psychopathic traits scores is necessary to affect group behaviour. Having only a small proportion of participants showing high psychopathic traits (20%) was not enough to provide a significant impact on cooperation. On the other hand, when half of the group was composed of high psychopathic participants, the group's behaviour changed significantly, showing more defections compared to groups with no high psychopathic individuals.

Another interesting aspect is the dissimilarity between the results reported by Rand and colleagues [132] and ours. Since our analysis showed no correlation between the level of cooperation and the rounds for both low and high conditions, we can state that the cooperation was maintained constant over time in these two cases. In other words, two of the three conditions of our experiment replicated Rand and colleagues [132] results: when specific network and payoff conditions are satisfied (static network and $\frac{b}{c} > k$), cooperation does not fluctuate over time. Nonetheless, the zero density condition did not corroborate Rand and colleagues [132] findings, showing an end-of-game effect. However, it is hard to give an interpretation as to why these differences emerged. A possible explanation could be that in the two conditions with high psychopathic traits (low and high density), the level of cooperation was already very low. Hence, it would be difficult to record an additional decrease in cooperative actions. Alternatively, the difference in the results could be explained by the different sample sizes adopted in the two experiments. While our groups were formed by maximum 11 players, Rand and collegues created much larger groups [132] (average of 24 players per group) for the static network setting (while smaller groups - average 8 - for the well-mixed network). Nevertheless, it would be interesting to address this point in future research to disentangle the end-of-game effect from other possible mechanisms not yet identified.

Furthermore, the experiment showed how some players' predispositions are important in the decision-making process. Trying to maximise both their own personal and their partners' payoffs led people to cooperate significantly more, while individuals focused only on their personal gain were more prone to defect, although not to a significant extent. Moreover, when influenced by partners' previous actions, participants cooperated less than average. This could suggest that only partners' defective behaviours had an influence on players' decisions, driving them towards less cooperative behaviours.

Although having a small range of psychopathic traits resulted in a strong impact of such traits on group dynamics, it would be interesting to collect a larger sample of participants to have a deeper understanding on how variations of psychopathic traits influence cooperation at the group level: a larger spectrum of psychopathic traits would allow us to understand the internal dynamics of the group, investigating how cooperation evolves over rounds for high and low psychopathic players.

This study addresses an important gap in the literature regarding the effect of individuals' personality traits in a group context. Our work is one of the first experimental investigation of the effect of individual psychopathic traits on cooperation in groups, and we showed that individuals' psychopathic traits do influence group behaviours, even when only small variations are present between group participants. With this study, we aimed to integrate the effect of individual personality traits into the large body of literature investigating how to promote cooperation, to highlight how individual differences are determinant for a more comprehensive study of the evolution of cooperation.

Chapter 5 Individual-based model: can psychopathic traits be evolutionarily adaptive?

5.1 Model background

Psychopathic traits have been described in some detail in the previous chapters; and I have analysed the impact of personality traits at the individual and at the group level through experimental evidence.

This third part of the thesis will approach the study of psychopathic traits and human behaviours from a different point of view. As described in the Introduction, individual-based models have often been used to describe the evolution of populations, allowing for the specification of details at the individual level. Building upon previous literature, I model the evolution of a population in which individuals' personality traits are considered. Specifically, I focus on those personality traits that are the most defining features of psychopathy. The main question I aim to address with this model is whether it is possible that some aspects of psychopathy can be beneficial for the survival and the evolution of a community, under specific circumstances. In other words: *"Can traits belonging to the psychopathy construct contribute positively to the evolution of a community? Do individuals expressing those traits invade the general population? Can those traits be evolutionarily adaptive?"*

The following chapters address these questions through an individual-based model composed of two main stages: we consider a population in which individuals (1) have to gather resources from the environment for their own well being, and (2) have to decide how much to contribute to the community's wealth by donating part of their gathered resources. By implementing this framework over a number of generations, I aim to disentangle the beneficial (or harmful) contribution of some dimensions of psychopathy in a community over a large span of time. In this framework, I consider two phenotypes of players, **Selfish Risk-Seekers (S)** and **Generous Risk-Averse (G)**, where the former incorporates some of the most distinctive traits of psychopathy such as risk-seeking, selfish attitudes and anti-social behaviours.

In the first stage, individuals face the risky situation of gathering resources provided by a variable and unpredictable environment. The decision as to whether to harvest resources is based on a number of factors such as the availability of supplies, the ratio between the benefit and the risk deriving from that action, the psychological attitudes of the individuals, and many more. I assume that the environment provides a certain amount of resources, and they are associated with a certain risk related to the possibility of being harmed while harvesting them. The two phenotypes react differently to risky conditions as shown by the literature. Psychopathy is often associated with low fear, lack of recognition of the consequences of actions, boldness, disinhibition and increased impulsivity [104]. Numerous experiments have been conducted to measure the correlation between psychopathy and risk-seeking behaviours. Dark Triad traits (psychopathy, narcissism and Machiavellianism) were shown to have positive relationships with both impulsivity and sensation-seeking when playing betting games and Stop-Signal tasks [145, 146]. This second task has been extensively used to assess aspects of inhibition. Individuals are instructed to respond as quickly as possible to a visual signal ("go"), but to withhold the response as soon as a second signal is presented ("stop"). The test estimates the time between the stop signal and the individual's reaction, measuring in this way the impulsivity in responses and the behavioural inhibition. Another test, the Balloon Analogue Risk Task (BART), was designed to assess impulsive decision-making and risky behaviours [147]. This task is a computer-simulated assessment and provides a novel behavioural measure of risk-taking [148]. Participants are presented with a simulated balloon and are asked to inflate the balloon to a desired level, knowing that the bigger the balloon, the larger the amount of money they would be rewarded with. However, the balloon has a probability of exploding and no specific information about this is provided to the participants. In the case of an explosion, the participant receives no monetary compensation. High levels of psychopathic traits were found significantly predictive of increased risk-taking attitudes [147] and, more specifically, boldness was found to be significantly correlated with BART risk-taking behaviours [149]. Furthermore, narcissism and psychopathy were found to significantly predict adolescent risky behaviours [150]. Participants high in psychopathy were negatively correlated with the ARQ subscales of judgment components (Adolescent Risk-taking Questionnaire [151]). Other evidence, such as from the Iowa Gambling Task (IGT), have been employed to assess risk-seeking behaviours, finding significant correlations between secondary psychopathy and risky IGT performances [152]. This test was developed to simulate real-life risky decisions: it required the examination of different card decks leading to different rewards. Psychopathic individuals seemed to be unable to control their impulses towards large reward decks, which also led to large losses.

The second stage of the model involves a Public Goods Game (PGG). Participants have to decide whether or not to contribute to the community's resources, knowing that the total amount collected will gain in value and then will be divided equally amongst all the members, independent of their initial contribution. The literature distinguishes three behavioural types based on their contributions [153]:

1. Free-riders: selfish players who do not contribute to the public good;
2. Pure cooperators: generous players who contribute all their resources to the public good;
3. Conditional cooperators: players whose contribution depends on other players' contributions to the group.

Which personality factors are correlated with which strategy type is still unclear. However, some correlations between players' personalities and their strategies have been assessed. Specifically, a significant negative correlation was recorded between the total amount of contribution to the public goods and Machiavellianism [154]. This result suggests an association between free-riders and high Machiavellianism. At the same time, being high in this personality measure was also correlated with a higher total gain in the game. Hence, it seems that people showing traits belonging to the Dark Triad (Machiavellianism, narcissism and psychopathy) behave more rationally, aiming for a higher personal gain. Looking at the trends found by Czibor, Vinexe and Bereczkei (2014), the average donation for low-Machiavellian subjects is around 80% of the total resources, while for high-Machiavellian participants is around 50% [155]. Thus, also in this case, it is possible to state that a high level of Machiavellianism is strongly correlated with a lower overall contribution to the community. Although Koenigs, Kruepke and Newmann (2010) adopted an Ultimatum game and a Dictator game, they confirmed a lower trend of offers from high psychopathic subjects, compared with non-psychopaths [79]. Thus, psychopathy is related to less cooperative attitudes and less generous behaviours towards other people.

Another aspect that is included in the model is related to the tendency of people high in psychopathy to engage in antisocial and criminal behaviours. Data shows that, although psychopathic people represent a small percentage of the population, they comprise over 15% of incarcerated prisoners and they commit almost half of the most serious crimes [34]. In this sense, the community has to pay a cost due to these behaviours. Individuals diagnosed as psychopaths are indeed more prone to engage in criminal activities, due to their callousness, manipulativeness, deceitfulness, indifference towards the others, and their lack of empathy and remorse [104]. Furthermore, some dimensions of psychopathy, such as antisocial deviance, affective detachment and interpersonal features, have been found to predict a history of suicide attempts [156]. Thus, highly psychopathic individuals represent a cost to the community as well as to themselves. To capture this, both individual and communal costs were introduced in the simulation model. The cost imposed on the community is also driven by the resistance of psychopaths to punishment. In one of his works, Hare noted that "in most jurisdictions, psychopathy is considered to be an aggravating rather than a mitigating factor in determining criminal responsibility" [157](p.205). Due to their resistance to punishment, psychopaths are considered less likely to redeem themselves when incarcerated [50, 52, 53]. Therefore, the cost they enforce on the community is considered higher than that caused by non-psychopathic offenders.

The final part of the simulation describes how individuals reproduce. To model this phase, I researched previous findings looking at the heritability of psychopathic traits in the general population. Genetic factors were discovered to have a strong influence, explaining approximately up to 49% of the variance in psychopathic personality [70]. On the other hand, a strong impact was also exercised by non-shared environmental influences. Several studies investigated these two factors (genetic and environmental) with regard to the heritability and genetic nature of psychopathy [158, 159]. A recent study discovered that psychopathy elevates fertility although diminishes the quality (with respect to physical and mental health and expected future reproduction ability) of the offspring [160]. They collected data from 635 individuals at the end of their reproductive phase with at least one child. Data showed that individuals with higher levels of psychopathic traits were more prone to have a larger number of offspring. At the same time, they were less likely to offer adequate care to the offspring, investing less time in parenting. Furthermore, the offspring born from high psychopathic people were less likely to have a future healthy life, as judged by responses to questions about their physical and mental health. Another interesting result was found by Međedović (2019) [161]: harsh environment in childhood and high levels of psychopathy (which are often positively correlated) lead to shorter relationships and lower parental effort. He tested 320 individuals with at least one child, measuring their psychopathic traits, the harshness of their childhood, their mate-seeking attitudes, the duration of their longest relationship and their care for children. Results showed that individuals with higher levels of psychopathy were significantly more likely to invest time in seeking a partner but were also unable to maintain a stable relationship.

Supported by the evidence presented here, I modelled some aspects of psychopathic individuals, discerning two main phenotypes in the community: SELFISH RISK-SEEKERS (S) and GENEROUS RISK-AVERSE (G). Due to the complexity of psychopathy, I focused on those aspects that (1) received more attention, and hence provided more empirical evidence from the academic perspective, and (2) are more likely to be observed in the general population.

In the next section, I will present the formalisation of the individual-based model. Results are then presented in the following chapters, where different steps are implemented to improve the ecological validity of the model.

5.2 Model formalisation

5.2.1 Purpose

The purpose of this model is to investigate whether, and if so under which circumstances, the presence of individuals with different levels of psychopathic traits affects the population dynamics. In particular, it aims to explore whether traits related to generosity and risk propensity can affect the evolution of a community under different conditions. The final goal is to model some of the main distinctive aspects of psychopathy, and to examine how individuals expressing those traits affect the growth of a population.

This is a temporally explicit individual-based model. I consider a population composed of two phenotypes: selfish risk-seeking (S) and generous risk-averse (G). I model the evolution of a community in different scenarios over time and I observe whether changing the parameters that describe various aspects of individuals' behaviour affects the overall evolution of the population size and composition.

5.2.2 Process Overview and Scheduling

The model consists of four main stages: harvesting, public contribution, reproduction and mutation. Firstly, individuals have to decide whether to gather resources from the environment (harvesting phase). During this first step, individuals might perish as a consequence of engaging in the risky action of harvesting (mortality phase).

Secondly, they participate in a public goods game in which they have to decide how much of their resources to donate to the communal pot, knowing that the total amount will be multiplied by a constant factor and equally redistributed among all citizens, regardless of their initial contribution (PGG phase). After having gathered all the citizens' contributions, the community has to pay a cost proportional to the number of selfish risk-seeking citizens (community cost phase). Thereafter, the remaining resources are equally redistributed among all citizens. The decisions in both the harvesting and the PGG phase depend entirely on the individual's behavioural type.

Thirdly, each individual reproduces proportionally to the amount of resources owned at the end of the PGG phase (reproduction phase). If they did not gather enough resources to meet the survival threshold, they perish without offspring. The offspring's phenotype is determined by a reproduction mechanism which takes into account both the genetic component and the phenotype expressed by the parent.

Lastly, a mutation in the reproduction probabilities is introduced. At each generation, the reproduction probabilities are subject to a small mutation, drawn from a probability distribution (mutation phase).

The entire cycle is then iterated over T generations and, in order to have robust results, the model is repeated over 10^3 independent realisations.

The flowchart in Figure 5.1 presents the different stages of the model in chronological order. The blue boxes represents phases that depend on the initialisation of the model; the orange boxes are stages depending on the individuals' phenotype; the red boxes are aspects that are imposed on the individuals/community; while the green box represents the evolutionary part of the model.

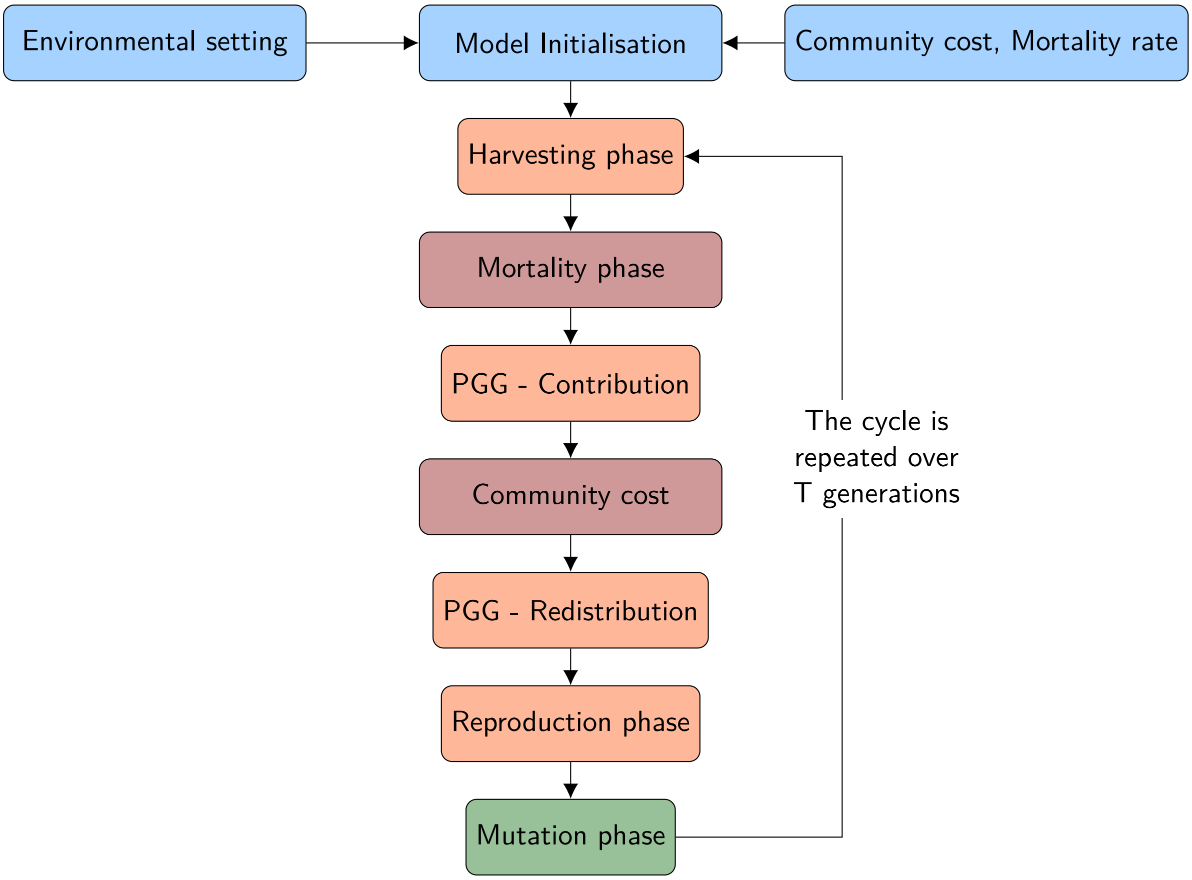
5.2.3 State Variables

The model comprises three hierarchical levels: environment, community and individual.

Individuals are entirely characterised by their phenotype: their decisions to harvest and contribute are determined by the behavioural type they express, either selfish risk-seeking (S) or generous risk-averse (G). Hence, expressing either one of the two phenotypes leads individuals to behave differently in the harvesting and the PGG phases. Furthermore, being risk-seeking leads individuals to engage in more dangerous actions, making them more likely to perish in such actions. Thus, a mortality rate is introduced for risk-seeking people. Each individual has a maximum number of offspring o they can reproduce, and a minimum amount of resources s required to be able to procreate. The phenotype the offspring will inherit is determined by the reproduction probabilities of the parent $\varphi_{G,G}$ and $\varphi_{S,S}$. $\varphi_{G,G}$ ($\varphi_{S,S}$) represents the probability that generous (selfish) individuals will pass on their own phenotype to their offspring. Each individual has both probabilities at the moment of birth and they will be then passed on to the offspring.

The community is composed of all the individuals present in each generation. It is responsible for paying the costs of sustaining troublesome citizens such as selfish risk-seekers. This cost was introduced to give a more realistic representation of aspects concerning psychopathy. In

Figure 5.1: Flowchart explaining the model phases.



fact, psychopathic people are more likely to engage in anti-social and criminal activities, which have repercussions on the community as well as on the individuals themselves. Therefore, a community cost proportional to the number of selfish risk-seeking individuals incorporates this aspect in the model.

The environment describes the amount of resources available to each individual in generation *t*. The resources can be maintained constant over time or they can vary from periods of abundance to moments of scarcity. The numerical values representing abundant and scarce environments have been deduced by trial and error. By implementing different values of the environmental offer, I observed which one led to an exponential increase in the population (abundant environment) and which resulted in a slow but constant decrease of the community size (scarce environment). A summary of the parameters controlling the evolution of the model can be found in Table 5.1

Table 5.1: Summary of model parameters.

Level	Parameters		Range
Environment			
	Resources offered in generation t	e_t	[0,5] units
	Carrying capacity	K	$K > 0$
Community			
	Community cost for S individuals	λ	[0%,100%]
	PGG Multiplier	ρ	$\rho > 1$
Individual $\equiv$ Phenotype $p \in \{S, G\}$			
	Harvesting rate	h_p	[0%,100%]
	Contribution rate (decimal format)	c_p	[0,1]
	Mortality rate	m_p	[0%,100%]
	Reproduction probability	$\varphi_{p,p}$	[0,1]
	Maximum number of offspring	o	$o > 0$
	Survival level	s	$s \geq 0$

5.2.4 Design Concepts

Emergence

Individuals' behaviour is entirely described by their phenotype, and their decisions are determined by a set of deterministic and stochastic rules. Population dynamics emerge from individuals' behaviours with respect to the different environmental conditions experienced and from the different parameters selected. Emergent system dynamics include:

- Population size
- Population composition
- Reproduction probabilities

Adaptation

The reproduction probabilities $\varphi_{G,G}$ and $\varphi_{S,S}$ are mutated over generations. Mutations allow the population to adapt to the environmental and social conditions experienced over time.

Interaction

Individuals interact globally in the Public Goods Game phase, when they all contribute part of their resources to the communal pot. Group composition also influences each community member as the collective cost is proportional to the number of selfish risk-seekers present in the population. This cost is paid with the collective money gathered during the PGG.

Stochasticity

The model includes only two elements that are not deterministically defined. The mortality rate is a stochastic parameter which describes the probability of an individual engaging in risky action to perish. The mutation rates are also a stochastic element of the model as they are drawn from probability distributions.

Observation

The key outputs of the model are:

1. Population size
2. Population composition
3. Reproduction probabilities

For the model analysis, the dynamics at the community level (population size and composition, community cost), as well as those at the individual level (resources gathered, reproduction probabilities and mortality rate) were saved at each generation.

5.2.5 Initialisation and Input

Table 5.2 reports the initial values of those parameters that were maintained constant in almost all models. Differences in the initialisation values of these parameters are reported in the overview section of each model chapter.

Table 5.2: Overview of parameters and initial values of parameters.

Variables	Description	Initialisation value
N_0	Initial sample size	100 / 250
T	Number of generations	200 / 10^3
I	Model realisations	10^3
Carrying capacity	Maximum population size that the environment can sustain	$2 * N_0$
PGG Multiplier	Public goods game multiplication factor	1.5
Survival level	Minimum amount of resources necessary to each individual to survive	1
Maximum resources	Maximum amount of resources each individual can gather at each generation	4
Maximum offspring	Maximum feasible number of offspring per individual	10
Harvesting rate	Proportion of resources each individual harvests from the environment , based on its phenotype	$h_S = 80\%$, $h_G = 50\%$
Contribution rate	Percentage of resources each individual contributes to the public pot, based on its phenotype	$c_S = 20\%$, $c_G = 100\%$

5.2.6 Submodels

The model algorithm is hereafter presented:

Initialisation

1. An initial population of size N_0 is generated. Each individual is assigned a phenotype and both reproduction probabilities $\varphi_{S,S}$ and $\varphi_{G,G}$.
2. The parameters describing community costs and mortality rate are assigned according to the scenario depicted.
3. An environmental condition is selected.

Game dynamics

1. Individuals harvest the resources offered by the environment according to their phenotype.

2. As harvesting is considered risky, a mortality rate is applied to account for the risk of perishing during harvesting.
3. Individuals participate in a Public Goods Game, contributing to the communal pot. Their contribution is proportional to their personal resources and the proportion is defined by their phenotype. In some models, individuals' contributions depend on previous overall contribution, as explained in chapter 9.
4. The community pays a cost, deducted from the communal pot, that is proportional to the percentage of S individuals present in the population.
5. The remaining communal resources are redistributed equally among all individuals independent of their initial contribution.

Reproduction

1. Individuals that did not gather enough resources to meet the survival threshold perish.
2. Individuals that gathered enough resources to survive are replaced by a number of offspring proportional to their personal resources, up to a maximum number o of offspring .

Mutation

1. Individuals' reproduction probabilities are mutated and carried on by the offspring.

Repeat 'Game dynamics' , 'Reproduction' and 'Mutation' for T generations.

Hereafter, I present the model steps in more detail.

Harvesting

In this first stage, individuals gather the resources the environment offers according to their phenotype. Individuals with risk-seeking attitudes are more likely to engage in dangerous situations to gather as much as they can for their own benefit. On the other hand, risk-averse individuals are more prone to engage in actions only if the risk is low and the reward is accessible.

After the harvesting phase in generation t, individual i has an amount of resources $r_{i,t}$ that depends on both the environmental offer e_t and his phenotype p_i:

$$r_{i,t} = e_t h_{p_i}. \tag{5.1}$$

Mortality

In pursuing the resources, individuals encounter the risk of perishing with a probability m_{p_i}. As the mortality parameter is related to engaging in risky actions, I modelled it to be always zero for risk-averse citizens. Following this step, the population size changes accordingly:

$$< N_t > = < N_t > - m_S < S_t >, \tag{5.2}$$

where S_t is the proportion of S members in the population at generation t.

Public Goods Game

Thereafter, each individual invests part of his resources to the public pot. Generous citizens behave as pure (or conditional) cooperators, investing all (or a part) of their resources in the communal pot. On the other hand, selfish citizens contribute a smaller proportion of their resources. The total amount of communal resources in generation t is therefore:

$$\tilde{C}_t = \sum_{j=0}^{N_t} r_{j,t} c_{p_j}. \tag{5.3}$$

Finally, after having collected the donations, the community pays a cost due to the presence of S individuals. The cost is proportional to the density of selfish risk-seekers and it is deducted from the total amount gathered by the population:

$$C_t = \tilde{C}_t (1 - \lambda * S_t), \tag{5.4}$$

where λ describes the percentage of communal resources that the community would have to pay if the population were entirely composed of selfish-risk seekers.

The communal pot is then equally redistributed among all citizens, providing them with a fitness:

$$f_{i,t} = \frac{C_t \rho}{N_t} + r_{i,t}(1 - c_{p_i}). \tag{5.5}$$

Reproduction

Finally, each individual is replaced by a number of offspring which is linearly proportional to its fitness:

$$n_{i,t} = \begin{cases} 0, & \text{if } f_{i,t} \leq s \\ \lceil \frac{o}{M-s}(f_{i,t} - s) \rceil, & \text{if } s < \ f_{i,t} < M \\ o, & \text{if } f_{i,t} \geq M \end{cases} \tag{5.6}$$

where M is the necessary fitness for an individual to reproduce o offspring. Each offspring is assigned with a phenotype according to the reproduction probabilities.

Mutation

The last step of the model is the introduction of mutations in the reproduction probabilities the offspring inherit. The mutation mimics an evolutionary process describing a variation in the probabilities that a certain phenotype will be passed on to the offspring. At each generation, a mutation η_t is drawn from a normal distribution $\mathcal{N}(0, \sigma^2)$. The reproduction probabilities will mutate in such a way as to favour one phenotype over the other.

$$\varphi_{p,p,t} = \begin{cases} 0, & \text{if } \varphi_{p,p,t-1} + \eta_t < 0 \\ \varphi_{p,p,t} + \eta_t, & \text{if } \varphi_{p,p,t-1} + \eta_t \in [0,1] \\ 1 & \text{if } \varphi_{p,p,t-1} + \eta_t > 1 \end{cases} \tag{5.7}$$

Chapter 6 Base model without mutation

6.1 Overview

To have a clear understanding of the model, I first implemented a simple version of the algorithm in which:

1. All the offspring inherit the phenotype of the parent: $\varphi_{G,G} = 1$, $\varphi_{S,S} = 1$.
2. No mutation in the reproduction probabilities is allowed: $\sigma^2 = 0$.

Different initial conditions determined the initial population composition (See Table 6.1), and various scenarios were implemented, as specified in Table 6.2.

Table 6.1: Population initial composition with respect to the density of selfish risk-seeking citizens.

Density	Initial percentage of S	Code colour
Low density	$S_0 = 1\%$	**Blue** lines
Medium-low density	$S_0 = 10\%$	**Red** lines
Medium-high density	$S_0 = 20\%$	**Green** lines
High density	$S_0 = 30\%$	**Yellow** lines

Table 6.2: Parameter initialisation for the model.

Parameter	Initialisation values
Community cost λ	$\lambda \in \{0\%, 50\%, 100\%\}$
Mortality rate m_{p_i}	$m_G = 0\%$; $m_S \in \{0\%, 25\%, 50\%\}$

Three possible percentages λ were considered for the cost the community has to pay to sustain selfish risk-seeking citizens: (a) $\lambda = 0\%$ means that the community pays no cost for having selfish risk-seeking citizens; (b) $\lambda = 50\%$ indicates a linear increase of the costs such that, if the society is entirely composed of selfish-risk seekers, the cost will be equal to half of its total resources; (c) $\lambda = 100\%$ denotes an infeasible scenario: it indicates a linear increase in this cost such that, in a community composed only of selfish-risk seekers, all the communal resources will be used to sustain selfish citizens, leaving no money to redistribute to the citizens.

Moreover, as the mortality rate is related to risky actions, the mortality rate for risk-averse individuals is equal to zero in all scenarios. On the other hand, risk-seeking individuals have either $0\%, 25\%$ or 50% probability of perishing during the harvesting phase.

Finally, a few different environments were implemented to observe how the community evolved when changing the available resources.

Two main environmental conditions were imposed:

1. Fixed environment
2. Variable environment

In the first case, the resources provided remain constant over generations, and the amount individuals can collect, $e_{t,i}$, depends on the population size:

$$e_{t,i} = \frac{e_0}{N_t}, \tag{6.1}$$

where e_0 is the fixed amount of resources the environment provides.

In the latter case, the environment provides a variable amount of resources over generations, describing situations of fluctuations of supplies over time. In this sense, the population will experience periods of abundance alternating with periods of scarcity.

6.2 Results

6.2.1 Fixed Environment

Three fixed environments were considered, simulating different stages of scarcity and abundance of resources. The environmental offer ranged between 1.2 and 4, where the former represents a period of strong shortage of supplies, while the latter mimics an era of profusion of resources.

To understand the population dynamics, I observed both the evolution of the population size and the population composition over 200 generations. The results report the mean over the 10^3 independent realisations to obtain robust outcomes. The grey shadow represents the variation area in which the mean values lie, calculated as the mean value $\pm$ the standard error over the 10^3 independent realisations.

The following Figures (6.1 to 6.6) show the evolution of the population size and composition under different initial conditions and environmental scenarios.

Figure 6.1: Evolution of the population **size** in an **abundant** fixed environment, $e_0 = 4$. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.

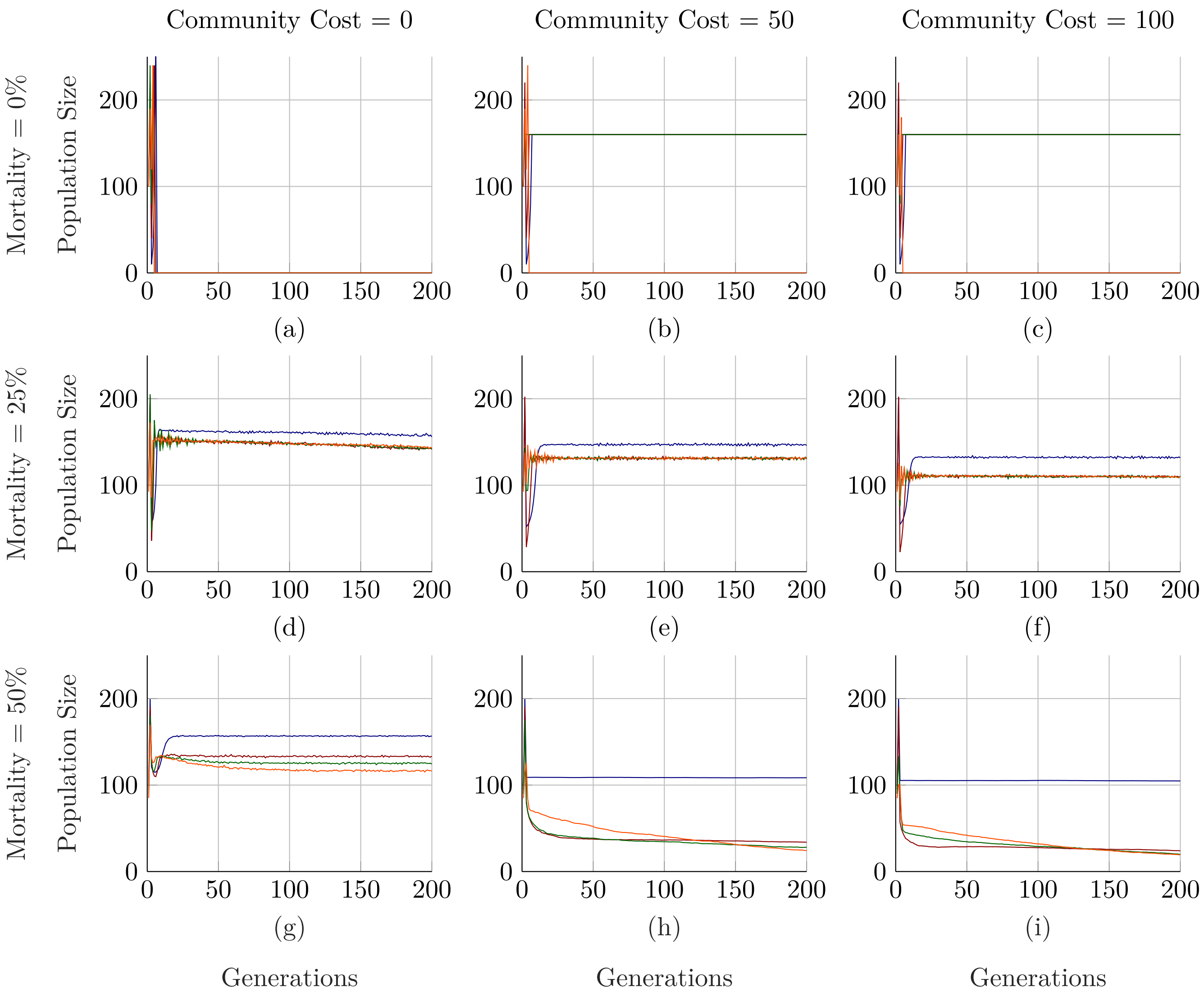
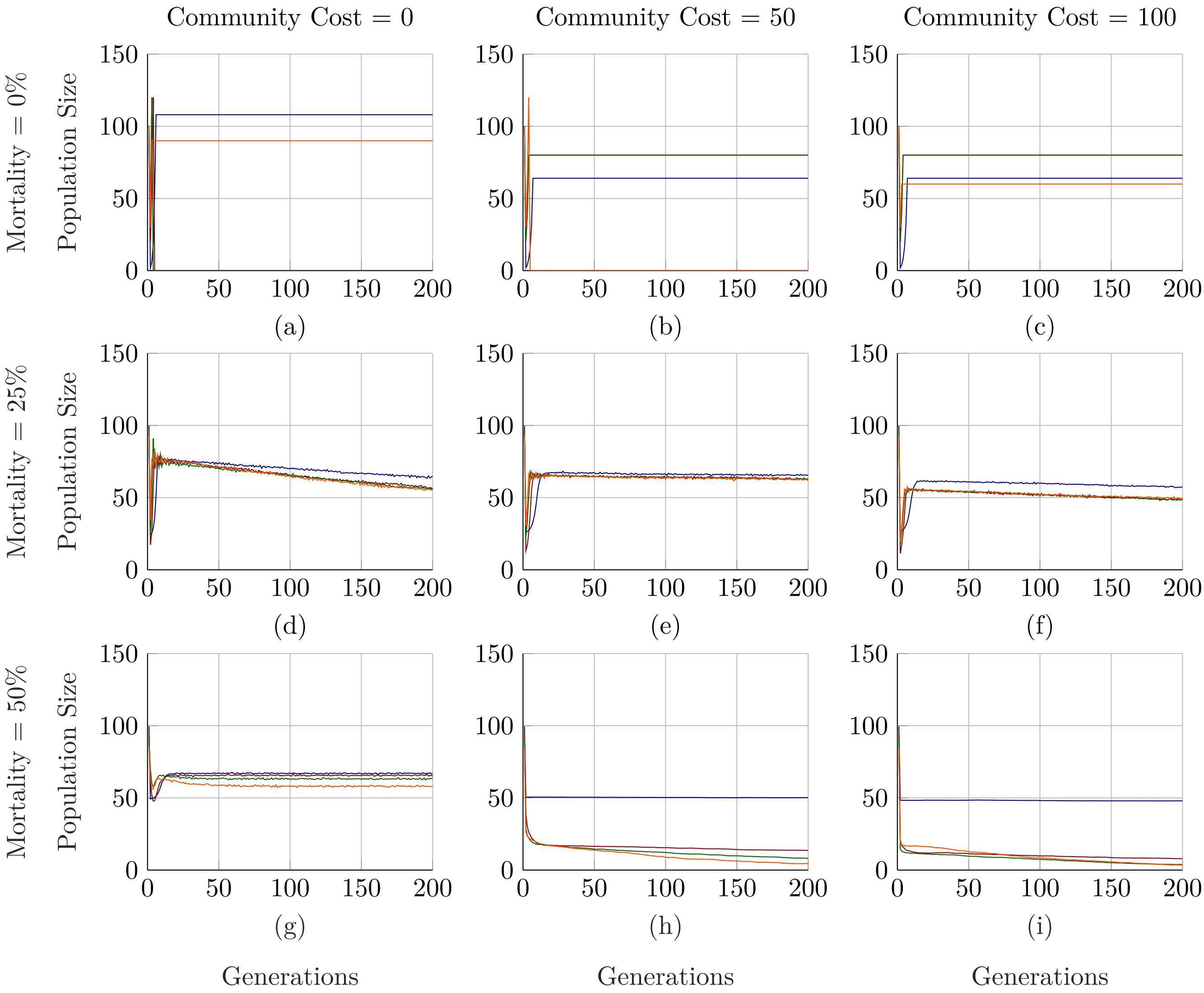


Figure 6.2: Evolution of the population **size** in a **moderate** fixed environment, $e_0 = 2$. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.

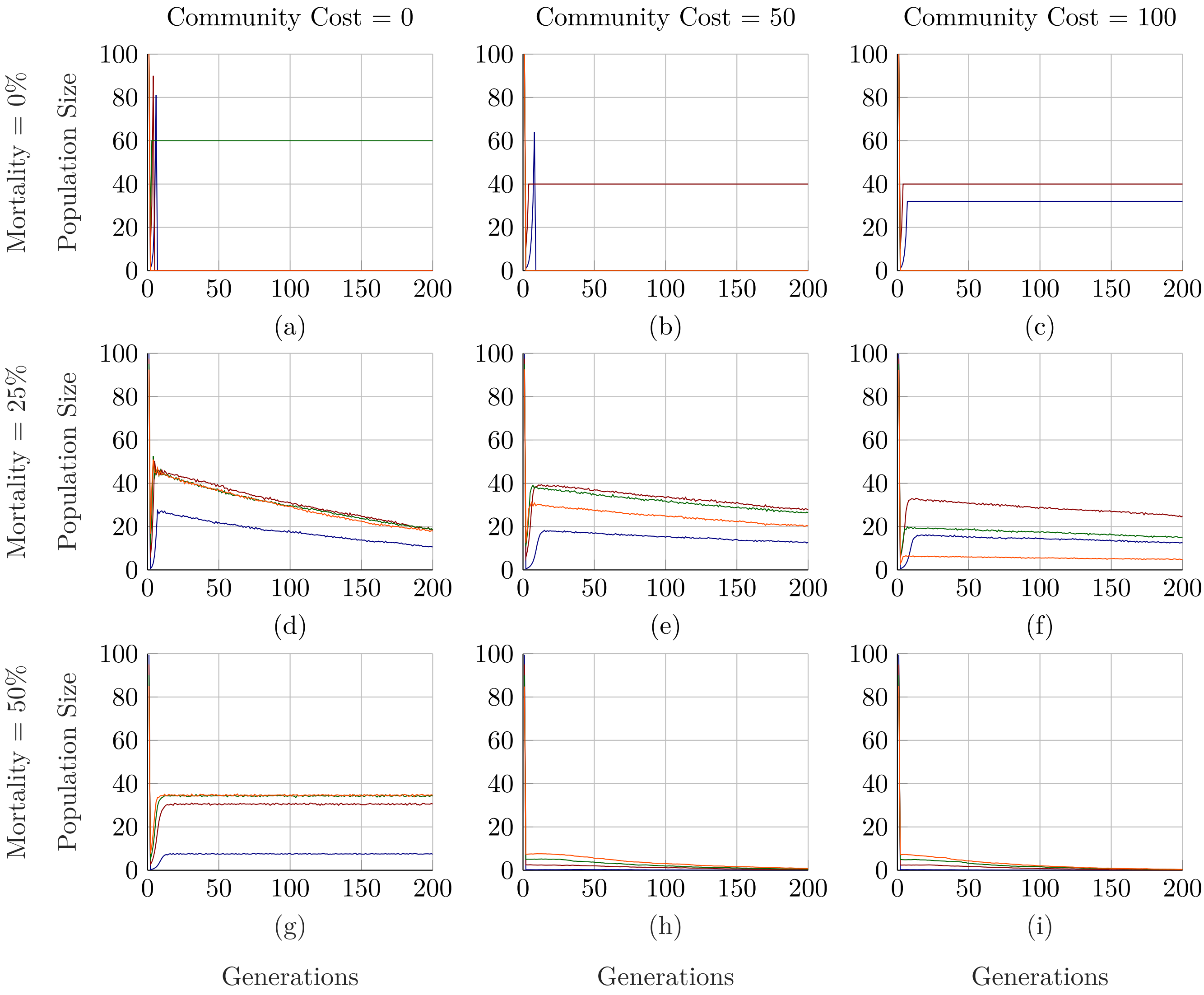


(a) (b) (c)

(d) (e) (f)

(g) (h) (i)

Figure 6.3: Evolution of the population **size** in a **scarce** fixed environment, $e_0 = 1.2$. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.



(a) (b) (c)

(d) (e) (f)

(g) (h) (i)

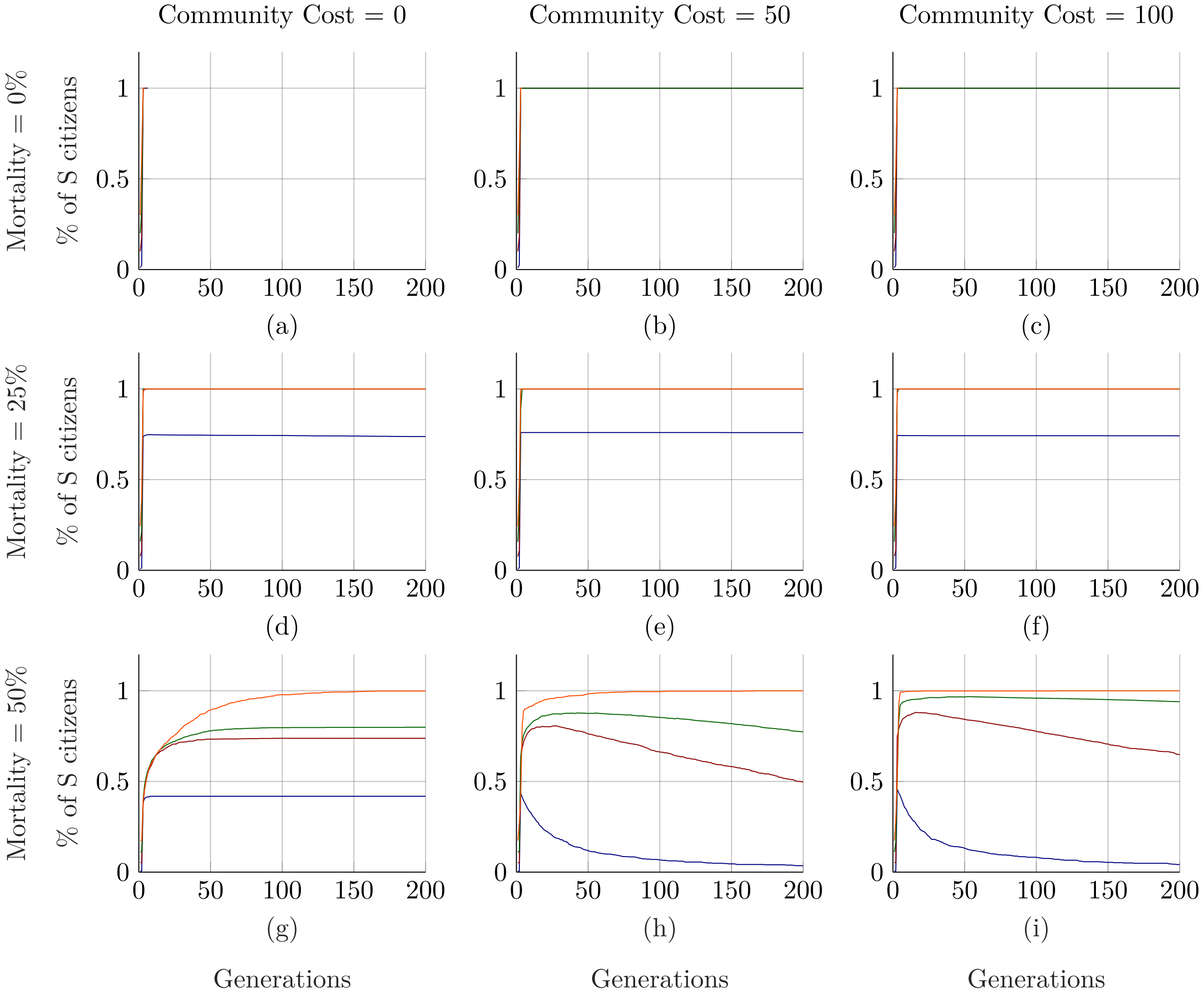
The first three Figures (6.1 to 6.3) illustrate the evolution of the population size over generations.

First, I analyse the evolution of the population in a scenario of abundance (Fig. 6.1), as the initial composition of the community, the mortality rate for selfish risk-seekers and the community cost are manipulated. Interestingly, when the population is not subjected to any cost and the mortality rate for S is equal to zero (Figure 6.1 (a)), it only survives for a short time, independent of the initial composition. This phenomenon is due to the fact that the environment can only sustain a fixed number of individuals (carrying capacity) and, in positive conditions, the population tends to grow rapidly, leading to overcrowding and the consequent extinction of the community itself. A similar phenomenon is present also in the other conditions, although some of the communities survive (Figure 6.1 (b-c)). When the mortality rate for selfish risk-seekers is increased, communities that started with a small percentage of S individuals outperform communities with an initially high percentage of S, having a larger size at the end of the 200 generations (Figure 6.1 (d-i)). When setting the mortality rate to 25%, the populations initialised with a percentage higher than 1% of S, performed similarly although with different equilibrium composition (Figure 6.4 (d-f)). Overall, when the environment provides a large amount of resources, having a low density of selfish risk-seeking individuals leads the community to reach a larger population size over time.

A different result is presented when the resources available are reduced (Figures 6.2 and 6.5). When the mortality is fixed at zero (Figure 6.2 (a-c)), the only communities that survive are entirely composed of selfish risk-seeking citizens, independent of the costs they have to pay. In such cases, the initial composition leads to different population sizes at equilibrium. Nevertheless, when the mortality increases to 25%, the communities initially composed of only 1% of S tend to reach a stable percentage of S (roughly 75%), obtaining larger population sizes compared to the other communities (Figure 6.2 (d-f)). Increasing the mortality rate to 50% leads to greater differentiation in the population size and composition over time (Figures 6.2, 6.5 (g-i)). If the community cost is set to zero, all communities reach a similar equilibrium size. However, when the community cost is increased, populations composed in majority of generous risk-averse individuals reach a stable size, while in all other scenarios the communities decline toward extinction.

Finally, when the environment offers resources that are close the individual's survival level, the beneficial aspect of selfish risk-seeking behaviours is unmistakably evident. As presented in Figure 6.6, the only communities that survive are entirely composed of selfish risk-seeking citizens. The only scenarios in which populations reach an equilibrium (as opposed to declining towards extinction) are those in which there is no mortality rate (Figure 6.3(a)-(c)), and those where the mortality rate is at maximum but no community cost is imposed (Figure 6.3(g)). In all these situations, the communities reach a stable configuration and the differences in sizes are determined by the initial conditions imposed on the density of selfish risk-seeking. Overall, when the community experiences a constant period of deprivation, selfish and risky behaviours support a stabilisation in the population size, avoiding its extinction.

Figure 6.4: Evolution of the population **composition** in an **abundant** fixed environment, $e_0 = 4$. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.
% of S citizens = 1: Population entirely composed of selfish risk-seekers,
% of S citizens = 0: Population entirely composed of generous risk-averse.



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

Figure 6.5: Evolution of the population **composition** in a **moderate** fixed environment, $e_0 = 2$. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.
% of S citizens = 1: Population entirely composed of selfish risk-seekers,
% of S citizens = 0: Population entirely composed of generous risk-averse.

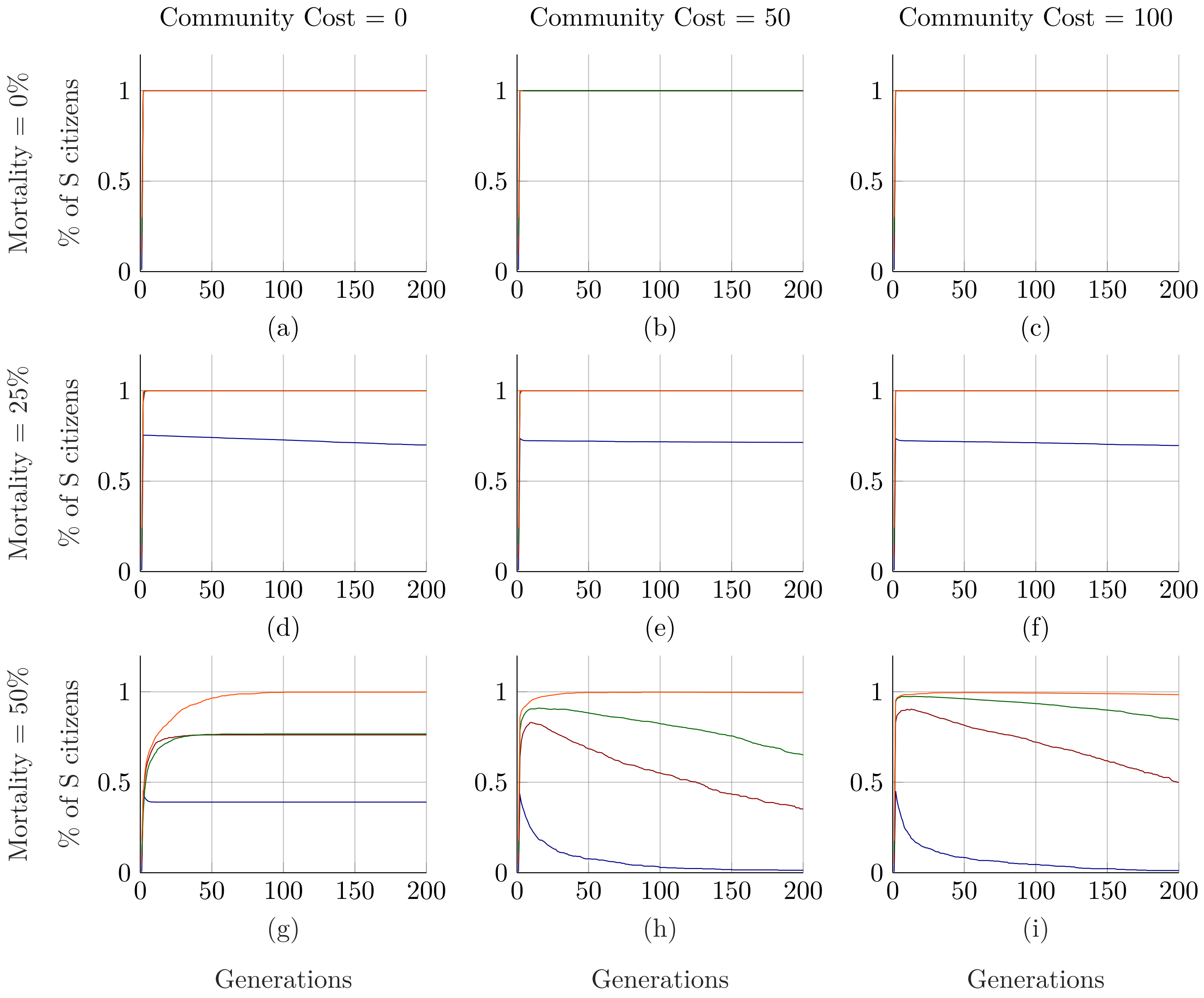
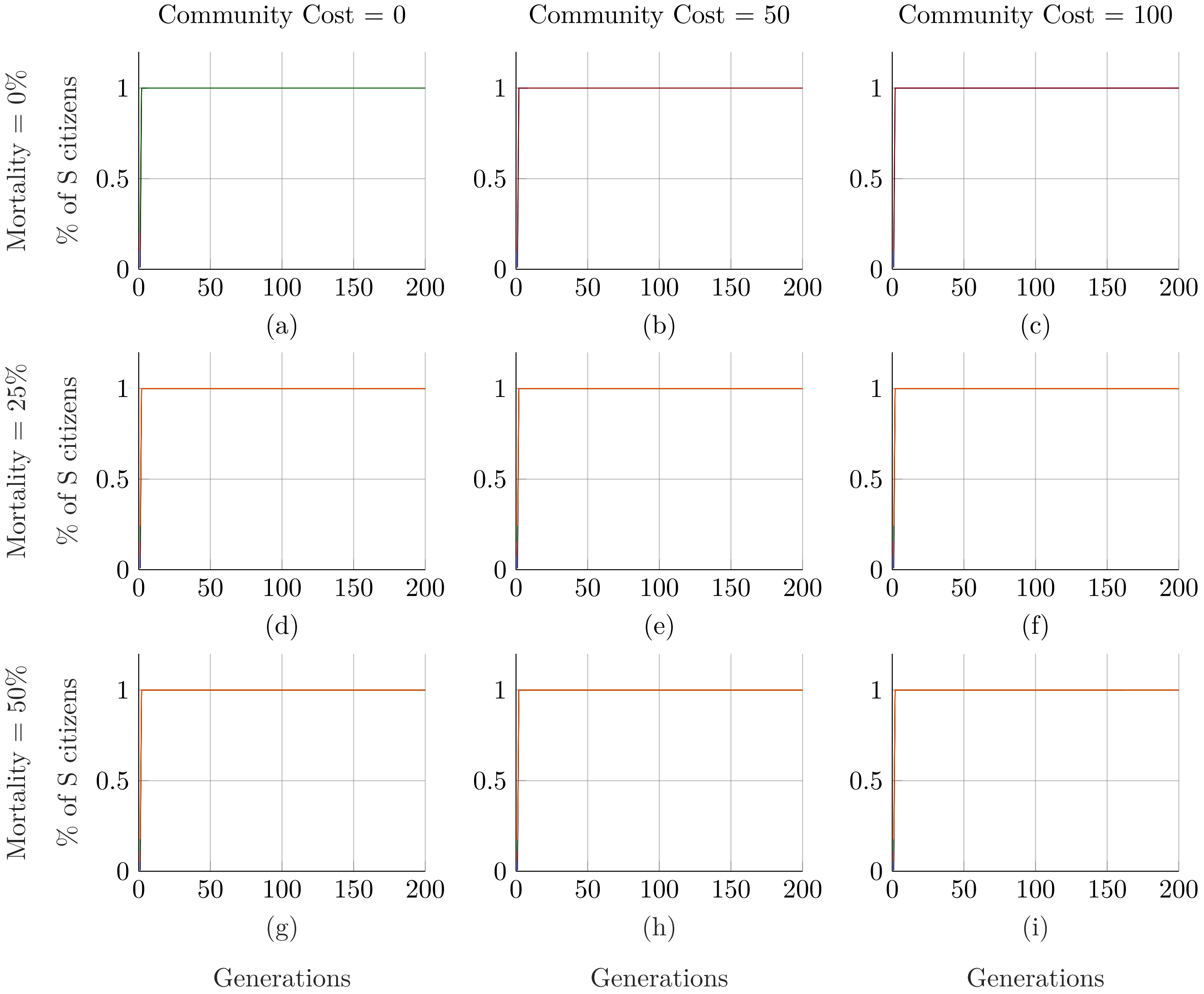


Figure 6.6: Evolution of the population **composition** in a **scarce** fixed environment, $e_0 = 1.2$. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.
% of S citizens = 1: Population entirely composed of selfish risk-seekers,
% of S citizens = 0: Population entirely composed of generous risk-averse.

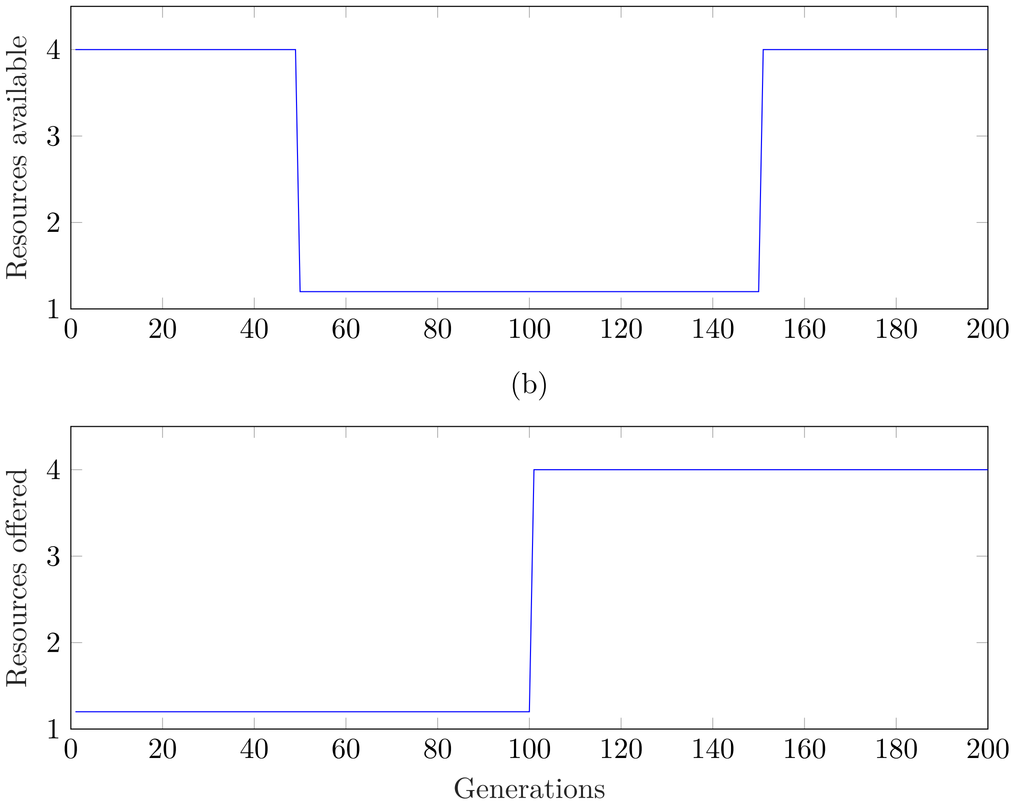


6.2.2 Variable Environment

A natural extension of the fixed environmental scenario is produced by an alternation of periods of scarcity and abundance in the environmental offer.

To model this, I implemented variable environments that switch between stages in which the environment offers a large amount of resources (e=4 or e=2), and stages where there are not enough supplies to survive (e=1.2), as shown in Figure 6.7.

Figure 6.7: Example of variable environmental offer.



(a)

(b)

I considered populations initialised with different densities of selfish risk-seekers as in the previous section. Results report the evolution of populations when moving from a negative environment ($e = 1.2$) to moderate or positive environments ($e = 2$ or $e = 4$), at different times of the evolution.

Figure 6.8: Evolution of the population **size** in a variable environment, starting with a **negative** $e = 1.2$ environmental condition and switching to a **positive** $e = 4$ environmental offer. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.

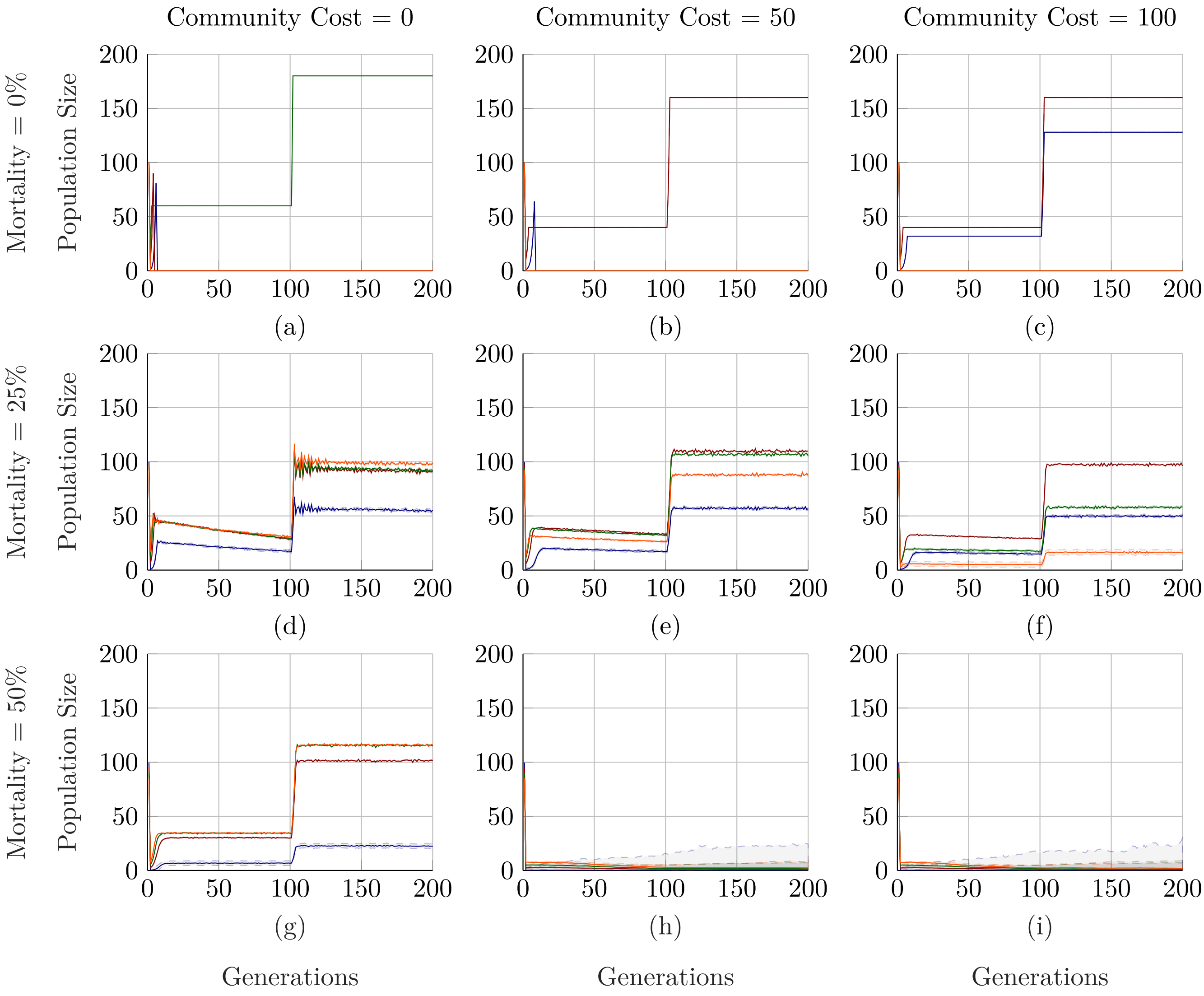


Figure 6.9: Evolution of the population **composition** in a variable environment, starting with a **negative** $e = 1.2$ environmental condition and switching to a **positive** $e = 4$ environmental offer. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.
% of S citizens = 1: Population entirely composed of selfish risk-seekers,
% of S citizens = 0: Population entirely composed of generous risk-averse.

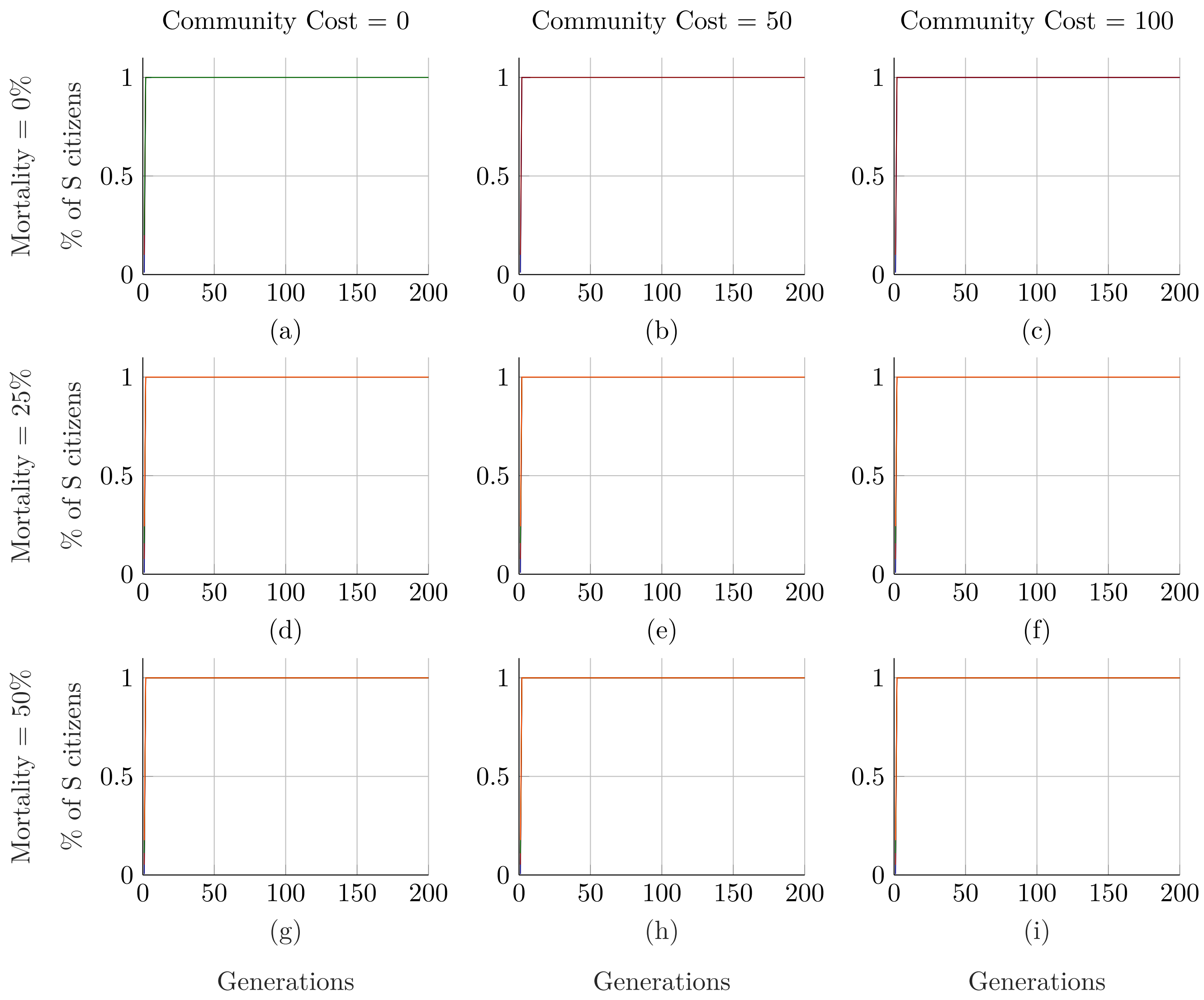


Figure 6.10: Evolution of the population **size** in a variable environment, starting with a **negative** $e = 1.2$ environmental condition and switching to a **moderate** $e = 2$ environmental offer. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.

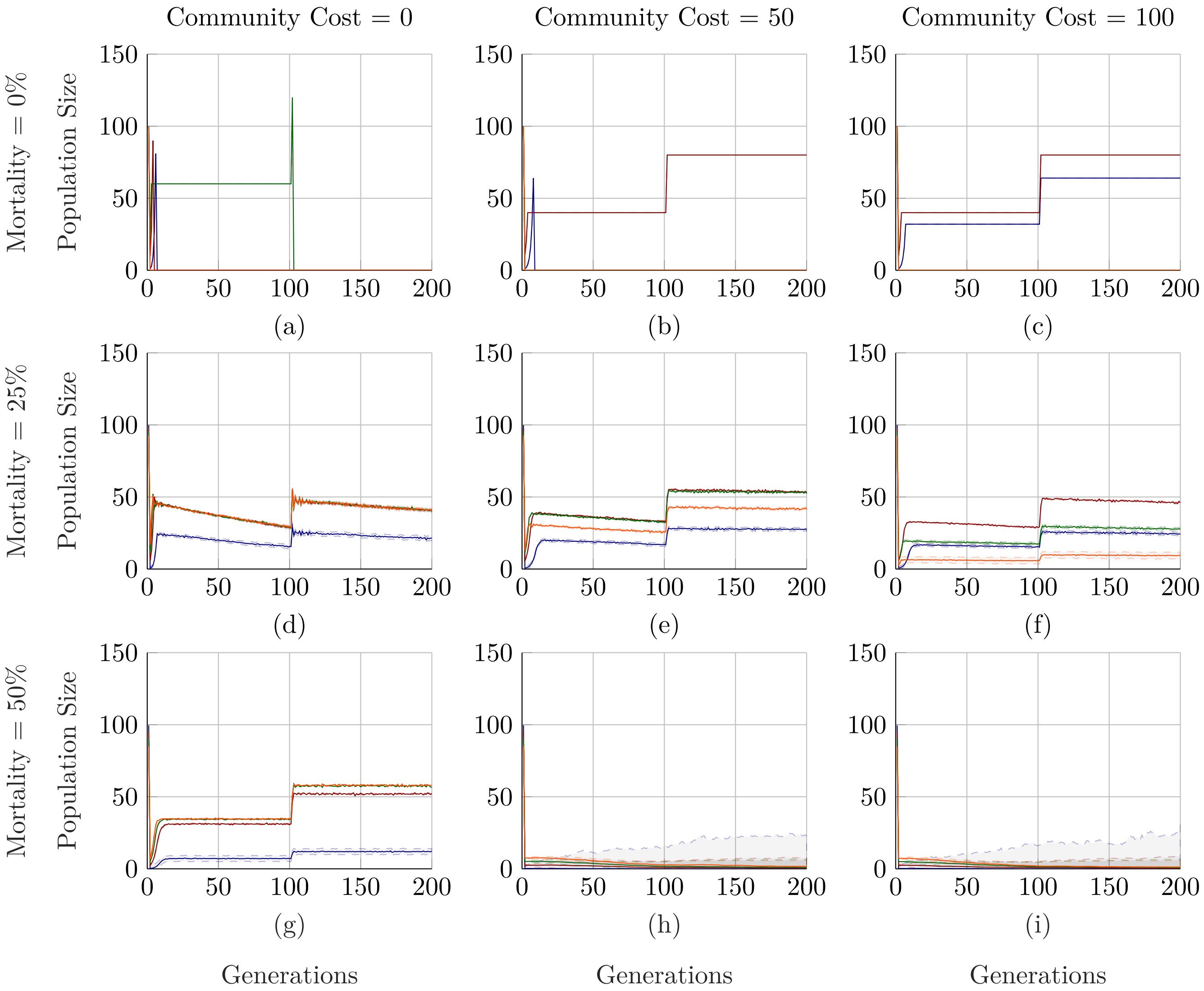
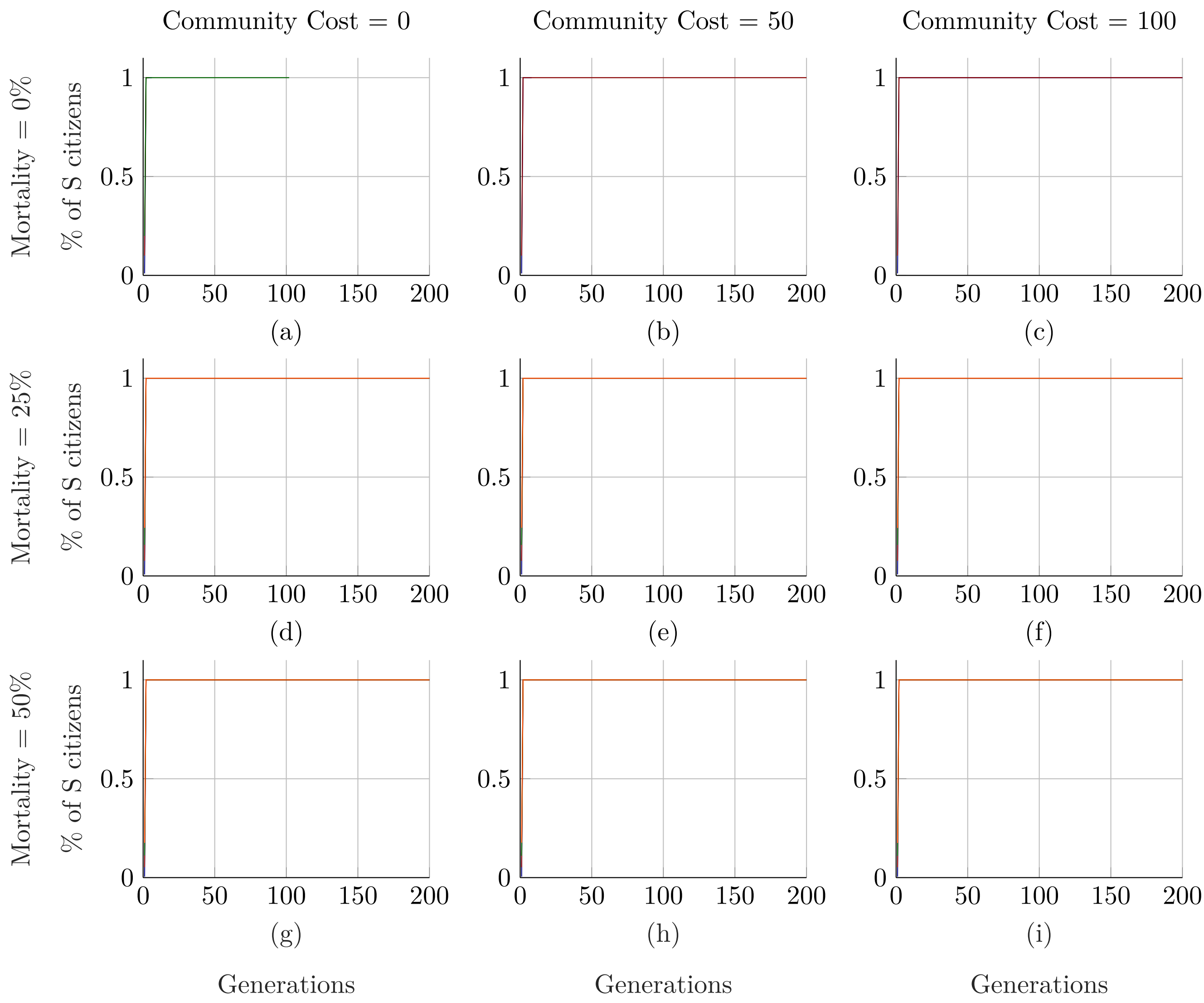


Figure 6.11: Evolution of the population **composition** in a variable environment, starting with a **negative** $e = 1.2$ environmental condition and switching to a **moderate** $e = 2$ environmental offer. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.
% of S citizens = 1: Population entirely composed of selfish risk-seekers,
% of S citizens = 0: Population entirely composed of generous risk-averse.



When the population experiences a harsh environment at first, the only surviving populations are entirely composed of selfish risk-seekers, as expected from the results reported for the fixed negative environment. As Figures 6.8 and 6.10 show, starting with high percentages of S citizens leads to larger communities only when no community cost is introduced (Figures 6.8, 6.10(d),(g)). In the other scenarios, having roughly 10 or 20% of selfish risk-seekers allows the community to grow more than conditions with a higher (30%) or a lower (1%) percentage of S individuals (Figures 6.8, 6.10 (b),(c),(e),(f)). In Figure 6.10, the overcrowding phenomenon previously presented in the fixed environment is presented again when no mortality nor community costs are introduced.

When no mortality rate is selected for risk-seekers, some populations struggle to survive from the very beginning, consistently with previous results (Figures 6.8, 6.10 (a-c)). Furthermore, when both the mortality rate and the community cost are high, the population never recovers from the initial harsh situation (Figures 6.8, 6.10 (h-i)). The grey shadows are due to the different time at which the various realisations get extinct, which lead to a higher variation across realisations.

The difference in the environmental offer after the critical period (either 2 or 4 units) did not highlight a relevant evolution discrepancy of the population size in the various scenarios. Populations reach a higher equilibrium size when they receive more resources, but the patterns remain constant across the two conditions.

Different evolutionary dynamics are observable when the critical period follows an initial state of abundance (e=4) (Figure 6.12). As expected from previous results, in the first hundred generations the population behaves as in the fixed benign environment scenarios previously analysed. However, when the environmental resources drop, only a few populations manage to survive: those initially composed of 30% of selfish risk-seekers, and only in those settings where the mortality rate is set at its maximum (Figure 6.12 (g-i)). As presented in Figure 6.13, when the population size drops as the critical period occurs, the only surviving individuals are selfish risk-seekers.

A similar pattern is also presented in Figure 6.14 although having an initial lower environmental offer (e=2) allows more communities to survive when the crisis occurs. This is due to the fact that the larger is the population during the flourishing time, the less resources each individual will have in the moment of shortage. Nevertheless, in both settings (initial environment = 2 or 4) the only individuals who survive in the harsh condition exhibit selfish risk-seeking behaviours, as reported in Figures 6.13, 6.15.

Figure 6.12: Evolution of the population **size** in a variable environment, switching between a **positive** $e = 4$ and a **negative** $e = 1.2$ environmental offer. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.

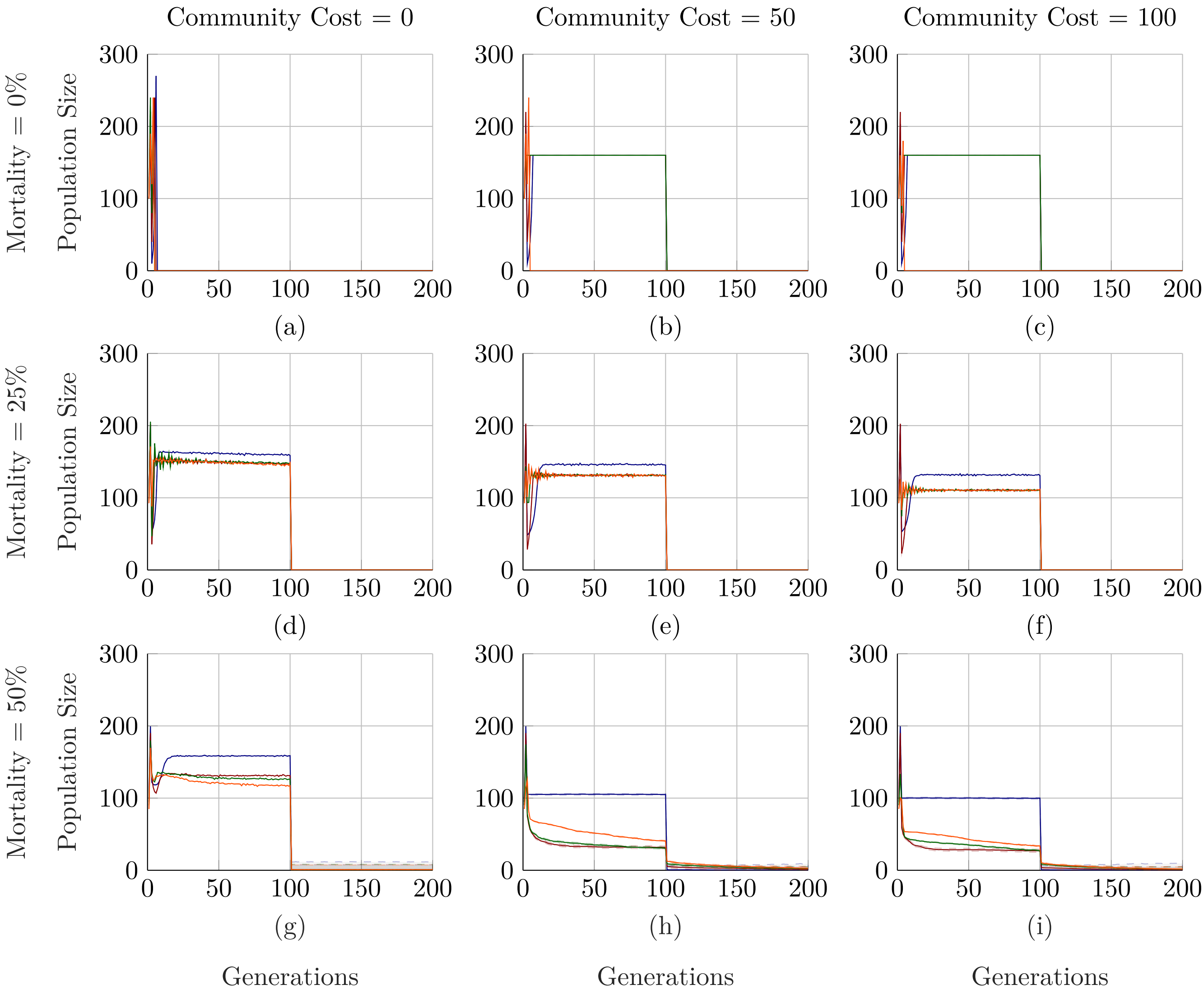


Figure 6.13: Evolution of the population **composition** in a variable environment, switching between a **positive** $e = 4$ and a **negative** $e = 1.2$ environmental offer. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.
% of S citizens = 1: Population entirely composed of selfish risk-seekers,
% of S citizens = 0: Population entirely composed of generous risk-averse.

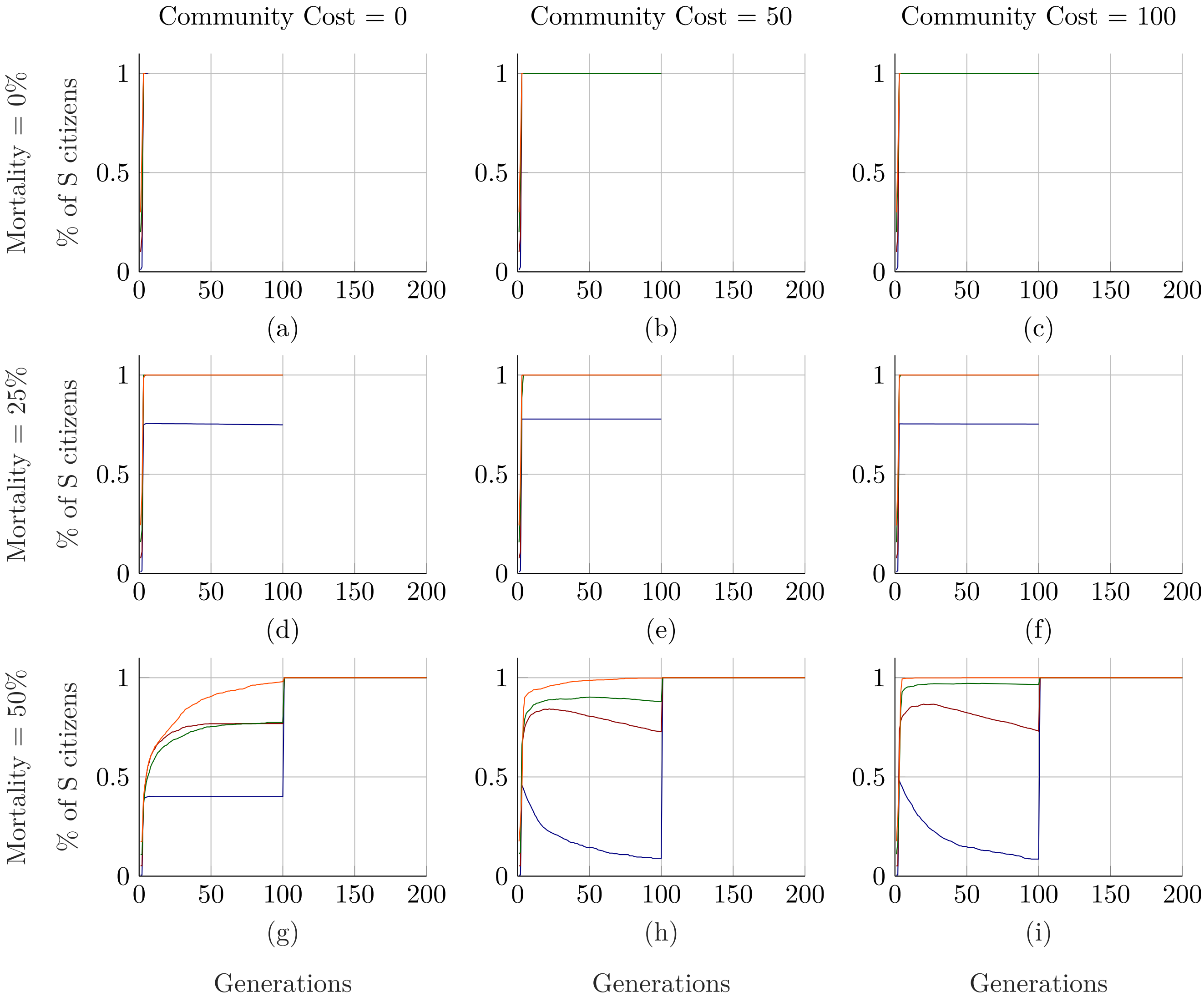


Figure 6.14: Evolution of the population **size** in a variable environment, switching between a **moderate** $e = 2$ and a **negative** $e = 1.2$ environmental offer. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.

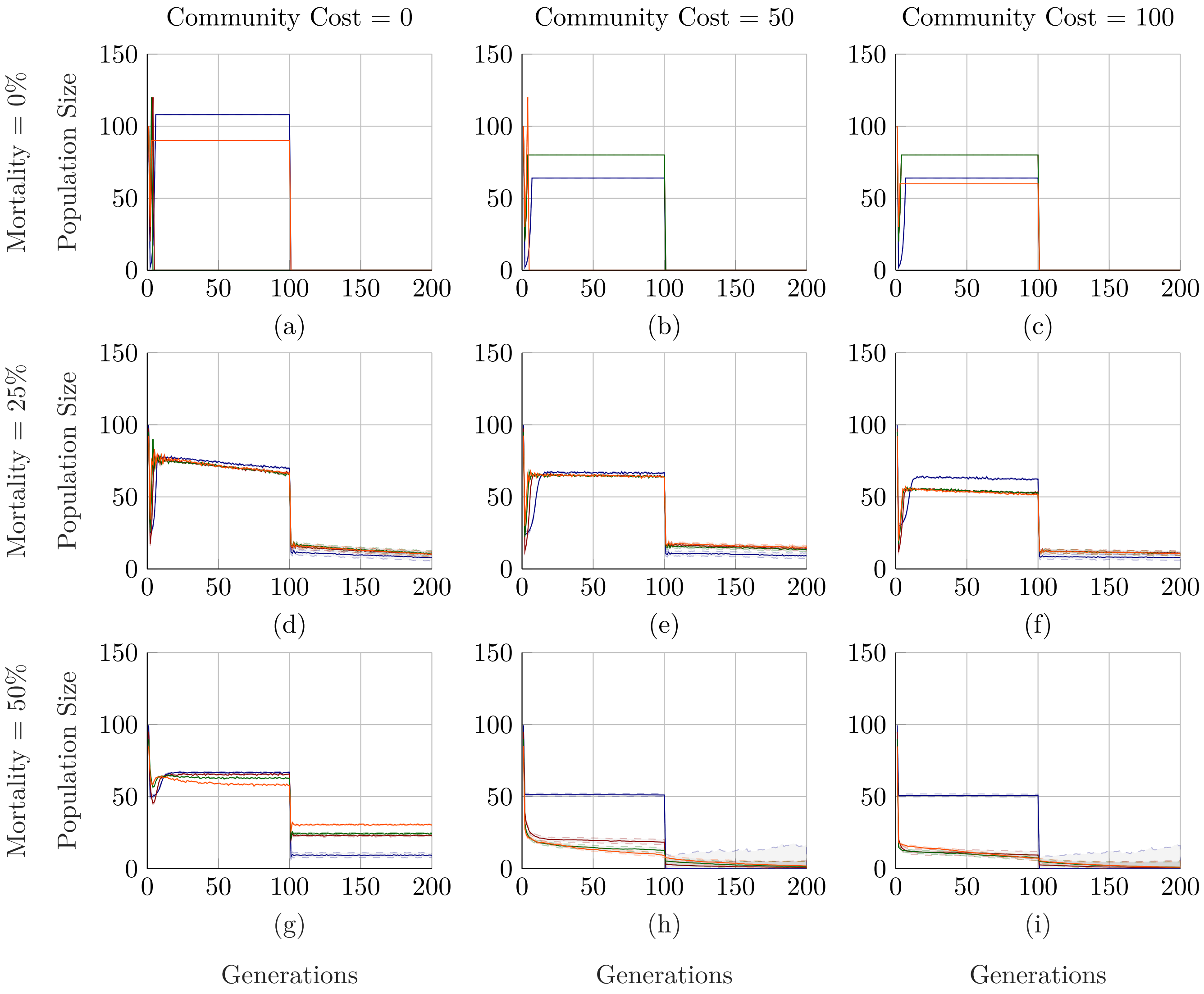
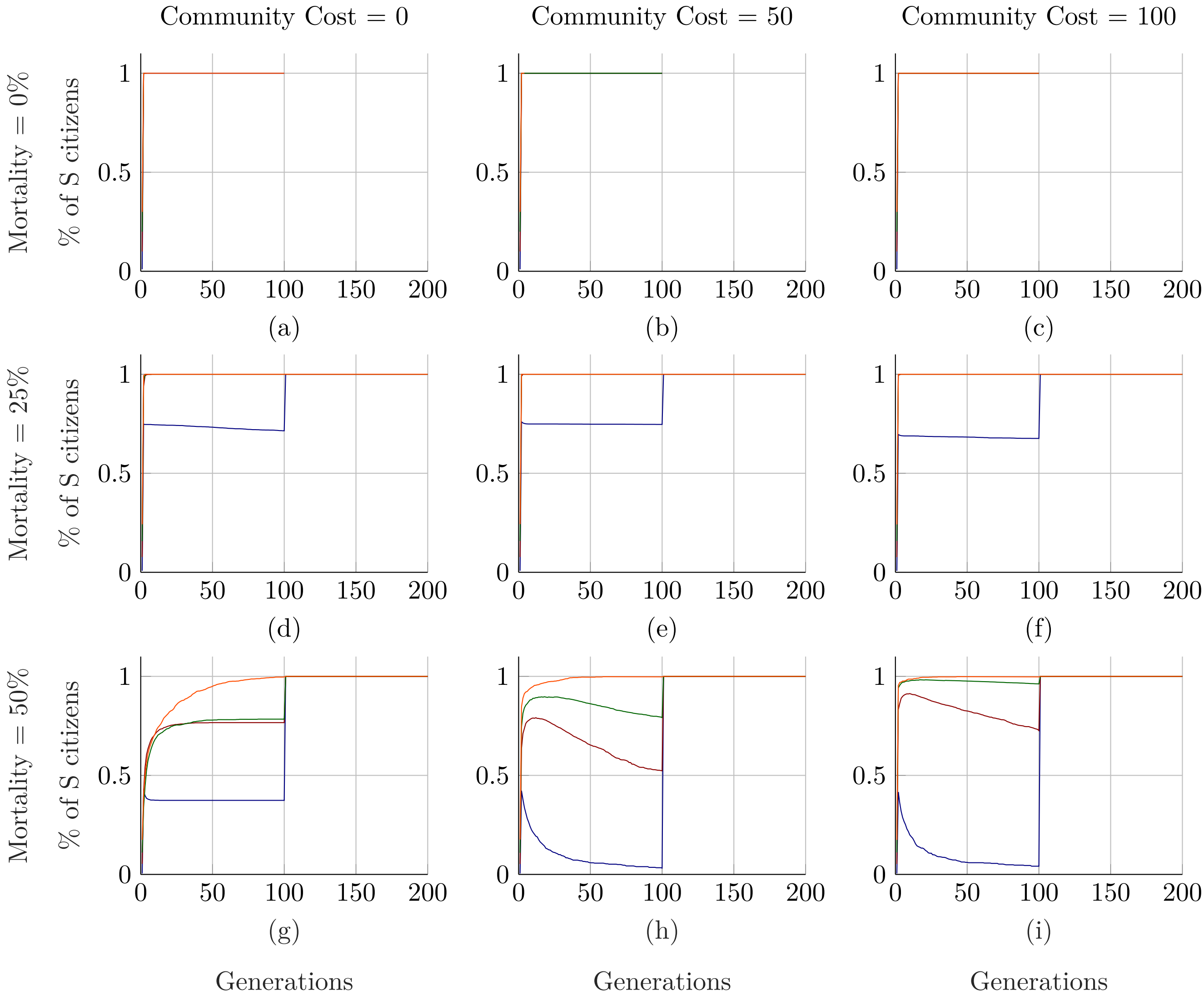

(a) (b) (c) (d) (e) (f) (g) (h) (i)

Figure 6.15: Evolution of the population **composition** in a variable environment, switching between a **moderate** $e = 2$ and a **negative** $e = 1.2$ environmental offer. Results show how the evolution differs when changing the percentage of selfish risk-seekers, their mortality rate, and the community cost λ.
Yellow lines: $S_0 = 30\%$,
Green lines: $S_0 = 20\%$,
Red lines: $S_0 = 10\%$,
Blue lines: $S_0 = 1\%$.
% of S citizens = 1: Population entirely composed of selfish risk-seekers,
% of S citizens = 0: Population entirely composed of generous risk-averse.



6.3 Discussion

This simplified version of the model aims to present the basic dynamics of the population evolution in response to various environmental offers and different parameter values (such as mortality rate, community cost and initial percentage of selfish risk-seeker citizens).

These results clearly show the advantages and disadvantages for both generous risk-averse and selfish risk-seeking individuals. Showing a risk-seeking attitude in a condition of deprivation allows individuals to survive when others perish. On the other hand, when the environmental conditions are benevolent, communities evolve to a larger equilibrium size when having lower percentages of generous risk-averse individuals.

Another aspect that arises from this first basic model is the importance of the environmental resources available: offers below 1.2 do not allow any population to survive, while environmental offers over 4 can lead to overpopulation and extinction of the population in the early stages. Moreover, I observed how the difference between environmental offers (either 0.8 or 2.8 units) affects the survival of some communities, but does not change the evolutionary pattern of the population, once it has survived the initial obstacle.

Lastly, the importance of the initial conditions for a community is clear: the initial composition of the population (percentage of selfish risk-seeking individuals) leads to very different population evolution, not only with respect to the final population size but also its equilibrium composition.

The next step of the model is to include mutation in reproduction percentages between the two phenotypes to observe whether the population will stabilise around an equilibrium, especially with respect to the final population composition, that is independent of the initial composition.

Chapter 7 Model with mutation

7.1 Overview

The previous chapter presented a simplified version of the model which fixed the reproduction probabilities of each individual. In this chapter, I incorporate the mutation phase first presented in Figure 5.1: at each generation, the probability of inheriting the parent's phenotype is controlled by a reproduction probability which mutates and is then passed on to the offspring.

Results represent the evolution of a population with an initial 10% of selfish risk-seekers. In contrast to the previous chapter, the initial population composition was not found to have an effect on the evolutionary dynamics. Furthermore, in chapter 6, there was no difference in the evolution patterns between the moderate and benign environment or between different levels of benign environment (e=*2* or e=*4*). Thus, in this chapter results are reported only for the two extreme environmental cases: negative (e=*1.2*) and abundant (e=*4*) environment. The parameters describing the model and their values are summarised in Table 7.1.

Table 7.1: Overview of the parameters values for the models with mutation.

Parameters	Initialisation value
N_0	250
T	10^3
I	10^3
S_0	10%
e_0	1.2 or 4
h_S, h_G	80%, 50%
c_S, c_G	20%, 100%
λ	$\lambda \in \{0\%, 50\%, 100\%\}$
m_p	$m_G = 0\%$; $m_S \in \{0\%, 25\%, 50\%\}$

The model was run over 10^3 generations (an increased time span compared to the previous 200 generations) to provide enough time for the reproduction rates to reach equilibrium. All results report the mean over 10^3 independent realisations to obtain robust results.

In this chapter, I present two models with the same reproduction mechanism, but while in the first case I consider a single population, I look at two initial separate populations in the second case. These models are presented hereafter in two separate sections.

7.1.1 Single population

Individuals are initialised as either generous or selfish. They both have a likelihood of reproducing a selfish offspring which evolves over time. At the same time, the phenotype of the parent has an effect on the reproduction rate which is expressed by γ or ω. Thus, in this model I introduced ϕ as the population baseline likelihood of reproducing a selfish individual, while γ/ω embody the effect of having a selfish/generous parent on the reproduction probabilities:

$$\begin{aligned} \varphi_{G,G} &= 1 - \phi + \omega, \\ \varphi_{G,S} &= \phi - \omega, \\ \varphi_{S,S} &= \phi + \gamma, \\ \varphi_{S,G} &= 1 - \phi - \gamma; \\ \\ 0 \leq \omega &\leq \phi, \\ 0 \leq \gamma &\leq 1 - \phi. \end{aligned}$$

That is, a selfish risk seeker will reproduce a selfish offspring with probability $\phi + \gamma$ and a generous risk-averse individual will reproduce a generous offspring with probability $1 - \phi + \omega$. The parameter ϕ is initialised accordingly to the initial percentage of selfish individuals in the community (i.e. $S_0 = 10\%$), while both γ and ω are set equal to 0.01. All three parameters are then evolved over generations. Mutations $\eta_{\phi,t}$ are drawn from a $\mathcal{N}(0, 0.1)$, for consistency with the previous chapter. The mutations $\eta_{\gamma,t}$ and $\eta_{\omega,t}$ for the phenotype parameters γ and ω are drawn from a $\mathcal{N}(0, 0.01)$. The parameters ω, γ are allowed to evolve in the model as there could be aspects that evolve over time, such as the offspring's sensitivity to parenting over generations. Thus, the reproduction probabilities are mutates at each generation as follow:

$$
\begin{aligned}
\varphi_{G,G,t} &= 1 - \phi_t + \omega_t, \\
\varphi_{G,S,t} &= \phi_t - \omega_t, \\
\varphi_{S,S,t} &= \phi_t + \gamma_t, \\
\varphi_{S,G,t} &= 1 - \phi_t - \gamma_t;
\end{aligned}
$$

$$
\begin{aligned}
\phi_t &= \phi_{t-1} + \eta_{\phi,t}, \\
\omega_t &= \omega_{t-1} + \eta_{\omega,t}, \\
\gamma_t &= \gamma_{t-1} + \eta_{\gamma,t}.
\end{aligned}
$$

The reproduction parameters are initialised as presented in Table 8.1. It is important to note that results show that different values of the mutation variances $\sigma^2_\phi, \sigma^2_\omega, \sigma^2_\gamma$ do not influence the dynamics of the population, they simply speed up or slow down the achievement of the equilibrium state. This was tested by allowing the mutation variances to vary between 0.01 and 0.5.

Table 7.2: Initial values for the reproduction parameters.

Parameters	Initial values
ϕ=S_0	0.1
γ, ω	0.01
$\sigma^2_\gamma = \sigma^2_\omega$	0.01
σ^2_ϕ	0.1

7.1.2 Two initial sub-populations

In the second model, the community is initialised as composed of two separate sub-populations, one entirely composed of selfish risk-seekers and the other entirely composed of generous risk-averse citizens. The reproduction mechanism is similar to the one presented above, although the initial values for the two populations are different and they are not evolved separately as in the previous chapter. In this section, indeed, the parameters $\varphi_{G,G}, \varphi_{S,S}$ are evolved instead of the three components ϕ, ω, γ. Nevertheless, $\varphi_{G,G}, \varphi_{S,S}$ can still be interpreted as the combination of ϕ, ω, γ, where they evolve simultaneously at each generation. The goal is to investigate whether one of the two populations can invade and overcome the other. Table 7.3 reports the initial values for the two sub-populations reproduction probabilities.

Table 7.3: Initial reproduction rates for the two subpopulations.

Initial phenotype	$\varphi_{G,G,0}$	$\varphi_{S,S,0}$
Selfish Risk-seeking	0.90	0.2
Generous Risk-Averse	0.99	0.02

In other words, individuals initialised as generous risk-averse have a 99% probability of passing on their own phenotype and a 1% chance of reproducing a selfish risk-averse individual. Any selfish offspring that they reproduce have a 2% chance of producing a selfish risk-seeking offspring themselves and a 98% probability of having generous risk-averse offspring. In contrast, individuals initialised as selfish have a 20% chance of passing on their own phenotype and a 80% probability of reproducing generous offspring. When their offspring exhibit a generous risk-averse behaviour, their offspring have a 90% probability of reproducing generous offspring of their own and a 10% chance that the offspring will exhibit selfish risk-seeking behaviours. The two populations are merged into a single population and their evolution is monitored over generations. The reproduction rates are mutated at each generation, and mutation coefficients are drawn from a normal distribution $\eta_t \sim \mathcal{N}(0, 0.1)$:

$$\begin{aligned}\varphi_{G,G,t} &= \varphi_{G,G,t-1} + \eta_{\varphi_G,t}\\ \varphi_{S,S,t} &= \varphi_{S,S,t-1} + \eta_{\varphi_S,t}.\end{aligned}$$

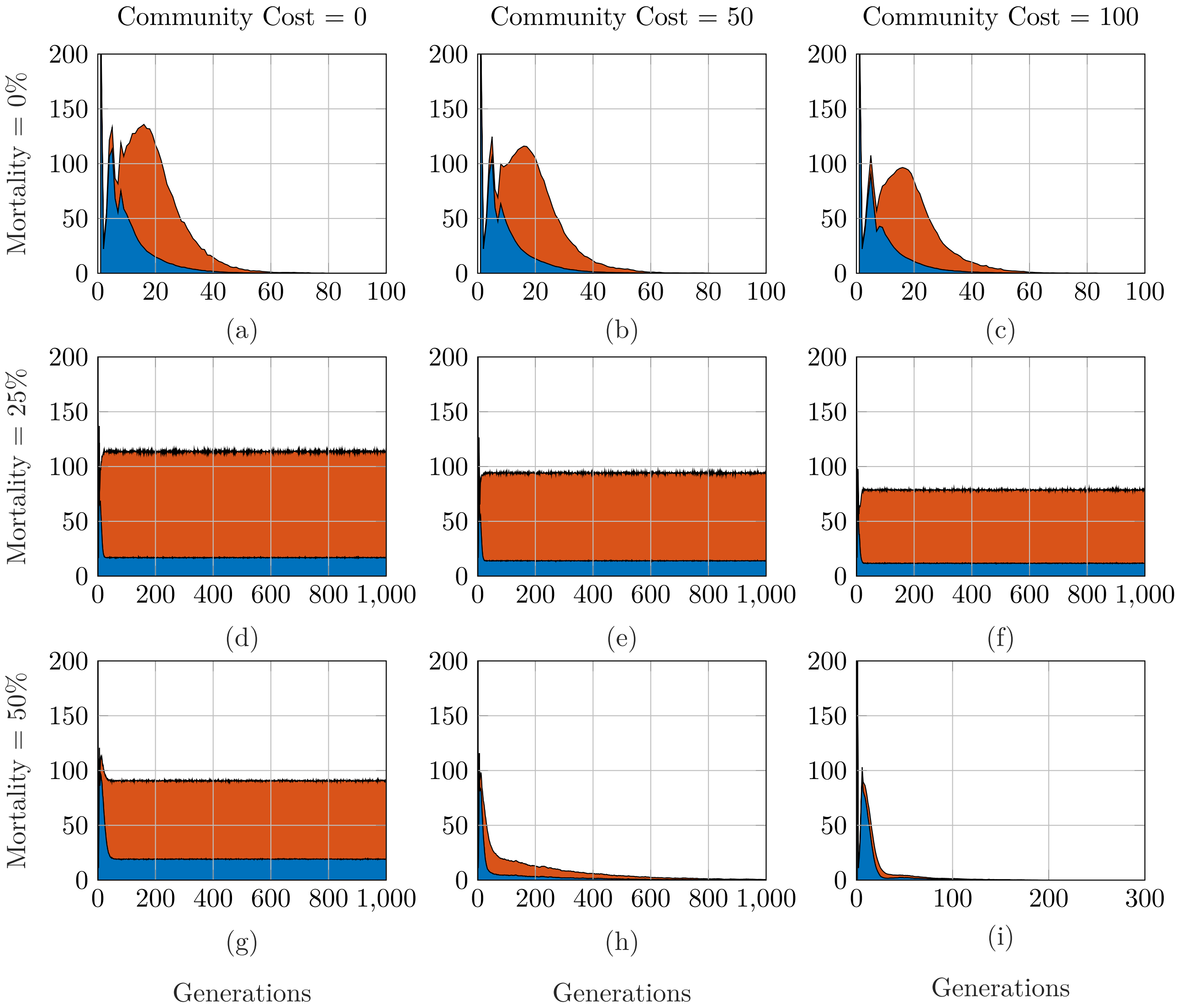
7.2 Results

7.2.1 Single population

Firstly, I present the results where the community is initialised as composed of a one single population. The results reported here are for γ and ω different from zero. Figures 8.1 and 8.2 show the evolution of the population and its composition in the different scenarios, when the environment is harsh and when it is benevolent. The first thing to notice is that, although the overall level of the population varies in the two environmental scenarios, the evolutionary patterns are similar, suggesting that the difference in the availability of resources does not affect the community dynamics. The parameter that most strongly affects the evolution is the rate at which selfish risk-seekers perish during the harvesting phase (mortality rate). When no mortality rate is introduced, the population grows without limitations and exceeds the carrying capacity of the environment, leading to the extinction of the population in roughly 100 generations. By introducing a small mortality risk for risk-seekers ($m_S = 25\%$), the population survives in both a benign and a harsh environment, reaching equilibrium. Selfish risk-seeking citizens comprise the majority of the community, leaving little space for generous risk-averse individuals. In this setting ($m_S = 25\%$), the effect of the community cost on the evolution dynamics is also visible: the larger the cost the community has to pay to sustain selfish individuals, the fewer citizens can be sustained at equilibrium. This is even more evident when the mortality rate is increased to 50%. In this case, the population survives and reaches equilibrium only if no community cost needs to be paid. In this case (Figures 8.1 (g),8.2 (g)), a larger proportion of generous citizens is present, although the majority is still composed of selfish individuals. When the community cost is set to 50 or 100% (Figures 8.1 (h,i), 8.2 (h,i)), the population rapidly decreases toward extinction.

The Figure 8.3 shows the evolution of $\varphi_{G,G}$ and $\varphi_{S,S}$ over generations, as composed by both ϕ and ω,γ respectively, while their separate evolution is presented in figure 8.4. The evolution of ϕ (i.e. the population likelihood to reproduce selfish offspring) reaches the same equilibrium independent of the scenario considered. In the first row, only the first 60 generations are shown as the population perishes after that. Nonetheless, the parameter ϕ has already reached the stable equilibrium ($\phi \sim 88\%$) that is present in most of the other scenarios. In the situation where mortality risk is at its maximum and the community cost is equal to 50%, the equilibrium is approached but it is not stable (Figure 8.3 (h)), while when the community cost is increased ($\lambda = 100$) the genetic component oscillates around the lower value of $\phi \sim 75\%$ (Figure 8.3 (i)). This is due to the noise in the evolution of the population in the most critical conditions, which lead the population to get extinct in several of the independent realisations. As γ remains constant across zero in all scenarios, the probability for selfish individuals to reproduce selfish offspring is controlled by the likelihood component ϕ. Conversely, the reproduction probability for generous citizens evolves over time differently according to the exogenous conditions implemented. This difference in the evolution pattern is controlled by the parameter ω. As visible in Figure 8.4, ω evolves over generations and this evolution is more or less rapid according to the mortality rate. When there is no mortality, ω increases very slowly, leading to a slight change of $\varphi_{G,G}$ from the purely likelihood parameter ϕ. However, when the mortality rate is set to either 25 or 50%, generous citizens become more likely to reproduce generous offspring over time (apart from when $m_S = 50\%$ and $\lambda = 100$, Figure 8.4 (i)). Thus, the probability for generous citizens of passing on their own phenotype can vary from 20% to 40%. It is also possible to notice that, contrary to the evolution of $\varphi_{S,S}$, $\varphi_{G,G}$, ω does not reach an equilibrium but it steadily increases over time, suggesting that if the population could evolve over more generations, the parameter would keep increasing (apart from the case in which no mortality rate is introduced).

Figure 7.1: Evolution of the population over generations in a **scarce** fixed environment, $e_0 = 1.2$. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange area: Selfish risk-seeking individuals,
Blue area: Generous risk-averse individuals.

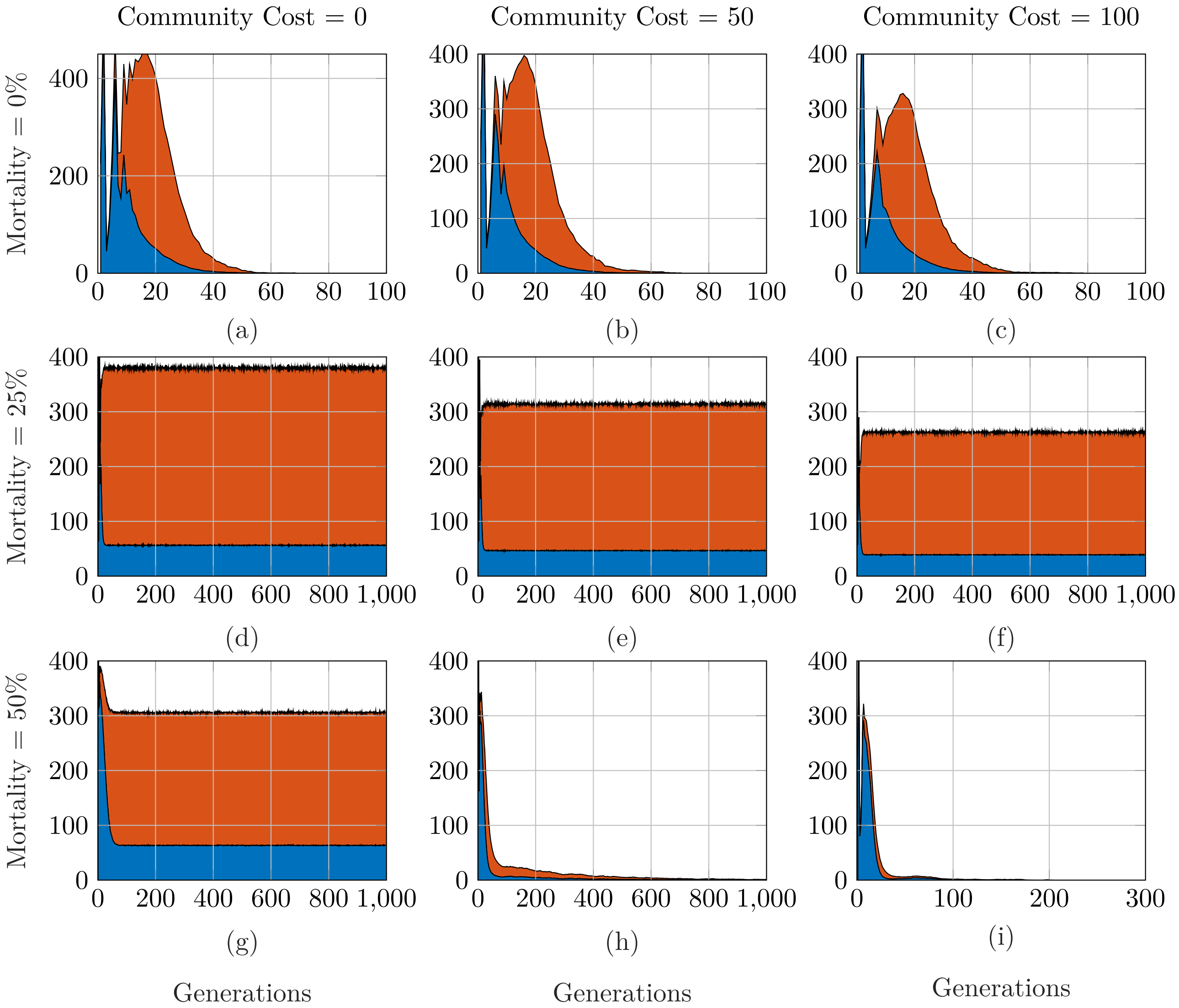


(a) (b) (c)

(d) (e) (f)

(g) (h) (i)

Figure 7.2: Evolution of the population over generations in an **abundant** fixed environment, $e_0 = 4$. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange area: Selfish risk-seeking individuals,
Blue area: Generous risk-averse individuals.



(a) (b) (c)

(d) (e) (f)

(g) (h) (i)

Figure 7.3: Evolution of the combined reproduction rates $\varphi_{S,S}, \varphi_{G,G}$ over generations. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange line: $\varphi_{S,S}$
Blue line: $\varphi_{G,G}$
$\varphi_{S,S}$=1 (/0) means that an S individual has a 100 (/0)% chance of reproducing an S offspring, $\varphi_{G,G}$=1 (/0) means that a G individual has a 100 (/0)% chance of reproducing a G offspring.

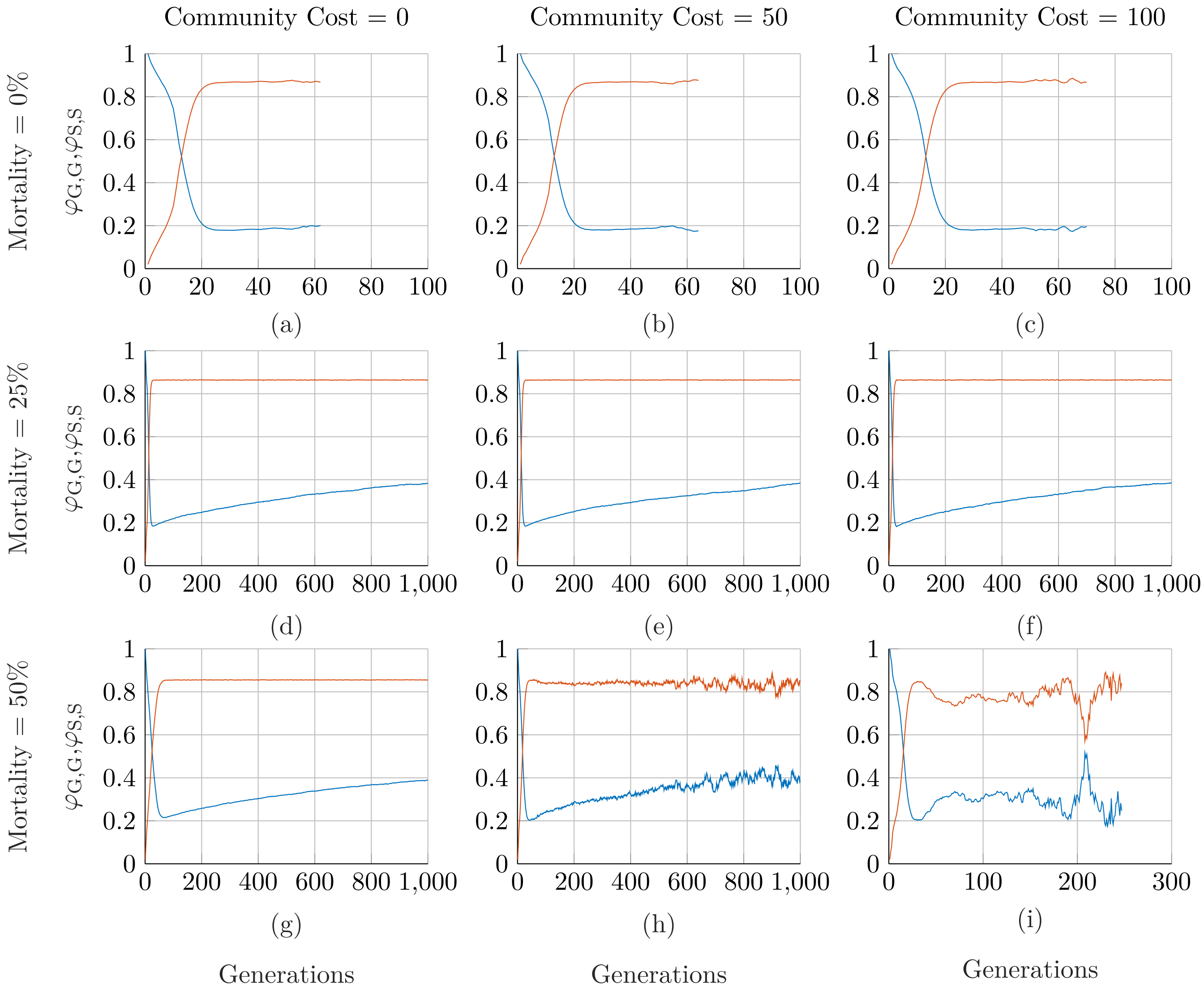


Figure 7.4: Evolution of the separate parameters regulating the reproduction mechanism parameters ω, γ and ϕ over generations. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.

Red line: ω

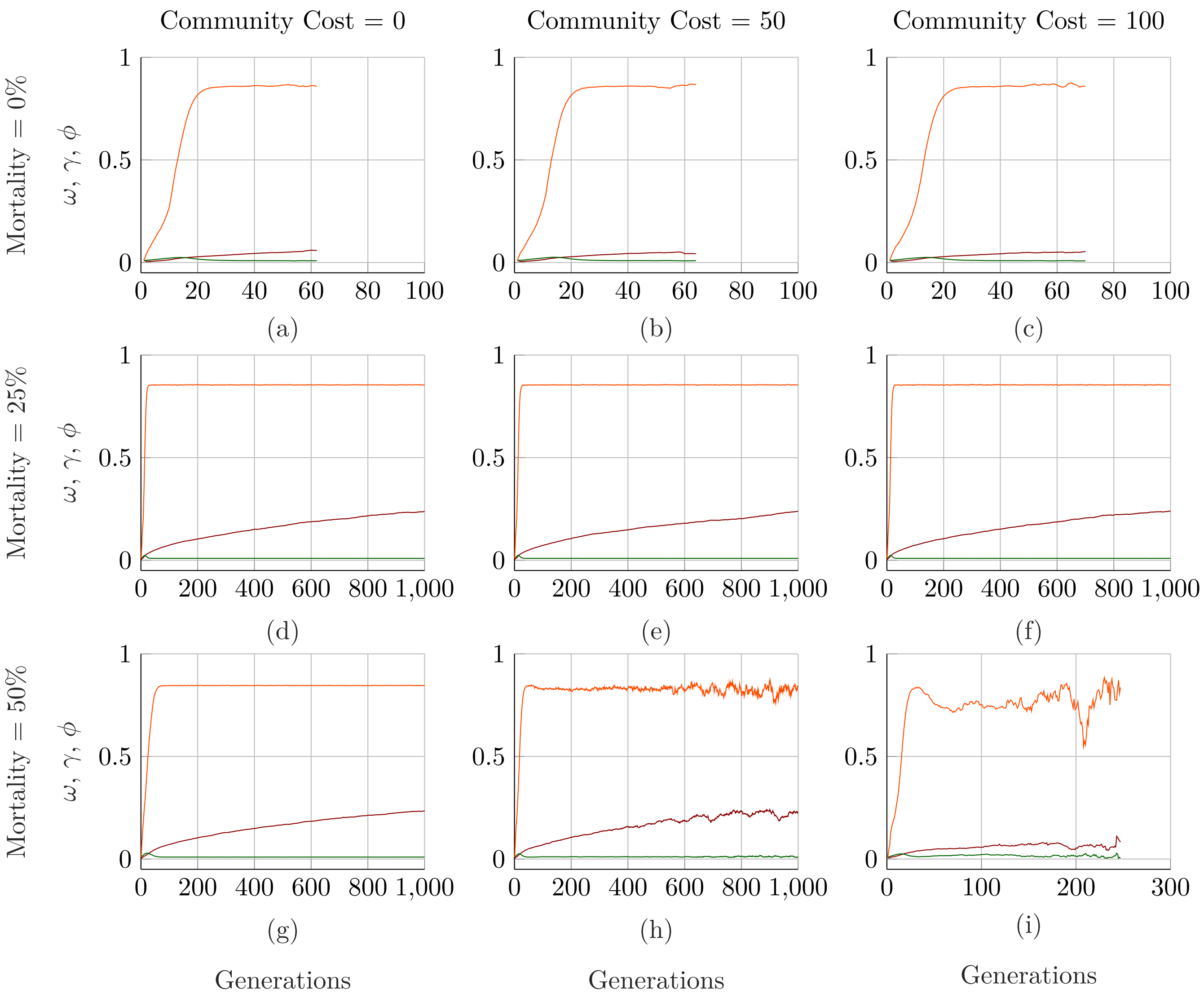
Green line: γ

Orange line: ϕ

ω, contribution of G parent to the probability of reproducing G offspring,

γ, contribution of S parent to the probability of reproducing S offspring,

ϕ, probability that an individual will reproduce a S offspring, independent of his own phenotype.



(a) (b) (c)

(d) (e) (f)

(g) (h) (i)

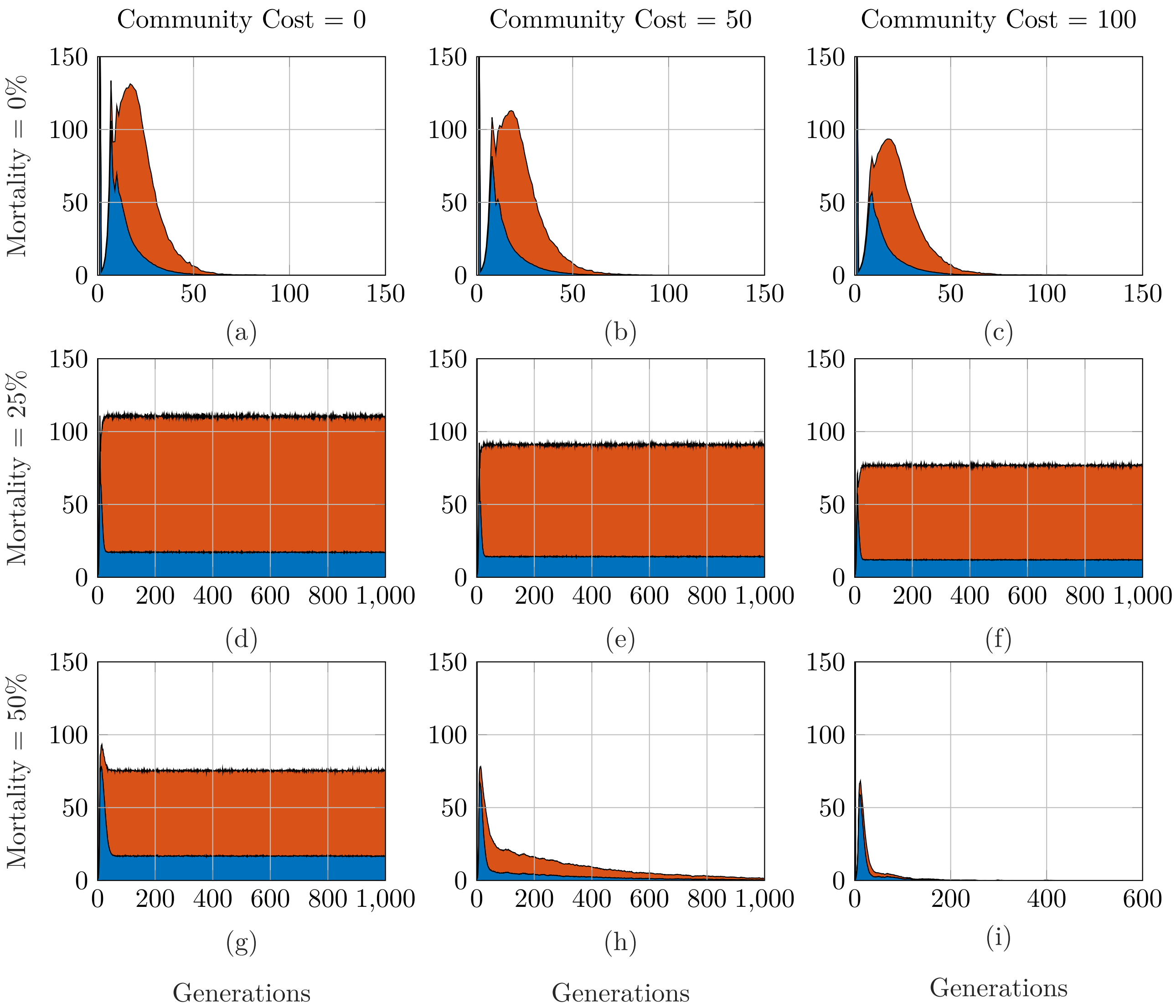
7.2.2 Two initial sub-populations

Secondly, I describe the evolution of the population initially composed of two separate sub-populations. Results show the evolution of the entire population and of the two initial sub-populations over generations, when altering the mortality rate and the community cost parameters, as well as the environmental conditions. The evolution of the population over generations is consistent with what was presented in the previous section (Figures 8.1, 8.2): selfish risk-seeking individuals comprise the majority of the population, when it does not collapse toward zero (figures 7.5, 7.6). Moreover, the environmental conditions do not impact the dynamics of the evolution but only the different population size at equilibrium.

Figures 7.7 and 7.8 show the evolution of the two initial sub-populations. In contrast to what was observed previously for the total population evolution, the environmental offer plays a role in the evolution of the two sub-populations. While both populations survive when resources are abundant, only individuals initialised as selfish risk-seeking survive when there is a paucity of resources. In the case of a benign environment, the two sub-populations coexist in roughly equal percentages when the mortality rate is set to 25%. However, by increasing this parameter to 50%, the majority of the community is composed of the initially generous risk-averse sub-population.

The other aspect to observe is the evolution of the reproduction rates $\varphi_{G,G}$, $\varphi_{S,S}$ over generations presented in Figure 7.9. The figure reports the evolution of the probability with which selfish risk-seekers (and generous risk-averse people) pass on their own phenotype to their offspring. Since the environment did not have a significant effect on the evolution of these parameters, results are shown for the evolution in a negative environment. $\varphi_{G,G}$ =1 means that a generous parent will reproduce a generous offspring with probability 1; similarly, $\varphi_{S,S} = 1$ means that an selfish parent will reproduce a selfish offspring with probability 1. Results show that the probability with which generous individuals pass on their own phenotype to their offspring reaches equilibrium at roughly 50%; meaning that 1 in 2 cases the offspring of a generous individual exhibit the same generous phenotype. Conversely, selfish individuals are much more likely to reproduce selfish offspring ($\varphi_{S,S} \sim 90\%$). The results are not strongly influenced by either community cost or mortality rate, and the oscillations present in figure 7.9 are due to the slow decrease of population size towards extinction. Moreover, these equilibria are independent of the initial values of both $\varphi_{G,G}$ and $\varphi_{S,S}$, as long as the relationship between the two parameters is satisfied ($\varphi_{G,G} >> \varphi_{S,S}$). This was observed by changing several initial values of the two parameters, considering $\varphi_{G,G} \in \{0.80, 1\}$ and $\varphi_{S,S} \in \{0, 0.20\}$. These values were chosen because of real-world evidence: we know that selfish risk-seeking individuals that exhibit anti-social behaviours are a minority in the community. Therefore, I selected reproduction rates that satisfied the condition of minority for selfish risk-seekers.

Figure 7.5: Evolution of the population over generations in a **scarce** fixed environment, $e_0 = 1.2$. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange area: Selfish risk-seeking individuals,
Blue area: Generous risk-averse individuals.



(a) (b) (c)

(d) (e) (f)

(g) (h) (i)

Figure 7.6: Evolution of the population over generations in an **abundant** fixed environment, $e_0 = 4$. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange area: Selfish risk-seeking individuals,
Blue area: Generous risk-averse individuals.

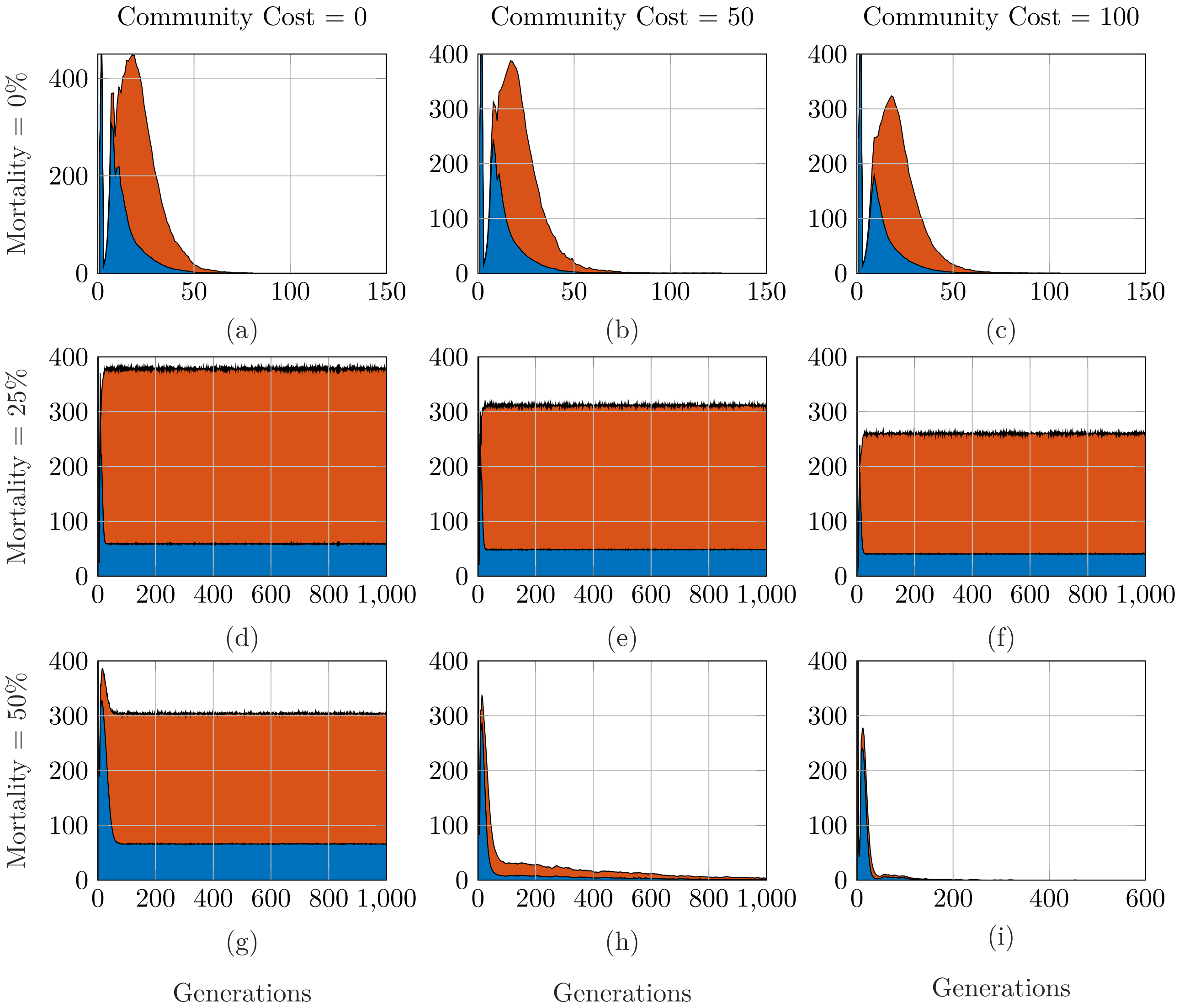


Figure 7.7: Evolution of the two initial populations over generations in a **scarce** fixed environment, $e_0 = 1.2$. Results show how the two populations evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Yellow area: Population initialised as selfish risk-seeking,
Purple area: Population initialised as generous risk-averse.

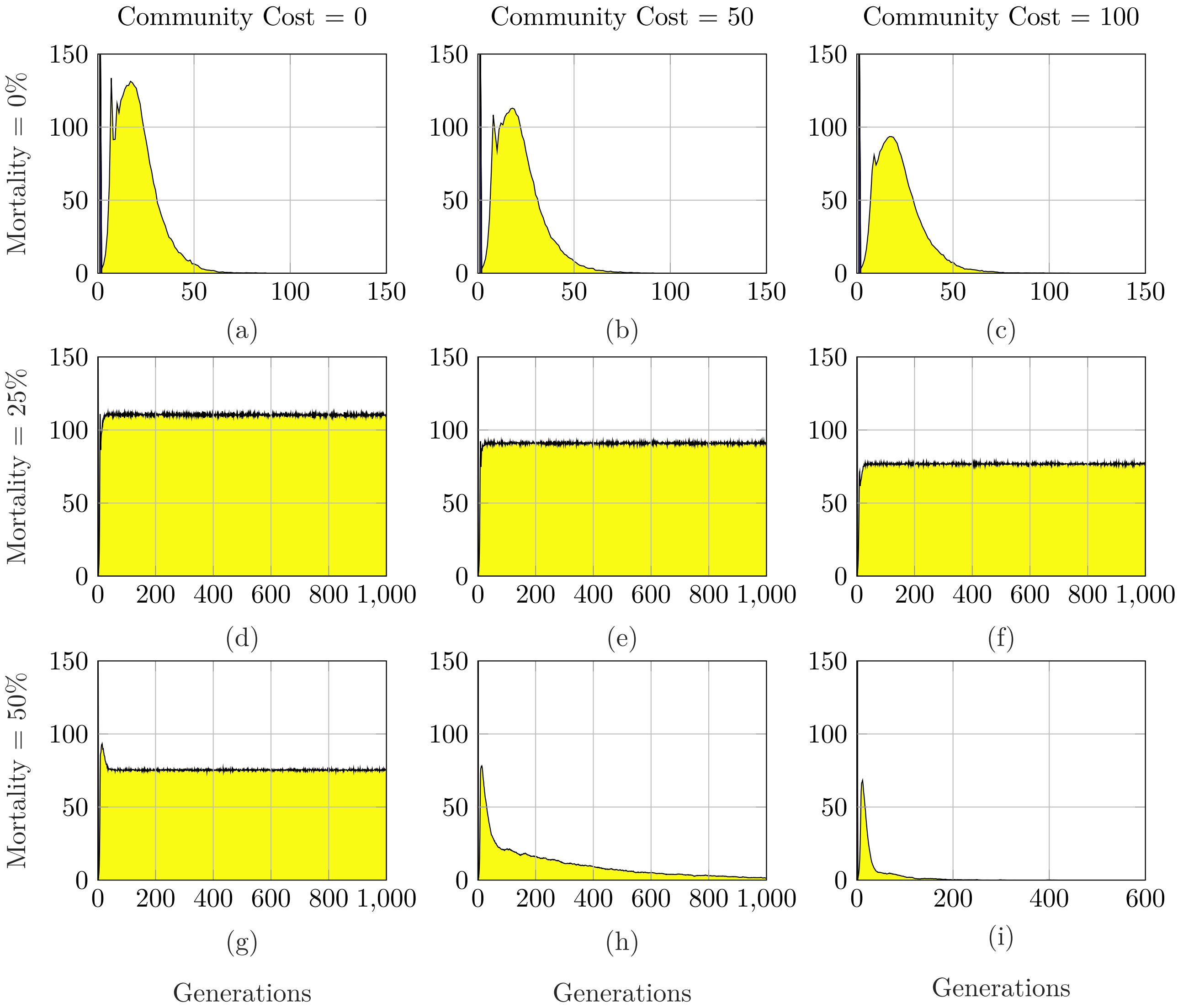
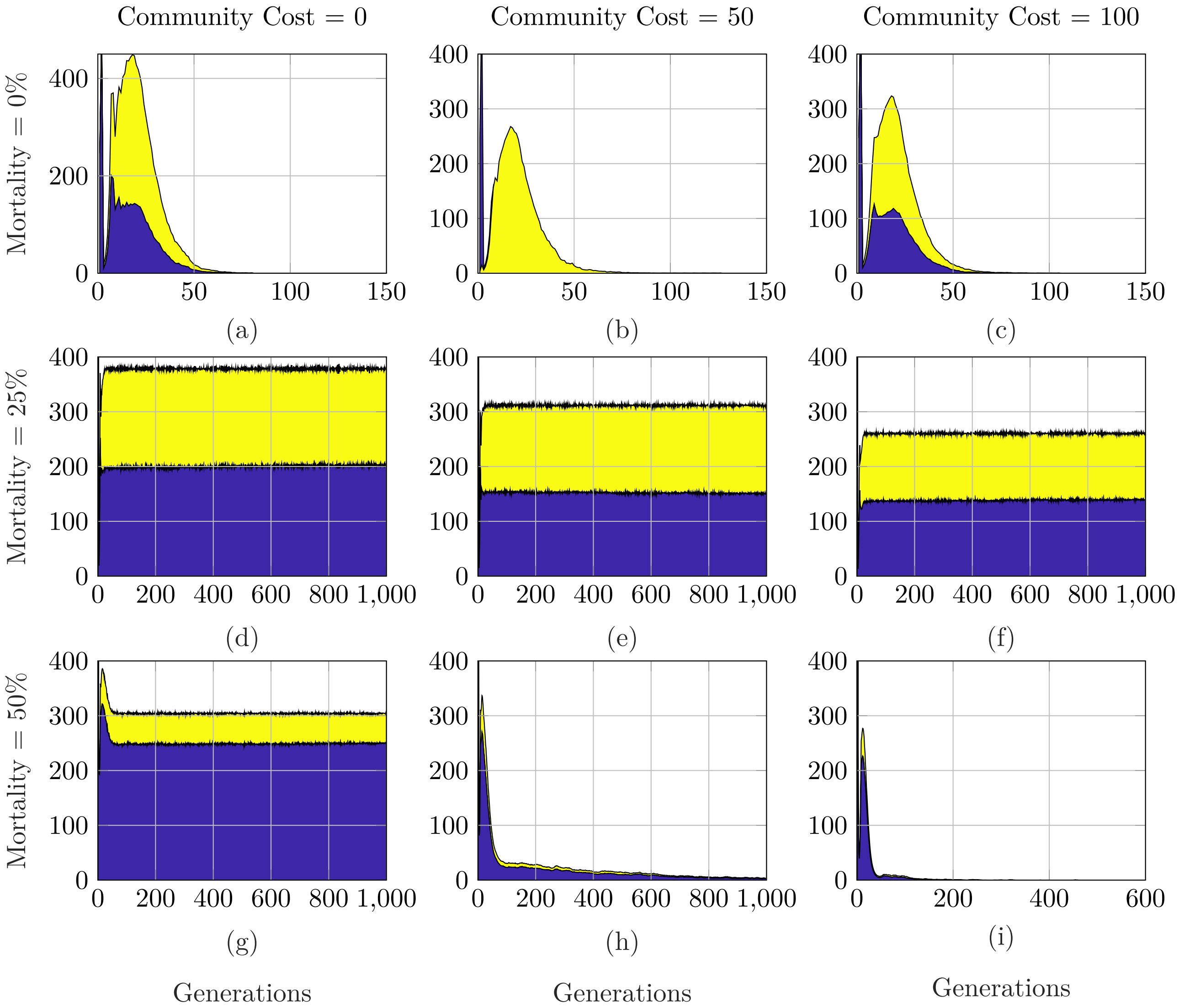


Figure 7.8: Evolution of the two initial populations over generations. Results show how the two populations evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Yellow area: Population initialised as selfish risk-seeking,
Purple area: Population initialised as generous risk-averse.



(a) (b) (c)

(d) (e) (f)

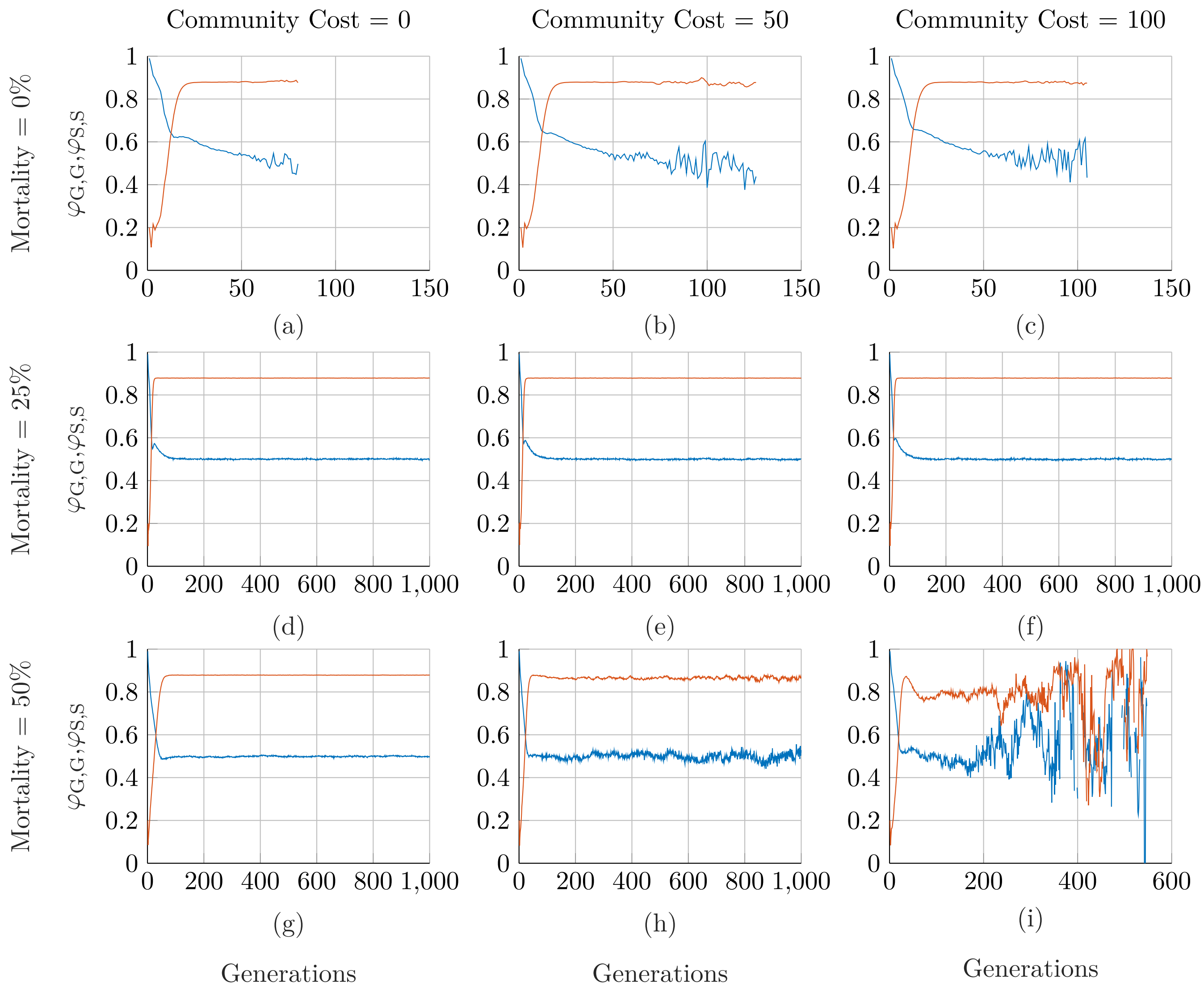
(g) (h) (i)

Figure 7.9: Evolution of the reproduction rates over generations. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.

Orange line: $\varphi_{S,S}$

Blue line: $\varphi_{G,G}$

$\varphi_{S,S}$=1 (/0) means that an S individual has a 100 (/0)% chance of reproducing an S offspring, $\varphi_{G,G}$=1 (/0) means that a G individual has a 100 (/0)% chance of reproducing a G offspring .



7.3 Discussion

This chapter provided the first example of population evolution in which mutation is introduced. The first striking outcome that arises when comparing both mutation models with the non mutation one is the role of the environment. When mutation was not included, the environmental offer played a substantial role in the population composition evolution, leading to a greater proportion of selfish risk-seekers when the environment was harsher, and fewer selfish citizens when the conditions were more benign. In the mutation models, however, the different environmental conditions only lead to different equilibria for the population size, given that more resources are able to sustain more individuals, independent of their phenotype. Nevertheless, an environmental effect arises for the model initialised as composed of two sub-populations, when analysing the evolution of the two initial sub-populations. While individuals initialised as generous risk-averse survive when the environmental conditions are favourable, they perish in a harsh environment. In this sense, we can observe the advantage of having even a small percentage of selfish risk-seeking individuals in the community: without their presence, the population would have not survived the critical period and would have perished immediately. Thus, behaving selfishly and taking risks can be evolutionarily adaptive for the survival of the population under harsh conditions.

Another difference between the mutation and the non mutation models is the evolution of the population in the context of high mortality rate ($m_S = 50\%$). When no mutation was introduced, the population survived independent of the community cost. On the contrary, the population declines towards extinction as soon as some community cost is introduced when mutation is present in the model. The fast decline of the population size in the mutation models might be driven by the evolution of the reproduction rates that strongly favour selfish individuals. In fact, the fewer selfish people were present in the community in the non mutation model, the larger the community population size was, in scenarios of high costs and high mortality ($m_S = 50\%, \lambda \in \{50, 100\}$). However, as the selfish phenotype is clearly favoured over the generous one, once mutation is introduced, the population does not survive the high costs and the high mortality risks present in these scenarios. This dynamic suggests that selfish and risk-seeking behaviours are not always beneficial for the evolution of the population, although they induce more personal gain overall.

The main difference that emerges between the two models is the evolution of the reproduction probabilities, as the overall population dynamics are consistent across the two models. The reproduction probabilities $\varphi_{G,G}$ and $\varphi_{S,S}$ evolve to equilibrium very quickly when they are not divided into the components ϕ, ω, γ. Moreover, they both evolve to the same equilibrium values respectively, independent of any external condition (environmental offer, community cost and/or mortality rate). Contrariwise, when the components ϕ, ω, γ are evolved separately, results show more variation in the dynamic patterns and equilibria. Although selfish risk-seekers are genetically strongly favoured also in this scenario $\phi \sim 85\%$, γ, ω do contribute to the development of either a selfish or a generous behaviour for the offspring. The component related to having a generous parent ω does increase as the mortality rate increases, suggesting that selfish individuals are not always the optimal behaviour to adopt as the cost they endure increases. Note also that such differences between the two models might have been influenced by the population initialisation (e.g. a single versus two separate sub-populations).

Overall, the dynamics presented in this chapter suggest that selfish individuals are mostly favoured. The large advantage of selfish risk-seeking individuals is driven by their ability to gather more resources and their tendency to share a smaller percentage of them with the community, compared to generous citizens. In this way, the community cost is almost entirely paid by generous individuals who contribute 100% of their resources to the public pot. Therefore, even though risk-seekers might perish during the first phase of the model, they are assured to succeed once they survive. This evolution is not realistic as individuals engaging in anti-social and criminal activities are usually either isolated from the community or they are asked to pay for their actions with detention. Another cause of the strong advantage of selfish risk-seekers is rooted in the strategy of generous citizens. Indeed, they are modelled as pure cooperators (they contribute all their resources to the public good), who do not adapt to the environment or to the other individuals in the community. This behaviour is rarely observed in experimental set up and in everyday life. To address these issues, the next two chapters present two models in which first (1) generous individuals adapt their contributions to the community, playing a conditionally cooperative strategy; and secondly, (2) selfish risk-seekers pay an individual cost for engaging in anti-social behaviours.

Chapter 8 Model with mutation and genotype plus phenotype reproduction

8.1 Overview

This chapter presents a different reproduction system which includes the genotype and the phenotype contributions to the reproduction probabilities with which offspring inherit their behavioural type.

In the second one, the parent's phenotype directly affect the development of the offspring's phenotype. Although there is dependency between parent and offspring's phenotypes also in the previous model, in this case there is a direct effect that can be interpreted as the parental effect. As explained in the introduction of the model 5.1, parents that exhibit selfish risk-seeking attitudes are less likely to provide an adequate care to their offspring. Therefore, by investing less time in child care, the offspring are more likely to develop behavioural problems. This second mechanism model this mechanism explicitly.

Each individual has a set of genes that evolve over time, independent of the phenotype expressed. Genetic factors have been discovered to have a strong impact on the development of psychopathic traits [70, 159]. Furthermore, individuals are influenced by external factors when developing personality traits, such as parenthood, environmental conditions and harsh childhood [70, 158]. For this reason, I introduced the two components separately when modelling the reproduction probabilities for both generous and selfish individuals. Thus, the reproduction rates of each individuals are composed of two features, the gene part ϕ and the phenotype part γ or ω:

$$\begin{aligned}
\varphi_{G,G} &= 1 - \phi + \omega, \\
\varphi_{G,S} &= \phi - \omega, \\
\varphi_{S,S} &= \phi + \gamma, \\
\varphi_{S,G} &= 1 - \phi - \gamma;
\end{aligned}$$

$$\begin{aligned}
0 &\leq \omega \leq \phi, \\
0 &\leq \gamma \leq 1 - \phi.
\end{aligned}$$

where ϕ represents the propensity of each individual to reproduce selfish individuals, only depending on genetic factors; γ embodies the effect of having a selfish parent in the development of personality traits; while ω embodies the effect of having a generous parent in the development of personality traits. γ represents an incentive to develop psychopathic traits due to the lack of time invested in parenting and the harsher environment experienced during childhood. That is, a selfish risk seeker will reproduce a selfish offspring with probability $\phi + \gamma$ and a generous risk-averse individual will reproduce a generous offspring with probability $1-\phi+\omega$. The parameter ϕ is initialised accordingly to the initial percentage of selfish individuals in the community (i.e. 10%), while both γ and ω are set equal to 0.01. All three parameters are then evolved over generations. Mutations $\eta_{\phi,t}$ are drawn from a $\mathcal{N}(0, 0.1)$, for consistency with the previous chapter. The mutations $\eta_{\gamma,t}$ and $\eta_{\omega,t}$ for the phenotype parameters γ and ω are drawn from a $\mathcal{N}(0, 0.01)$. The parental effects are allowed to evolve in the model as there could be aspects of parenting that evolve over time, such as the offspring's sensitivity to parenting over generations. Thus, the reproduction probabilities are evolved over generations as follow:

$$\begin{aligned}
\varphi_{G,G,t} &= 1 - \phi_t + \omega_t, \\
\varphi_{G,S,t} &= \phi_t - \omega_t, \\
\varphi_{S,S,t} &= \phi_t + \gamma_t, \\
\varphi_{S,G,t} &= 1 - \phi_t - \gamma_t;
\end{aligned}$$

$$\begin{aligned}
\phi_t &= \phi_{t-1} + \eta_{\phi,t}, \\
\omega_t &= \omega_{t-1} + \eta_{\omega,t}, \\
\gamma_t &= \gamma_{t-1} + \eta_{\gamma,t}.
\end{aligned}$$

The reproduction parameters are initialised as presented in Table 8.1, while the other parameters describing the model are consistent with the previous models (see Tables 7.1).

It is important to notice that different values of σ^2 do not influence the dynamics of the population, they simply speed up or slow down the achievement of the equilibrium state.

Table 8.1: Initial values for the reproduction parameters

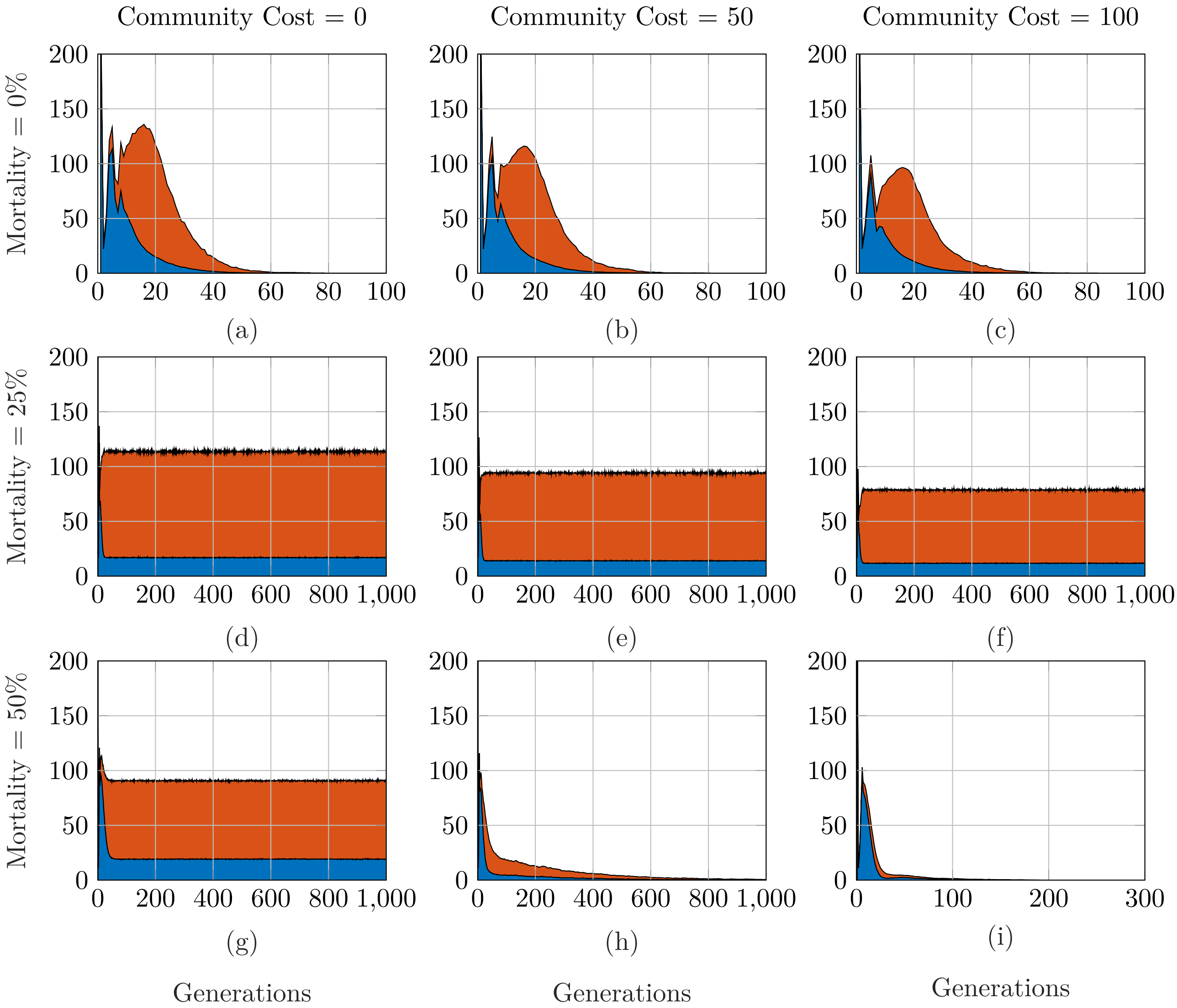
Parameters	Initial values
$\phi = S_0$	0.1
γ, ω	0.01
$\sigma_\gamma^2 = \sigma_\omega^2$	0.01
σ_ϕ^2	0.1

8.2 Results

The results here reported are for γ and ω different from zero, meaning that parental contribution does make an impact on the development of offspring's phenotypes. However, if phenotypes contributions ω, γ were set to zero, the evolutionary dynamics are similar to the one reported in the previous chapter. Also, since the evolution of ϕ is independent of the individual's phenotype, the evolution of the reproduction rate is visible in Figure 8.4. The evolution of the population over generations is consistent with what presented in the previous model (Figures 7.5, 7.6): selfish risk-seeking individuals comprise the majority of the population, when it does not collapse toward zero (figures 8.1, 8.2). Moreover, the environmental conditions do not impact the dynamics of the evolution but only the different population size at equilibrium.

The Figure 8.3 reports the evolution of $\varphi_{G,G}$ and $\varphi_{S,S}$ over generations, as composed by both ϕ and ω,γ respectively, while their separate evolution is presented in figure 8.4. While the reproduction probability for selfish individuals remains constant over generations ($\varphi_{S,S} \sim 88\%$), the reproduction probability for generous citizens changes over time. In fact, the probability for generous individuals to pass on their own phenotype to their offspring increases over generations, slowly reaching the same equilibrium presented in figure 7.9. Such convergence is confirmed when allowing the reproduction parameters ϕ, ω, γ to mutate at a faster pace. The parent's phenotype does make an impact on how likely generous parents pass on their own phenotype to their offspring. The parameter γ increases over time, leading generous individuals to reproduce fewer selfish offspring. This evolution is more or less steep according to the mortality rate: as there is no mortality, γ increases very slowly, leading to a slight change in the G reproduction probability from the purely genetic parameter ϕ. However, when the mortality rate is set to either 25 or 50%, generous citizens become more likely to reproduce G offspring over time (a part from when $m_S = 50\%$ and $\lambda = 100$, Figure 8.4 (i)).

Figure 8.1: Evolution of the population over generations in a **scarce** fixed environment, $e_0 = 1.2$. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange area: Selfish risk-seeking individuals,
Blue area: Generous risk-averse individuals.

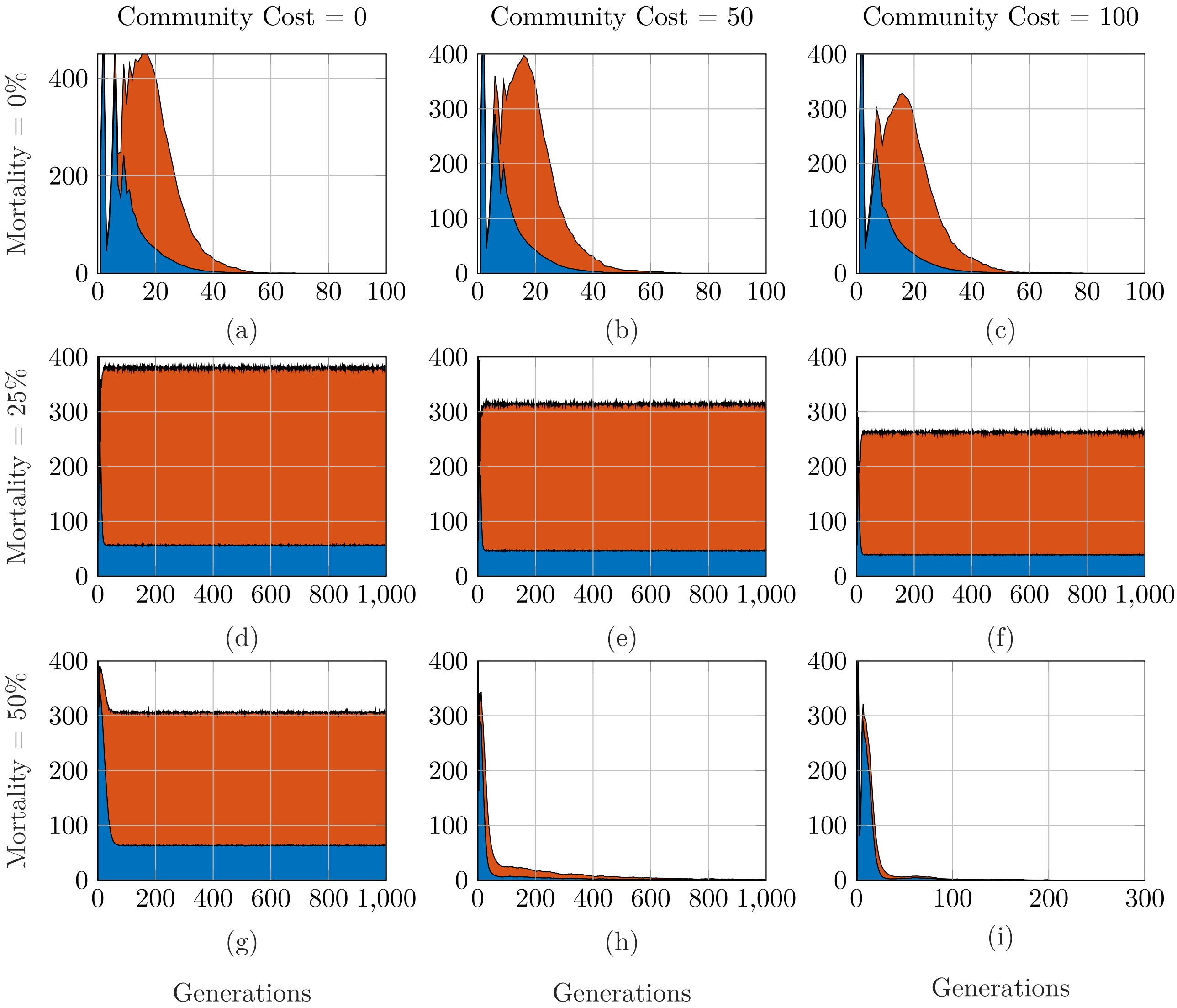


(a) (b) (c)

(d) (e) (f)

(g) (h) (i)

Figure 8.2: Evolution of the population over generations in a **abundant** fixed environment, $e_0 = 4$. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange area: Selfish risk-seeking individuals,
Blue area: Generous risk-averse individuals.



(a) (b) (c)

(d) (e) (f)

(g) (h) (i)

Figure 8.3: Evolution of the combined reproduction rates $\varphi_{S,S}, \varphi_{G,G}$ over generations. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.

Orange line: $\varphi_{S,S}$

Blue line: $\varphi_{G,G}$

$\varphi_{S,S}$=1 (/0) means that a S individual has 100 (/0)% chances of reproducing a S offspring,
$\varphi_{G,G}$=1 (/0) means that a G individual has 100 (/0)% chances of reproducing a G offspring .

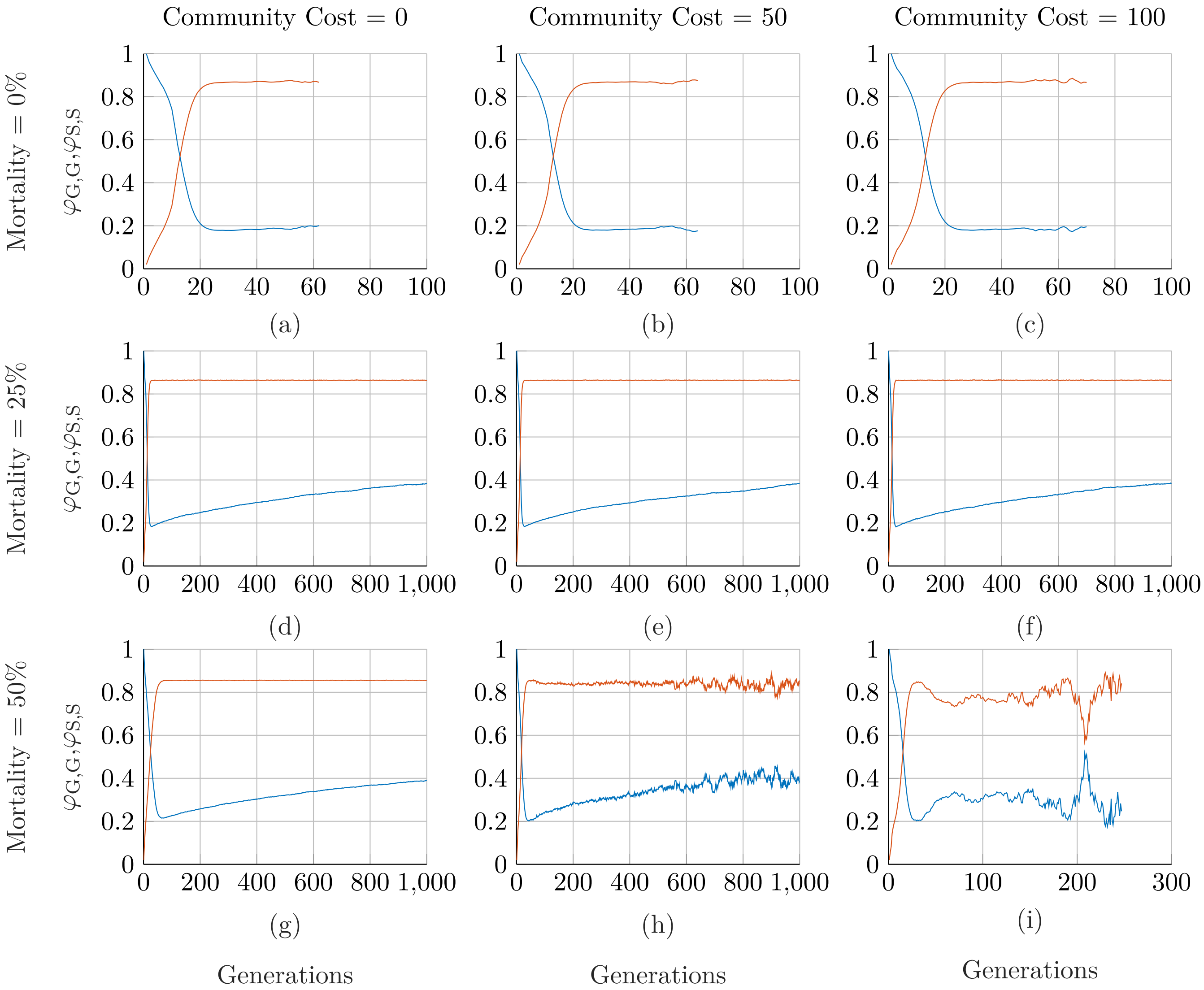
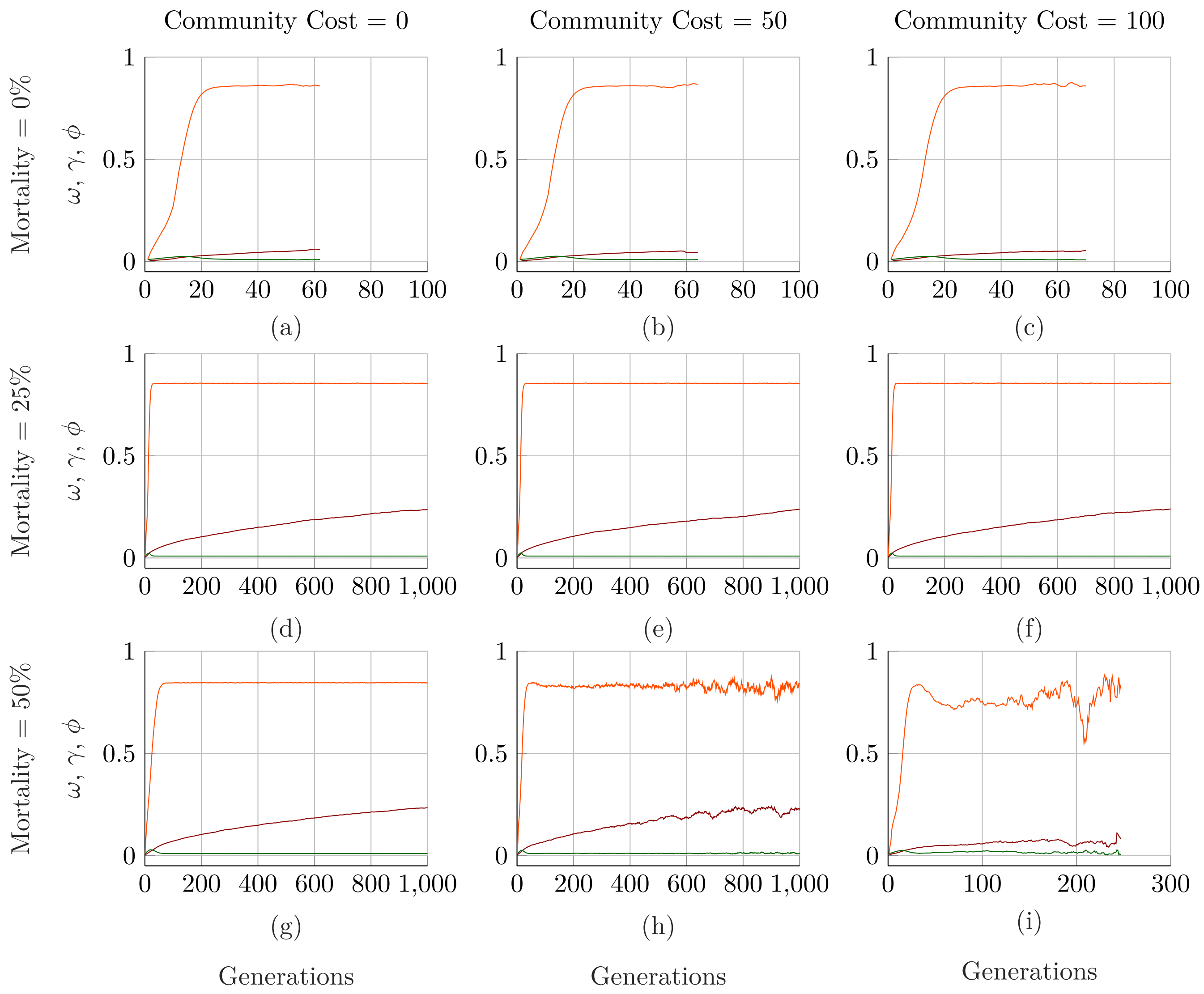


Figure 8.4: Evolution of the separate parameters regulating the reproduction mechanism parameters ω, γ and ϕ over generations. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Red line: ω
Green line: γ
Orange line: ϕ
ω , contribution of G phenotype on the probability of reproducing G offspring,
γ , contribution of S phenotype on the probability of reproducing S offspring, ϕ, probability that an individual will reproduce a S offspring, independent of his own phenotype.



8.3 Discussion

This chapter illustrates the effects of a different reproduction mechanisms, examining how the population evolved when considering the impact of parent's phenotype on the development of offspring's personality traits.

Results show an evolutionary dynamic consistent to what already presented in chapter 7. In both benign and harsh environment, the population at equilibrium is composed in larger proportion of selfish risk-seeking individuals. The innovative contribution of this model is the disentanglement between the genetic and the environmental contribution to the development of individuals' behaviours.

Although genetically selfish risk-seekers are strongly favoured, the parent's phenotype does contribute to the development of either a selfish or a generous behaviour for the offspring. In fact, generous parents tend to have more generous offspring as generations pass. Nevertheless, the large majority of the population at equilibrium is composed of selfish individuals.

This dynamic suggests that selfish individuals are largely advantaged, which is not a realistic feature of the model. The large advantage of selfish risk-seeking individuals is driven by their ability to gather more resources and their tendency to share a small percentage of them with the community. In this way, the community cost is almost entirely paid by generous individuals who contribute 100% of their resources to the public pot. In this way, even though risk-seekers might perish during the first phase of the model, they are assured to succeed once they survive. This evolution is not realistic as individuals engaging in anti-social and criminal activities are usually either isolated from the community or they are asked to pay for their actions with detention. Another cause of the strong advantage of selfish risk seekers is rooted in the strategy of generous citizens. Indeed, they are modelled as purely cooperators (they contribute all their resources to the public good), who do not adapt to the environment or to the other individuals in the community. This behaviour is rarely observed in experimental set up and in every day life. To address these issues, the next two chapters present two mode in which first (1) generous individuals adapt their contributions to the community, playing a conditionally cooperative strategy. Secondly, (2) selfish risk-takers individuals pay an individual cost for engaging in anti-social behaviours.

Chapter 9 Model with mutation and conditional cooperation

9.1 Overview

As suggested at the end of the previous chapter, this model addresses the issue of purely cooperative strategies adopted by generous individuals. To have a more realistic depiction of how individuals behave, I modelled generous risk-averse citizens as conditional cooperators: they start by adopting a cooperative strategy in the first generation, $c_{G,0} = 1$, and they then change their strategy according to how the other citizens acted in the previous generation, $c_{G,t} = \frac{1}{N}\sum_{j=1}^{N} c_{j,t-1}$. In this sense, generous risk-averse individuals adapt to the surrounding environment, reconsidering their strategy on the basis of others' behaviour. Thus, generous individuals behaviour can be modelled as follows:

$$c_{G,t} = \begin{cases} 1, & \text{if } t = 1 \\ \frac{1}{N}\sum_{j=1}^{N} c_{j,t-1}, & \text{if } t > 1. \end{cases} \tag{9.1}$$

This model aims to investigate the impact of generous individuals' behaviour towards the public good on the evolution of the population over generations. Will the population reach different equilibria when modifying the cooperative behaviour?

The reproduction mechanism implemented here consider the three components affecting the reproduction rates separately as presented in the previous section 7.1.1. The other parameters describing the model (such as $\lambda, m_S, \gamma, \omega, \phi$) are consistent with the previous chapters (see Tables 7.1, 8.1).

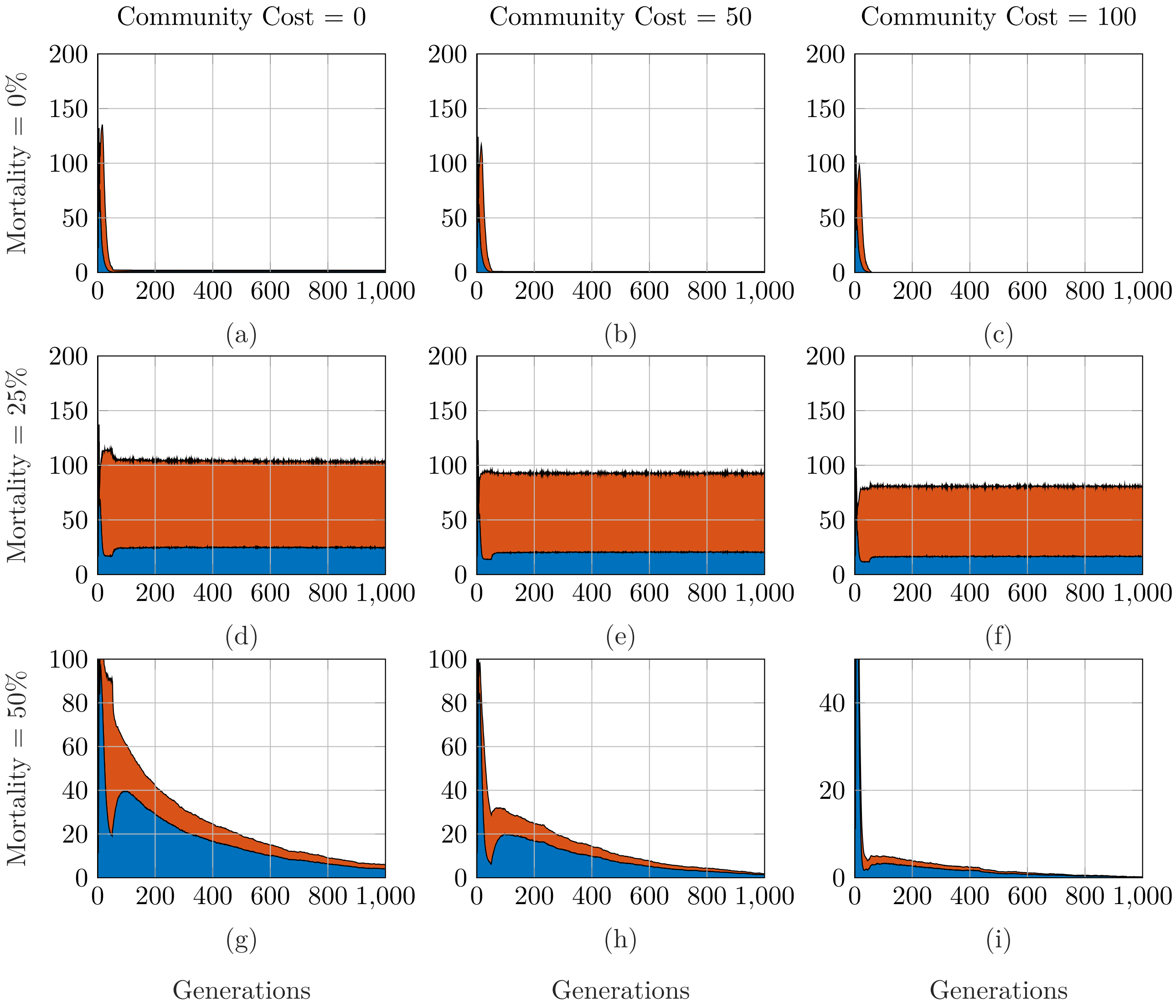
9.2 Results

Results show the evolution of the community over time, when allowing generous individuals to adapt their strategy according to their own experiences, adopting a conditionally cooperative strategy.

While results are consistent with previous models when no or low mortality rate is introduced ($m_S \in \{0\%, 25\%\}$), differences emerge when the mortality rate is set at 50%. In this setting, independent of the community cost, the population survives even though it reaches very low levels towards the end of the 1000 generations (Figures 9.1 (g-i), 9.2 (g-i)). More interestingly, in these cases the population is almost entirely composed of generous risk-averse individuals. Note that this is the first time that generous risk-averse individuals comprise the majority of the community, since the mutation was introduced. Enabling generous individuals to adjust to the surrounding environment and to respond to past experiences led the community to reach a different population composition in extreme cases such as high mortality rate and high community cots ($m_S = 50\%, \lambda \in \{50, 100\}$). Since the only parameter altered is the strategy of generous people in the Public Goods Game, it is evident that modifying the contribution according to the group average behaviour is the driving element of these changes in the evolution. Hence, generous risk-averse individuals can survive in both positive and negative environmental conditions and can outnumber selfish risk-seekers in certain situations, if they adopt a conditional cooperation strategy.

Finally, this model presents another notable change in the evolution of the reproduction rates (Figure 9.3). While $\varphi_{S,S}$ has always been close to 1 independent of the scenario implemented in the previous chapter, this model shows an alternative evolution of the probability with which selfish risk-seekers hand down their own phenotype to their offspring ($\varphi_{S,S}$). When no mortality is introduced, both selfish and generous individuals have a 55% chance of passing on their own phenotype to their offspring. Moreover, when the mortality is set at its maximum, $\varphi_{S,S}$ records its minimum value since mutation was introduced: less than half of selfish individuals reproduce S offspring. On the contrary, generous individuals have the highest probability to pass on their own phenotype to their offspring ($\varphi_{G,G} \sim 65\%$). When the mortality rate is set at 25%, $\varphi_{S,S}$ decreases to 80% compared to previous models where $\varphi_{S,S} \sim 90\%$. Conversely, $\varphi_{G,G}$ remains quite low in this scenario.

Figure 9.1: Evolution of the population over generations in a **scarce** fixed environment, $e_0 = 1.2$. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange area: Selfish risk-seeking individuals,
Blue area: Generous risk-averse individuals.



(a) (b) (c)

(d) (e) (f)

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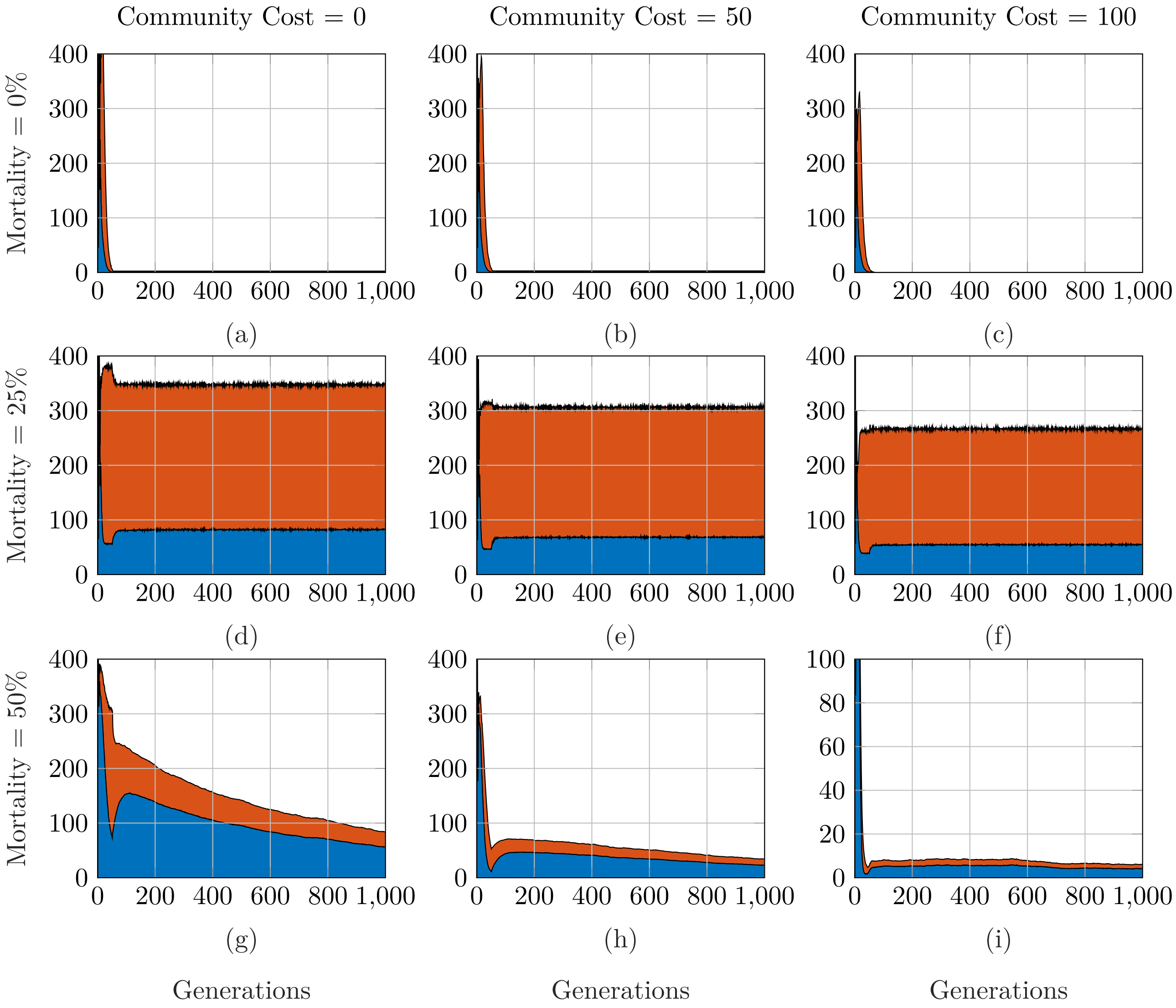
Figure 9.2: Evolution of the population over generations in an **abundant** fixed environment, $e_0 = 4$. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange area: Selfish risk-seeking individuals,
Blue area: Generous risk-averse individuals.



(a) (b) (c)

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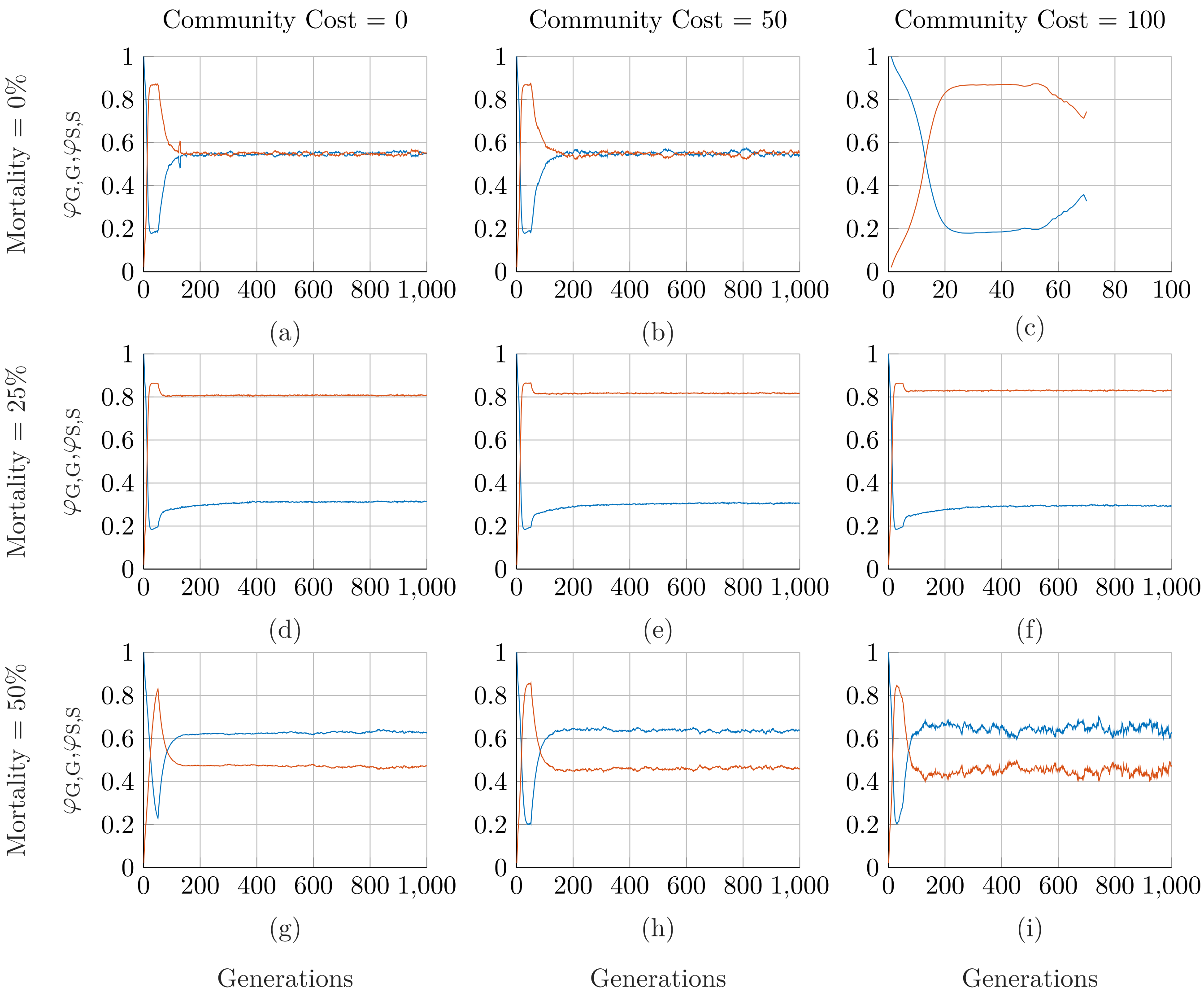
Figure 9.3: Evolution of the combined reproduction rates $\varphi_{S,S}, \varphi_{G,G}$ over generations. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange line: $\varphi_{S,S}$
Blue line: $\varphi_{G,G}$
$\varphi_{S,S}$=1 (/0) means that an S individual has a 100 (/0)% chance of reproducing an S offspring, $\varphi_{G,G}$=1 (/0) means that a G individual has a 100 (/0)% chance of reproducing a G offspring.



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9.3 Discussion

The model presented in this chapter aimed to provide a more realistic representation of individuals' strategies when contributing to a public good. Allowing the strategies to adapt to the community, the model reproduces a more accurate depiction of real-world interactions. As a consequence, the community cost is more homogeneously split among all citizens, compared to the previous model. That is because the contribution to the public good is now more homogeneous amongst the citizens. Since conditional cooperators adjust the contribution to the average contribution in the community, the average amount of contribution is equal across all citizens. Therefore, generous individuals do not spend most of their resources to support anti-social and criminal behaviours perpetrated by selfish risk-seekers, as was the case in the previous chapters.

Results report interesting findings regarding the evolution of the population. Despite the adaptive strategies of generous individuals, when the mortality risk is not too elevated ($m_S = 25\%$), behaving in a selfish and risky way does lead to higher payoffs and therefore selfish risk-seekers make up the largest portion of the total population. However, as the mortality risk increases ($m_S = 50\%$), the population does not go extinct as in the previous chapter. It adapts by changing its composition, favouring cooperative and risk-averse attitudes. Individuals who avoid risks and conditionally cooperate become the largest portion of the total population, allowing the community to survive for each community cost introduced.

Furthermore, the evolution of the two reproduction rates illustrates different outcomes, compared to all previous chapters, although the probability with which selfish individuals pass on their own phenotype to their offspring remains quite high ($\phi \in \{45\%, 80\%\}$). Indeed, this model is the first one to present an evolution that leads generous individuals to reproduce generous offspring with a higher probability than that with which selfish individuals procreate selfish individuals ($\varphi_{G,G} > \varphi_{S,S}$). In this sense, the generous risk-averse phenotype evolves as the evolutionarily adaptive behavioural type, as long as the mortality hazard for selfish individuals is high enough ($m_S = 50\%$). Nevertheless, when the mortality hazard for risk-seekers is set at 25%, adopting a selfish and risk-seeking behaviour is still the optimal behaviour. Lastly, when no mortality rate is introduced for risk-seekers, the community perishes in the first 100 generations, not providing insights on the evolution of the population.

The last variation of the model will include an individual cost borne by selfish risk-seeking citizens. This cost describes the cost that each individual who engages in anti-social or criminal behaviours has to pay.

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Chapter 10 Model with mutation, conditional cooperation and individual costs

10.1 Overview

This last chapter introduces an individual cost for selfish individuals into the model. As discussed in Chapter 7, after the harvesting phase selfish risk-seeking individuals are successful individuals, who gather more resources and share a smaller portion of what they gathered with the community, compared to generous citizens. However, when engaging in anti-social and disruptive behaviours, selfish citizens incur additional costs, due to either social costs (by being isolated from the rest of the population) or institutional costs (by being incarcerated). Therefore, this model includes an individual cost that selfish risk-seekers have to pay after the resources have been redistributed after the Public Goods Game. The fitness of selfish risk-seekers at the end of the generation is calculated as follows:

$$f_{i,t} = \frac{C_t \rho}{N_t} + r_{i,t}(1 - e - c_{p_i}), \tag{10.1}$$

where e (expense) is initialised as a fixed amount per individual. Different values have been selected, starting from a high value of 0.5, which is equal to half of the resources necessary to survive ($s = 1$), to a low cost of 0.1. This new parameter presents a more realistic representation of dynamics, not favouring selfish risk-seeking attitudes over generous risk-averse. The results are presented for the same initial settings adopted in the previous chapter, thus generous individuals behave as conditional cooperators and parameters are initialised as in Tables 7.1, 8.1.

This final model aims to integrate all previous aspects into a single model, which also presents a more realistic representation of the benefit and costs of adopting selfish and risk-seeking behaviours that sometimes culminate in antisocial occurrences.

10.2 Results

Results are shown for an individual cost equal to 0.1. In fact, results show that when the individual cost is increased, populations do not survive in a condition of scarcity of resources, while they evolve consistently across different cost values when the resources are abundant.

Figure 10.1 (Figure 10.2) shows the evolution of the population, highlighting the two phenotypes, when resources are scarce (abundant). Contrary to what was observed in the previous chapters, the population does not perish in the first 100 generations because of overpopulation when no mortality risk is included. In fact, this is the first model, since mutation was introduced, that shows a stable nonzero population when $m_S = 0\%$. With no mortality rate, the population only survives in a hostile environment if no community costs are introduced (Figure 10.1 (a)). When the resources are abundant, the community costs impact the equilibrium level of the population, which survives and stabilises to a constant nonzero value (Figure 10.2 (a-c)). In both environments, when $m_S = 0\%$ the equilibrium composition for those populations is around 50%, meaning that half of the population is composed of selfish risk-seekers and the other half exhibits a generous behaviour.

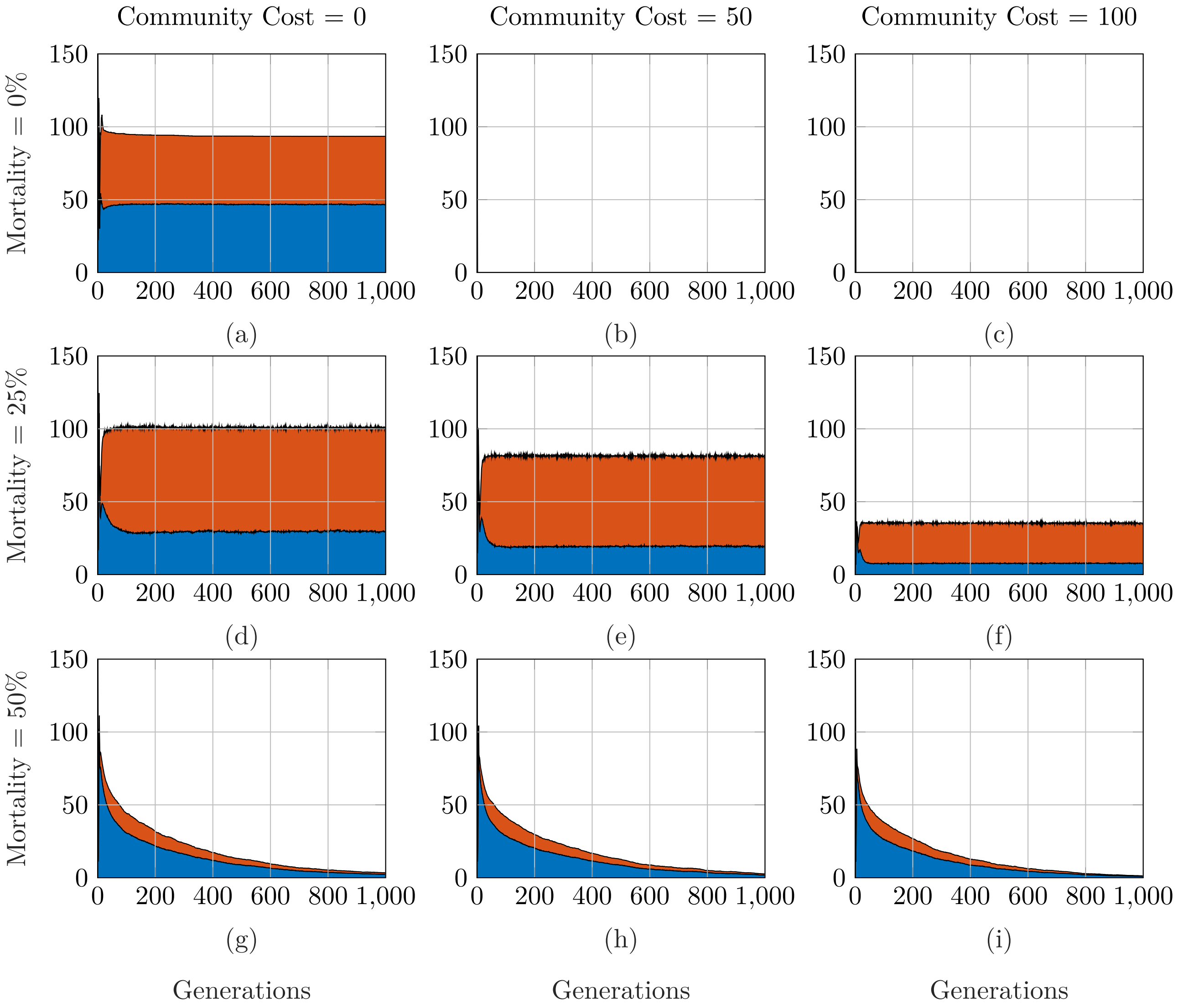
When the mortality rate for risk-seekers is increased to 25%, the evolution is consistent with what was reported in previous chapters: populations reach a stable equilibrium that is lower as the community cost increases. Selfish risk-seekers comprise the majority of the community, reaching roughly 80% of the population, which is slightly lower than the previous model (Figure 10.1 (d-f) versus 9.1 (d-f), and Figure 10.2 (d-f) versus 9.2 (d-f)).

Lastly, when the mortality rate is set at its maximum ($m_S = 50\%$), the population is mainly composed of generous risk-averse individuals, consistent with previous results. However, the population reaches higher equilibrium sizes compared to previous models, especially when both mortality rate and community costs are set at their maximum and the environmental offer is abundant. When there is abundance of resources, the population decreases over time, slowly stabilising around 80 citizens, independent of the community cost.

The reproduction probabilities show a stable evolution (Figure 10.3), confirming the results found for the conditional cooperation model (Figure 9.3). While selfish risk-seeking individuals are more likely to be reproduced in a scenario where the mortality rate is equal to 25%, generous risk-averse behaviours are favoured when the mortality is 50%. However, this evolution is different when the individual cost is increased. In fact, when the individuals cost $e = 0.5$, the reproduction rate evolution (independent of λ, m_S) is similar to that presented for $e = 0.1$ and $m_S = 50\%$. Finally, when no mortality rate is introduced, offspring have the same probability of inheriting either one of the two phenotypes.

The evolution of the different components of the reproduction probabilities ϕ, γ, ω presented in Figure 10.4 is also interesting. The likelihood of reproducing selfish offspring ϕ is quite large when $m_S = 25\%$, while it decreases significantly when the mortality rate either decreases to 0% or increases to 50%. This is the first time, since this reproduction mechanism was introduced, that the component ϕ reaches a stable equilibrium below 50%. Also, when $m_S = 25\%$ the contribution of generous parents ω evolves to a larger equilibrium compared to the selfish one γ, affecting the reproduction rate $\varphi_{G,G}$. In all other cases, the reproduction probabilities $\varphi_{G,G}$ and $\varphi_{S,S}$ are mainly controlled by the component ϕ.

Figure 10.1: Evolution of the population over generations in a **scarce** fixed environment, $e_0 = 1.2$. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange area: Selfish risk-seeking individuals,
Blue area: Generous risk-averse individuals.



(a) (b) (c)

(d) (e) (f)

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Figure 10.2: Evolution of the population over generations in an **abundant** fixed environment, $e_0 = 4$. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange area: Selfish risk-seeking individuals,
Blue area: Generous risk-averse individuals.

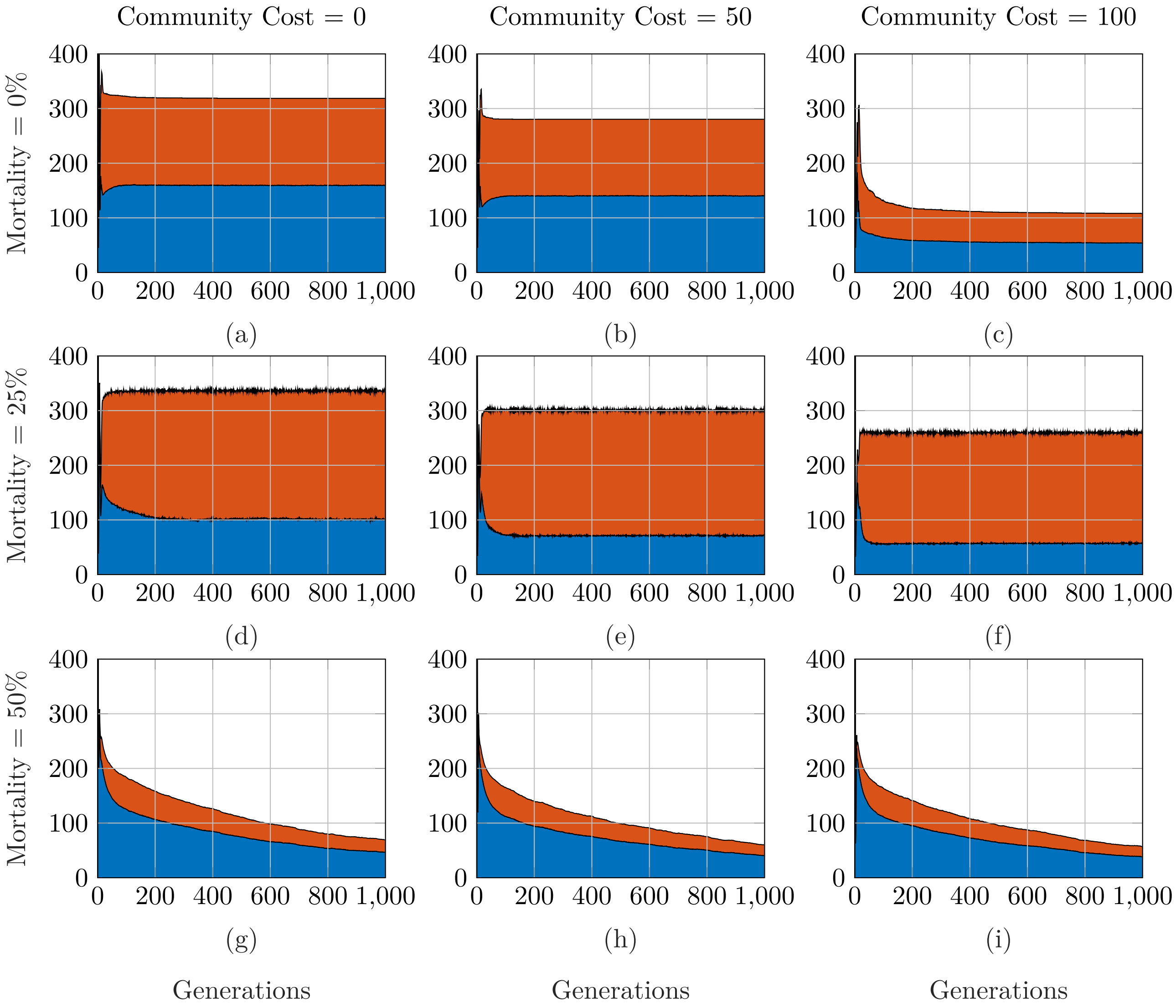
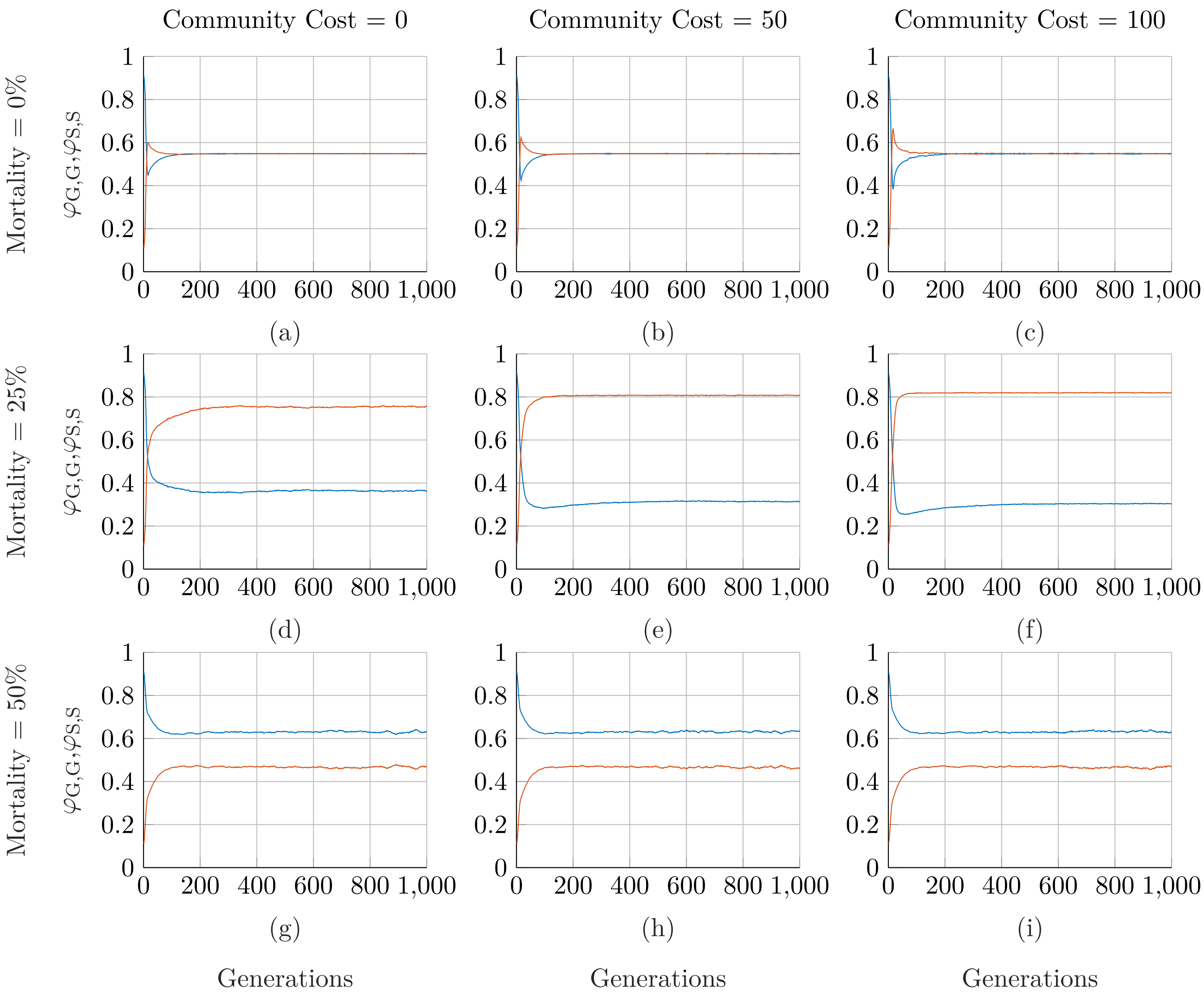


Figure 10.3: Evolution of the combined reproduction rates $\varphi_{S,S}, \varphi_{G,G}$ over generations. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.
Orange line: $\varphi_{S,S}$
Blue line: $\varphi_{G,G}$
$\varphi_{S,S}$=1 (/0) means that an S individual has a 100 (/0)% chance of reproducing an S offspring, $\varphi_{G,G}$=1 (/0) means that a G individual has a 100 (/0)% chance of reproducing a G offspring.



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(g) (h) (i)

Figure 10.4: Evolution of the separate parameters regulating the reproduction mechanism parameters ω, γ and ϕ over generations. Results show how the evolution differs when changing the percentage and the mortality rate of selfish risk-seekers, and the community cost λ.

Red line: ω

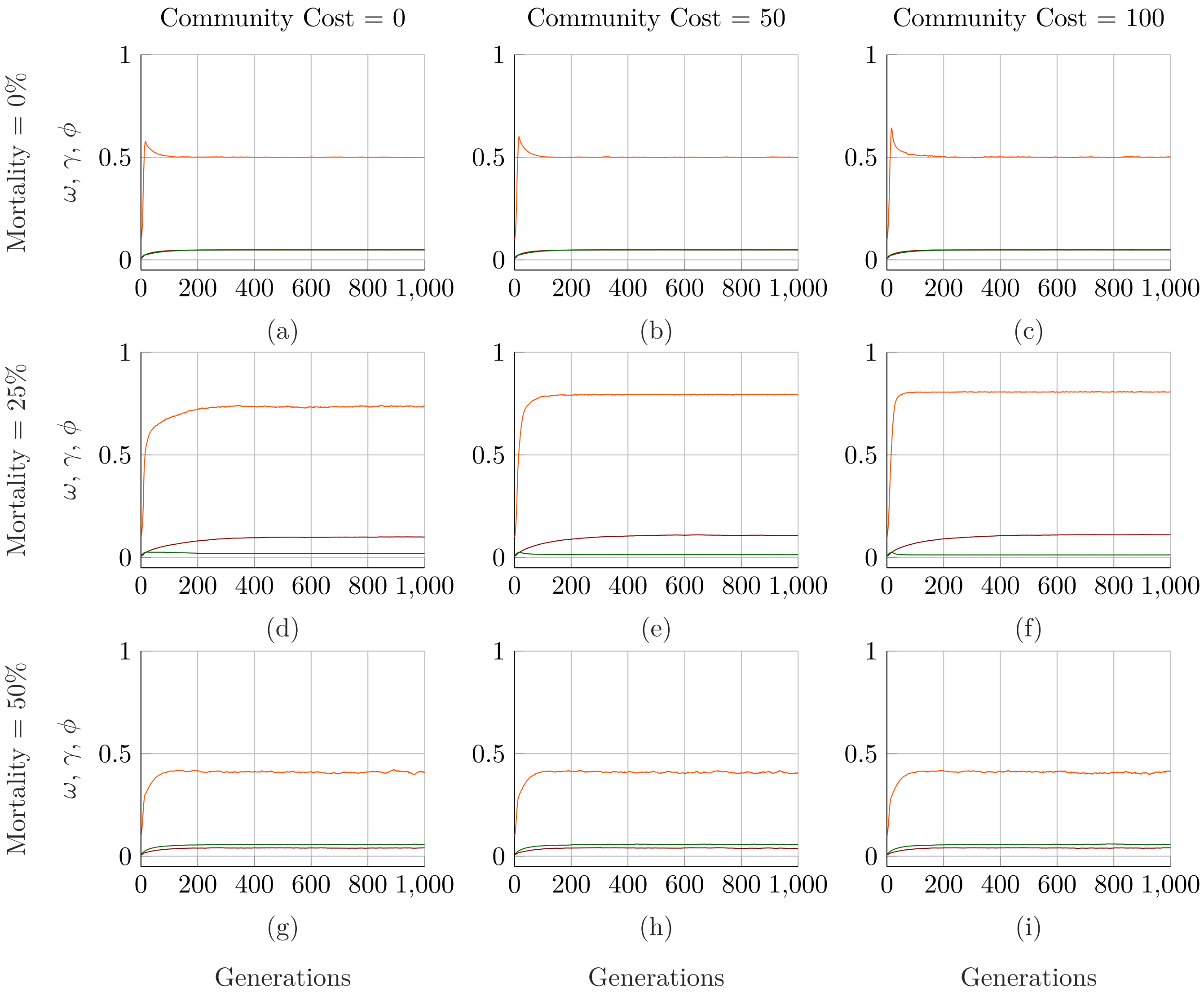
Green line: γ

Orange line: ϕ

ω, contribution of G phenotype to the probability of reproducing G offspring,

γ, contribution of S phenotype to the probability of reproducing S offspring,

ϕ, probability that an individual will reproduce a S offspring, independent of his own phenotype.



(a) (b) (c)

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10.3 Discussion

In this chapter, I incorporated the last element of the model, by including an individual cost for individuals who engage in antisocial and detrimental behaviours for the community.

Results showed for the first time in a mutating population a survival for the communities when no mortality risk is considered. This interesting new outcome underlines the importance of introducing individual costs for individuals who behave in such a way as to disrupt the community. In fact, both the mortality risk and the individual cost embed the personal costs those individuals incur when adopting either risky or antisocial behaviours. In all previous models, when no cost was introduced for selfish risk-seekers, the population reached very large sizes, overshooting the carrying capacity of the environment. However, by limiting the success of selfish risk-seekers, the population survives without overpopulation issues. Thus, this model presents a closer depiction of the real-world dynamics, suggesting that selfish, risk-seeking and anti-social behaviours are not always advantageous in a community.

Nevertheless, selfish behaviours are prevalent in the overall community in some scenarios. Populations reach equilibrium states when composed of 60% of selfish risk-seeking individuals, as long as the mortality risk is not too high ($m_S = 25\%$). These evolutionary dynamics highlight the large advantage that those behavioural traits can bring to the individual. Further investigations should include factors that relate to the community benefit: when citizens act for the wellbeing of the community and not only for their own, they have a positive return that enhances their personal fitness. This aspect is not yet included in my model, but it would be an interesting aspect for future research.

The results for the reproduction rates are also interesting. This model is the first one to show an equilibrium for the likelihood of reproducing selfish offspring that is below 50%. That means that overall generous individuals are favoured over selfish individuals when the mortality cost is high ($m_S = 50\%$). This result suggests that there are scenarios where behaving in a selfish and risk-seeking way lead to lower fitness values compared to individuals who behave generously and avoid risks.

Overall, this model presents a more realistic representation of real-world interactions, giving the opportunity to observe how different behavioural types can contribute to and coexist in a community, shedding light on the evolutionary equilibria under different environmental and individual circumstances.

Chapter 11 Overview and Conclusions

11.1 Thesis overview

The work presented in this thesis aimed at understanding the role of psychopathic traits in different contexts, answering to the research questions initially posed: *How do some aspects of psychopathy, that are common in the general population, affect the development of cooperative behaviours? Under which circumstances can those traits be beneficial for the evolution of the population?*

I addressed these questions by using empirical and simulated data, providing results on the impact of psychopathic traits on individuals decision-making as well as on group dynamics and humans evolution. Throughout my work, I investigated how psychopathic traits impact behaviours and outcomes in the general population.

More specifically, I investigated (I) the role of psychopathic traits at the individual level in competitive games, (II) the effects of high and low psychopathic individuals in group dynamics; and finally (III) the impact of some of the most defining traits of psychopathy on community survival. To address the different facets, I adopted knowledge from a variety of disciplines, from game theory to evolutionary biology, from psychology to statistics.

Chapter 2 contributed to the existing literature about cooperation and psychopathy highlighting the essential role of a realistic context when designing an experimental set-up to investigate cooperation in the context of player-opponent interactions. More importantly, it shed light on the importance of appropriate statistical methods when analysing experimental data, offering examples of badly fitting models and misleading results.

Chapter 3 reported negative results with respect to the effect of facial feedbacks on cooperation, but it also presented interesting evidence concerning the use of defective strategies by participants with high psychopathic trait levels. The chapter also contributed to consolidating the results of the already broad literature in the field about the negative impact of psychopathic traits (especially fearless dominance) on the propensity to act cooperatively in an iterated competitive game.

A particularly interesting and original result was presented in Chapter 4, where I carried out the first empirical investigation of the effect of group composition with respect to members' psychopathic traits on cooperative behaviours. By manipulating the number of high and low psychopathic members in each group, I tested how having more relatively high-psychopathic individuals in a group affects the cooperation of all group members. Results showed that, independent of the individual's personal psychopathic traits, belonging to a group with more relatively high psychopathic individuals leads the group members to cooperate less over time. This result was an innovative contribution to the literature, as no previous study empirically tested the effects of group composition on cooperative behaviours, when controlling for psychopathic traits.

Building on the previous chapters and existing literature, the model presented in Chapter 5 discussed the important role of some dimensions of psychopathy in the evolution of populations. The model mimicked the evolutionary dynamics of a population composed of two main types of agents: selfish risk-seeking and generous risk-averse. The population evolved in a series of different scenarios, examining how the availability of resources, the communal costs imposed on the population, as well as the mortality risks in the initial phase of the model affected the evolution of the population. Results provided interesting insight into the adaptive role of some dimensions of psychopathy: in line with adaptive theory, the model shows an advantageous facet of audacity and exploitativeness typical of psychopathy.

11.2 Conclusion

11.2.1 Ecological Validity remarks

> In order to behave like scientists
> we must construct situations in which our subjects...
> can behave as little like human beings as possible
> and we do this in order to allow ourselves
> to make statements about the nature of their humanity.
> Bannister, 1966, p. 24

This thesis employs mainly experimental (and computational) methods to investigate real world dynamics. While experiments have been recognised for their strong internal validity (which "refers to the approximate validity with which we infer that a relationship between two variables is causal or that the absence of a relationship implies the absence of cause", [162](p.37)); external validity (which "refers to the approximate validity with which we can infer that the presumed causal relationship can be generalized to and across alternate measures of the cause and effect and across different types of persons, settings, and times" [162](p.37)) is argued to be lacking. This is known as an important trade-off in lab experiments: "the more we ensure that the treatment is isolated from potential confounds in order to make certain that the observed effect is attributable to the treatment, the more unlikely it is that the experimental results can be representative of phenomena of the outside world, since typically, in the outside world, many factors interact in the production of events that we are interested in" [163](p.302). Despite the criticisms of the lack of generalization, several scholar have stressed the importance of experiments in social sciences and have addressed the issue of external validity through different means [164, 165]. An important point made in the discussion is that "rather than making predictions about the real world from the laboratory, we may test predictions that specify what ought to happen in the lab. We may regard even "artificial" findings as interesting because they show what can occur, even if it rarely does. Or, where we do make generalizations, they may have added force because of artificiality of sample or setting. A misplaced preoccupation with external validity can lead us to dismiss good research for which generalization to real life is not intended or meaningful." [164](p.379). Thus, when drawing conclusions from experiments, it is important not to oversell the results as applicable to the entire population. Moreover, it is important to remember that "participants in the lab are human beings who perceive their behaviour as relevant, experience real emotions, and take decisions with real economic consequences" [165](p.536). Therefore, the results obtained in lab experiments do relate to human behaviour, but scholars should indeed be careful when generalising their results to the entire population. Since lab experiments have been used more in economic and social sciences, game paradigms have been widely developed. Game paradigms based on game theory have allowed researchers to examine typical contextual decisions individuals frequently face in real-life. Although these games can seem quite far from the reality, they do tell us something about how individuals interact in different scenarios and they can provide insights on what are the causes behind such behaviours [166].

On the basis of real-world depiction and generalizability, scholars have argued the superiority of field data over lab data. However, these two research methodologies are complementary, and each one needs the other in order to derive conclusive results on human behaviour. Although field data are more representative of the real world, they are not able to determine causal effects between events, which is instead the domain of lab data. Thus, the two methodologies should be used in a complementary way to address a research question thoroughly. Especially in psychology, the increasing use of lab experiments has pushed towards the development of self-reported questionnaires to assess participants' personality traits. There has been considerable discussion over the validity of these measures and their employment. In this thesis, two different scales have been employed to assess participants' psychopathic traits. Both scales have been validated through several studies and have now been recognised as some of the most reliable measures for psychopathy. The clinical construct of psychopathy refers to "a pathologic syndrome involving prominent behavioural deviancy in the presence of distinctive and interpersonal features" [40](p.913). Several studies have been reviewed before constructing both the Triarchic and the PPI-R measures [39, 40]. Studies have been employed to test the convergence among different measures of psychopathy and they have also been tested for external validity in relation to theoretically relevant correlates of psychopathy [167]. Furthermore, the measures have been corroborated with both forensic psychiatric patients and community samples, making them widely used measures to assess psychopathy, mainly in sub-clinical samples [122, 168].

In light of this discussion, it is important to interpret the results of this thesis with the appropriate caution. Results from the lab experiments relate to individuals' psychopathic traits, but it is important to bear in mind that it is challenging to assess individuals' personality traits in our everyday life. Results from Chapter 4, for example, highlight how group composition (with respect to psychopathy) impacts group cooperation. The results were obtained by manipulating the group composition, so that some groups had more relatively high psychopathic members than others. Of course, a similar mechanism is not easily reproducible in the real world, since we would need to test all group members for their personality traits and then assemble the groups accordingly. Nevertheless, the result of the study does provide us with insights on how certain personality traits influence the group dynamics, as discussed in the next sections. Future study should try to investigate similar group dynamics in a more naturalistic way, for example by employing field studies, in which we examine the cooperativeness of groups and we then measure the personality traits of the group members. The findings of the studies could then help firms and offices to better arrange groups according to the task that need to be accomplished. That is, if the group is asked to carry out a cooperative goal, then individuals who exhibit behaviours characteristic of the psychopathy spectrum should not be grouped (over a certain threshold) with more cooperative and social individuals. On the other hand, it is possible that if the task is a competitive one, these individuals might boost the productivity of the group.

Finally, the merge of different techniques of research (such as lab and field experiments) would allow us to have a more coherent and realistic depiction of how individuals behave. The debate about validity is indeed an important one, and should always guide us in drawing the conclusions from the experiments we conduct, but it should not be used to promote one kind of research over the other. Future research should contemplate a more integrative use of multiple techniques to provide more robust results.

11.2.2 Psychopathic traits and decision-making

A key assumption in the study of human behaviour is that individuals' decision-making processes are influenced by a multitude of factors. Individual differences have been found to be a great source of major variability in the decision-making process and hence in people's behaviour.

A large branch of research has focussed on the impact of personality traits on individual choices. Among the large spectrum of personality traits an individual can be described by, I focused here on psychopathic traits, as they are characterised by specific interpersonal behaviours related to decision-making. In order to clarify open questions from existing research on the impact of psychopathy on cooperation, I investigated this relationship by (1) examining psychopathic traits and individual decision-making in the context of emotional feedback, and (2) by exploring the individuals' reactions to different group compositions in group tasks.

Previous research has highlighted the impact of context in the decision-making process, also considering the interactions with personality traits [111]. The role of emotional facial expressions was also discovered to affect individuals' choices [113]. The first two studies reported in this thesis provided a novel context of emotional feedback after each decision made by the participants. However, despite the literature assessing the role of smiling and frowning faces on cooperative choices [112], and the evidence of a dysfunctional recognition of emotional stimuli by psychopaths [104], results point towards no effect of emotional facial feedback. That is, results do not show any alteration in cooperation levels when emotional feedbacks were introduced, contradicting the initial hypotheses. Moreover, there was no interaction between psychopathic traits and emotional feedback on cooperative behaviours. That means that either psychopathic individuals can indeed recognise and react to emotional stimuli, contrary to previous findings [104], or that the treatment implemented did not work as expected. In line with this last point, I identified some limitations of both these works, which result from the unrealistic representation of the emotional feedback from the opponents, and the biased instructions of the experiment. By not believing in the authenticity of the stimuli presented, participants might not have reacted to them, leading to a null effect of the emotional feedback. Furthermore, instructing participants to compete in order to obtain higher gains might have biased participants' behaviour, giving a manipulative connotation to the stimuli received. The small percentage that believed in the experimental set up still did not react to the feedback (to a significant extent), posing the question of whether receiving an emotional reaction through a short computer video is the appropriate technique to test the effect of emotional stimuli on decision-making processes. In this sense, the first two experiments questioned the use of deceitful facial emotional reactions in the study of human decision-making mechanisms.

Nevertheless, interesting findings were derived from the experiments. These results corroborated the large body of literature confirming the negative impact of psychopathic traits on cooperation [41, 111]. Fearless dominance was the component driving this effect: higher levels of fearless dominance led participants toward defective strategies, in pursuit of higher gains. Thus, fearless dominance seemed to support an evolutionarily adaptive aspect of psychopathic traits, as individuals act so as to increase their own fitness. That is, when individuals are less anxious and abound in confidence, they tend to achieve higher fitness, making them more successful when interacting with other people. This is one of the main aspects that define successful psychopaths, who are known to excel in obtaining what they pursue [169]. To fully investigate the impact of emotional stimuli on individuals' decisions, future work should take into consideration a more realistic presentation of the experimental design, for example with real interactions between participants. This should allow participants to react to the emotional stimuli received and take them into account when making a series of decisions. Moreover, neutral instructions should be considered in order to avoid a bias in the participants' behaviour.

While the first two experiments examined decisions made by single individuals separately, the last experiment addressed the study of psychopathic traits by exploring the group dynamics. This is an innovative point of view presented in the thesis, as no prior experiment studied the impact of different group composition with respect to psychopathic traits on cooperation. The design of this experiment allowed me to manipulate the number of high and low psychopathic players in each group, without the use of deception. Findings showed how having a large number of high psychopathic players in a group is sufficient to drive the cooperation of each group member towards defective behaviours, independent of their own personality traits. The robustness of the result shed light on an unexamined phenomenon, opening the way for future research. By choosing a different experimental game (such as the Public Goods Game), researchers will be able to have a more comprehensive overview of group dynamics when manipulating the composition. By analysing a collective action as the one in the PGG, it would be possible to collect more evidence describing psychopathic individuals and their effects on group dynamics, when individuals' actions involve not only themselves but also the community they are part of. My experiment presented the first step in connecting group dynamics and members' psychopathic traits, but limiting the results to personal decision-making processes.

Furthermore, the study presented limitations with respect to the sample analysed, despite these robust results. The small variance of the participants' psychopathic measures might have contributed to an unclear pattern over time inside the groups. In fact, it is hard to clearly distinguish how the decrease in cooperation is driven by the actions of high psychopathic members. That is, my results show that high psychopathic people start defecting from the very beginning of the game, but how long does it take to observe an irreversible change in low psychopathic individuals' behaviour? Is there a threshold for when high psychopathic individuals start to manipulate the group behaviour towards significant and irreversible defective strategies? My results suggest that a threshold of 50% high psychopathic people does decrease the overall cooperation, but do not indicate whether a minimum number of interactions is necessary for the defective strategies to stabilise. This issue could be overcome by examining a more heterogeneous sample of the population, without restricting it to undergraduate students. A larger variance in psychopathic levels might allow to examine who is driving whom and in which way.

Another interesting aspect to investigate concerns the type of task the group has to accomplish. The current results indicate that groups with a large proportion of high psychopathic members under-perform in cooperative tasks, but do not indicate how performance might be affected in competitive tasks. Therefore, it would be interesting to investigate whether different tasks (creative, cooperative or competitive) can lead groups with a high percentage of psychopathic people to outperform groups only composed of healthy members. In this way, in organisations and also in educational contexts, the group setting could be manipulated according to the task in hand. Thus, further research in this direction will provide useful information on how individual variations affect the group performance, contributing in this way to more productive group dynamics, both in work environments and in educational scenarios.

The first three chapters of this thesis aimed at describing the influence of psychopathic traits in our everyday life, both at the individual and at the community level. Despite the limitations of the studies, results contributed to the discussion by providing statistical analysis and innovative experimental design. I also suggested future lines of research to expand the knowledge on individuals' personality traits and decision-making. Some of the queries arising from the data have been addressed by the simulation model developed in Chapters 6 to 10, but future research should work on these aspects through the use of experimental studies.

11.2.3 Psychopathic traits and evolution

Psychopathy has long been seen as a personality disorder, characterised by interpersonal, affective and behavioural problems. At the same time, other lines of research consider psychopathy as a "life history strategy that is evolutionarily adaptive" [65](p.1). The evolutionary advantage is driven by the ability of psychopathic people to be "cheater-hawks", i.e. individuals who use manipulation and deception to exploit cooperation, but also adopt intimidation and aggression to achieve their goal. As interestingly presented by Meloy et al. (2018) [65] (p.9): "[...] psychopathy is a genotype within our species, which is phenotypically expressed to different degrees depending on culture, and confers a genetic advantage". Glenn, Kurzban and Raine shed light on the positive evolutionary perspective of psychopathic traits [63]. They described the different dimensions of psychopathy, considering the benefits and the costs for each one of them. They then compared two main visions of psychopathy: (1) the adaptive perspective, in which psychopathic traits are considered an adaptive strategy developed over generations as a response to environmental stimuli; and (2) the pathology perspective, in which psychopathy is seen as a dysfunctional pathology deriving from a series of mutations over time unrelated to strategic advantages. Providing evidence supporting and weakening each of the two theories, the author concluded that both views could be sustained, and further research should investigate this more thoroughly. Previous research has also argued that differences arising from psychopathy can be evolutionarily advantageous [64]. In their work, Krupp et al. argue that psychopathy is not a disorder but an "evolved life-history strategy". Although they recognise the psychological differences between psychopaths and non-psychopaths, they assert that such differences are an evolutionarily advantage. Because of the main traits of psychopathy (e.g. manipulativeness, exploitativeness, deceiving attitudes, lack of fear and empathy, and superficial charm), psychopathy has been considered to be an "adaptation for social predation" [65]. Previous studies looked at successful psychopathy as a form of adaptation to the environment. The successful psychopath is defined as "one who embodies the essential personality characteristics of psychopathy but who refrains from serious antisocial behaviours" [66] (p.459). Manipulative interpersonal attitudes, as well as lack of guilt-aversion, can be interpreted as positive and adaptive behaviours when environmental conditions are harsh, as they lead individuals to gather more resources and therefore be more likely to procreate [67]. In their study, Međedović examined the relationship between psychopathy and fitness, considering the moderating role of the environment, where fitness is represented as the ability to reproduce [67]. Their data showed that some aspects of psychopathy (interpersonal and affective sphere) correlate positively with individuals' fitness, leading towards more offspring in the future. At the same time, other aspects such as impulsivity and recklessness are negatively correlated to reproductive success. Finally, studies looking at the correlation between professional success and psychopathy dimensions found that fearless dominance was positively correlated with success, whereas self-centred impulsivity was negatively linked to professional success [68]. The work here presented supports the adaptive theory suggesting that psychopathic traits may not be a dysfunction but rather a consequence of human evolution.

In this thesis, I investigated the evolutionary aspect of psychopathy through the design of a model aimed at simulating the evolution of a community where a portion of individuals express some of the most defining traits of psychopathy. More specifically, the models aimed at investigating the evolution of a community composed of two separate behavioural types: cooperative tendencies and risk-aversion attitudes. The goal was to find an answer to the research questions initially asked: *Can traits belonging to the psychopathy construct positively contribute to the evolution of a community? Can individuals expressing those traits invade the general population? Can those traits be evolutionarily advantageous?*

Chapters 6 to 10 presented the evolution of the simulation through different phases, each of them making the model a more realistic representation of real-world interactions and dynamics.

By introducing one new feature at the time, I disentangled the contribution of the different aspects on the evolution of the community. Starting from the basic mutation model in Chapter 7, I analysed how: (1) the inclusion of conditional cooperation (Chapter 9), and (2) the representation of a more exhaustive cost structure for selfish individuals (Chapter 10) affected the evolution of the population, for a set of different environmental, economical and ecological factors (such as the environmental offer, the community cost and the mortality rate).

From the first model without mutation, the positive contribution of individuals showing some dimensions of psychopathy was evident when resources were scarce. This advantageous contribution was then confirmed when introducing the mutation mechanism across individuals. In this first mutation model, a selfish risk-seeking population invaded the entire community in the case of paucity of resources, proving the evolutionary superiority of selfish risk-seekers over the general population composed of generous risk-averse individuals (Chapter 7). The advantage of those individuals showing some of the psychopathic traits was robust, and remained consistent also when the generous individuals were modelled as conditional cooperators (Chapter 9). The populations were indeed composed of both phenotypes, but selfish individuals were the majority as long as their mortality risk during the harvesting phase was not extreme ($m_S = 50\%$). Introducing lastly an individual cost for antisocial behaviours allowed the model to present a more realistic overview of the community dynamics (Chapter 10). Populations survived independent of the mortality probability for risk-seekers in all scenarios when resources were abundant and in most situations where the environmental conditions were harsh. Also, the equilibrium population showed a majority of citizens expressing behaviours typical of the psychopathy construct, suggesting their higher fitness in most of the scenarios simulated. This dynamic was inverted only when the probability of perishing for risk-seeking individuals was equal to 50%.

These results should be read in light of the large body of literature investigating the evolution of cooperation in humans. The behaviour expressed by generous risk-averse individuals can be described as cooperative, while selfish risk-seeking agents behave more similarly to free-riders. Several scholars have investigated how cooperation evolves amongst humans, using both simulations [115, 117, 128] and analytical models [25, 129, 170]. Cooperation has been proved to evolve and dominate as a strategy in different contexts, for example when reciprocity is introduced as a mechanism in interactions [115] or when kin selection, direct/indirect/network reciprocity and/or group selections are at work [171]. Punishment (either institutional or from peers) is another mechanism that allows the evolution of cooperation [172]. Most of these mechanisms rely on the fact that the benefits deriving from cooperative actions outweigh the costs. In the simulations presented here, results highlight that in most situations the costs for taking advantage of the community (by not contributing to the public good) are low enough to allow selfish and risk-seeking individuals to evolve and outweigh generous and risk-averse individuals. That is, the costs that the community has to pay are not sufficient to deter selfish behaviours from spreading and becoming the dominant traits in the population. However, when costs are imposed not only at the collective level but also at the individual one, results start to be more in line with previous literature. That is, cooperation is fostered and individuals behaving in a cooperative way tend to invade the community and become the dominant phenotype in the population.

Overall, all these models show how behaviours aligning with some of the core characteristics of psychopathy were advantageous for individuals, as long as the conditions were not extreme. Indeed, selfish and risk-seeking individuals comprised the majority of the population in most settings across the different models. Therefore, my findings support the theory that psychopathic traits can be evolutionarily adaptive. This evolution suggests that selfish and risk-seeking behaviours are favoured over generous and risk-averse attitudes, in most of the cases: results suggest that selfish individuals perform better than generous individuals, achieving higher fitness values. However, the fitness is here defined as an individual performance, which does not depend on how the community is performing as a whole. This is an interesting aspect that future research should take into account, especially considering the dominant dynamics in our modern society. Individuals benefit from living in a dense and cohesive community and the evolution of each citizen is indeed strongly correlated with the development of the community. Being part of a cohesive community gives the opportunity for citizens to benefit from a dense network of help and support. At the same time, a community that receives more contributions from its own citizens is able to provide more services that the citizens can benefit from. Thus, it would be important to understand how the fitness of the community influences the individuals' fitness, potentially changing the equilibria of the model. Another aspect that would be of interest for future research is to allow the single personality traits to evolve separately, allowing therefore more complex behavioural combinations to arise. That is, in this thesis I consider selfish and risk-seeking attitudes (as well as generous and risk-averse traits) as one unified behaviour profile that evolve together as a single personality trait. However, an individual can for example express generous attitudes and be prone to engage in risky actions, but this evolution of behaviours was not allowed in my model. By modelling each behaviour component (such as selfish/generous and risk-seeking/risk-averse) separately, it would be possible to observe whether the construct of psychopathy as a whole is evolutionarily adaptive or only some of its components. For example, in this simulation, is it the combination of selfish and risk-seeking behaviours that are evolutionarily adaptive? Would other combinations lead to the total invasion of the community? My conclusion on these questions is that the combinations of the two aspects (selfishness and risk-seeking) is what makes individuals more successful. That is because individuals who engage in risky actions gather more resources for themselves, improving in this way their own fitness. At the same time, given the heterogeneity of the community, behaving in a selfish way is the optimal solution to protect the resources gathered. In a community where the benefit of the population is strongly correlated with the individual fitness, more generous behaviours would be favoured over selfishness. Thus, depending on the society we are living in, different behaviours would arise as evolutionarily adaptive. In a work place where team work is essential, generous behaviours will be more advantageous. On the other hand, in a structured and hierarchical society, a more selfish and self-centred attitude will yield higher profits for the individual, making selfish and risk-seeking behaviours evolutionarily adaptive.

This individual-based model aimed at shedding light on the evolutionary role of some dimensions of psychopathy, using simulation techniques that have not been employed in the study of psychopathic traits and evolution so far. Although more work is necessary to give a robust answer to the questions posed initially, results point towards an evolutionarily adaptive role of psychopathy.

11.2.4 Summary

Results from the simulation model seem to suggest that psychopathic traits are essential for the survival of the community in specific conditions. On the other hand, results from the experiments conducted suggest that psychopathic people are detrimental for the cooperation of the groups. Highly psychopathic individuals are known to compose roughly 1 per cent of the entire population [173]. The costs for their anti-social and criminal behaviours are high for the community but they are much higher for the individuals, often including incarceration and ostracism from the society. My simulations depicted a milder scenario, in which the community had to pay the most of the costs for these behaviours, introducing only at the end a personal cost linked to these behaviours. Interestingly, when the costs were introduced at the individual level, the percentage of selfish risk-seeking individuals dropped drastically, although remaining slightly higher than what we observe in real life (high mortality rate and individual cost for selfish risk-seekers). Therefore, this suggests that psychopathic traits have indeed evolved to favour some individuals over generations, but only a small number could be sustained. This is also what we observe in real life. Successful psychopaths (i.e.,"one who embodies the essential personality characteristics of psychopathy but who refrains from serious antisocial behaviours" [174] (p.459)) have been found extremely prosperous in our society [66]. Manipulative interpersonal attitudes, as well as lack of guilt-aversion, can be interpreted as positive and adaptive behaviours when environmental conditions are harsh, as for example in highly competitive work environments [66, 169]. Nevertheless, these attitudes are only efficient in harsh and competitive environments (such as leadership and high power positions), and they are detrimental and self-destructive in more benign environments, where cooperation is the key. Thus, a world of only high psychopaths would not be sustainable as there would be no one to manipulate and free-riding would not be an option. Interestingly, situations such as the one presented in the experiment in Chapter 4 (in which groups are equally composed of high and low psychopathic people) might occur in extremely competitive and harsh scenarios, where usually groups are not performing cooperative but rather competitive tasks. Hence, although high psychopathic people do diminish the cooperation of the groups, this is not needed for the group task..

> "I think it inevitably follows, that as new species in the course of time are formed through natural selection, others will become rarer and rarer, and finally extinct. The forms which stand in closest competition with those undergoing modification and improvement will naturally suffer most."
>
> Charles Darwin, The Origin of Species

IBM Matlab Code

```
%% SIMULATION

% Two phenotypes are present in this simulation SELFISH RISK-SEEKING SUBJECTS (S) & GENEROUS RISK-AVERSE SUBJECTS (G).

function [N]= RUNSIMULATION()

%% Initialisation

% Initial population size - it will vary during the generations
INITIAL_N=250;
% Number of times the population will evolve
G=1000;
% Percentage of selfish risk-seeking individuals in the initial population
P=10;
% Number of independent realisations to obtain robust results
I=1000;

%% Store the variables for each of the I iterations and the G generations

% Community resources at each generation
C_Res = zeros(I,G);
% Environmental resources provided at each generation
Environment = zeros(I,G);
Environment_total = zeros(I,G);
% Population composition at each generation
Strat = zeros(I,G);
% Resources gathered by each individual in each generation before PGG
I_Res = zeros(I,G);
% Resources owned at the end of the game by each individual in each generation
I_Final_Res = zeros(I,G);
% Contribution made by each individual in each generation
I_Cont = zeros(I,G);
% Average resources for S individuals in each generation
S_Res = zeros(I,G);
% Average resources owned at the end of the game by S individuals in each
```

```
    generation
S_Final_Res = zeros(I,G);
% Average resources for G individuals in each generation
G_Res = zeros(I,G);
% Average resources owned at the end of the game by G individuals in each
    generation
G_Final_Res = zeros(I,G);
% Average contribution for S individuals in each generation
S_Cont = zeros(I,G);
% Average contribution for G individuals in each generation
G_Cont = zeros(I,G);
% Total number of S, G and total population size
Total_G = zeros(I,G);
Total_S = zeros(I,G);
Total = zeros(I,G);
Count_S = zeros(I,G);
Count_G = zeros(I,G);
% Cost of having S individuals in each generation
Cost = zeros(I,G);
% Reproduction probabilities
Genotype = zeros(I,G);
Genotype_S = zeros(I,G);
Genotype_G = zeros(I,G);
Phenotype_S = zeros(I,G);
Phenotype_G = zeros(I,G);
% Mutations
Mutations = zeros(I,G);
% Mortality
Mortality = zeros(I,G);
% S individuals dead in the harvesting phase
S_Mortality = zeros(I,G);


%% Run the complete game

for i=1:I % iterate the simulation I times

    for g=1:G % iterate the game over G generations

        % Players are randomly assigned to a behavioural phenotype:
        % 0 = generous risk-averse subjects
        % 1 = selfish risk-seeking subjects

        if g==1
            [strategies] = initialpopulation(INITIAL_N,P);
            N=INITIAL_N;
        else
```

```
             strategies = newstrategies;
             N=size(newstrategies,1);
         end

        % Mortality stage for S due to their risky behaviours

        count_S_before = sum(strategies(:,1));
        G_before = N;
        [strategies,N] = mortality(strategies,N);
        G_after = N;
        count_S_after = sum(strategies(:,1));
        Mortality(i,g) = G_before - G_after;
        S_Mortality(i,g) = count_S_before - count_S_after;

         % Environmental offer

         total_offer = 1.2;

         % Define the resources available per each individual

         if N == 0
             offer = total_offer/N_0;
         else
             offer = total_offer/N;
         end

         % Set the maximum amount each person can collect which is what we define as a positive environmental offer

         max_offer = 4;
         if offer>=max_offer
             offer = max_offer;
         end

        if g==1
             I_Cont_temporary = 0;
             I_Res_temporary = 0;
        end

         [i_res,i_cont,...
             c_res,i_final_res,cost] = game(N,strategies,offer,...
                                                    I_Cont_temporary,...
                                                    I_Res_temporary,g);

         % Save the mean of the different parameters

         Environment_total(i,g)=total_offer;
```

```

        Environment(i,g)=offer;

        C_Res(i,g) = c_res;

        I_Res(i,g) = nanmean(i_res(:,2));

        I_Cont(i,g) = nanmean(i_cont(:,2));

        Strat(i,g) = mean(strategies(:,1));

        I_Final_Res(i,g) = nanmean(i_final_res(:,2));

        Cost(i,g)=cost;

        I_Res_temporary = i_res(:,2);

        I_Cont_temporary = i_cont(:,2);

        % Save those parameters divided by S & G

        for j=1:N
            if (strategies(j,1)==0) % if G
                G_Res(i,g)=G_Res(i,g)+i_res(j,2);
                G_Final_Res(i,g)=G_Final_Res(i,g)+i_final_res(j,2);
                G_Cont(i,g)=G_Cont(i,g)+i_cont(j,2);
            else % if S
                S_Res(i,g)=S_Res(i,g)+i_res(j,2);
                S_Final_Res(i,g)=S_Final_Res(i,g)+i_final_res(j,2);
                S_Cont(i,g)=S_Cont(i,g)+i_cont(j,2);
            end
        end

        count_S=sum(strategies(:,1));    % Number of S in the community
        count_G=N-count_S;               % Number of G in the community

    % Control how the 2 population initialised are evolved
    % Count how many of the original S and G individuals are still alive in the population

    Count_S(i,g) = sum(strategies(:,4));
    Count_G(i,g) = N - Count_S(i,g);

        % Save the number of S & G in the community at time g, iteration i

        Total_G(i,g) = count_G;
        Total_S(i,g) = count_S;
```

```

        Total(i,g) = N;

        % Store the mean resources/contribution for phenotype at time g, iteration i

        if (count_G ~= 0)
            G_Res(i,g) = G_Res(i,g)/count_G;
            G_Final_Res(i,g) = G_Final_Res(i,g)/count_G;
            G_Cont(i,g) = G_Cont(i,g)/count_G;
        else
            G_Res(i,g)=missing;
            G_Final_Res(i,g)=missing;
            G_Cont(i,g)=missing;
        end

        if (count_S ~= 0)
            S_Res(i,g) = S_Res(i,g)/count_S;
            S_Final_Res(i,g) = S_Final_Res(i,g)/count_S;
            S_Cont(i,g) = S_Cont(i,g)/count_S;
        else
            S_Res(i,g)=missing;
            S_Final_Res(i,g)=missing;
            S_Cont(i,g)=missing;
        end

        % Control if the generation survives and determine the new set of strategies in the population

        [newstrategies, mutations,N_new]...
        = replication(strategies, N, i_final_res);

    N = N_new;

    % Save the updated reproduction rates & mutations

    Mutations(i,g)=nanmean(mutations);

    % Mean Reproduction Rates Over generations

   Genotype(i,g) = nanmean(strategies(:,2));
   Phenotype_S(i,g) = nanmean(strategies(:,3));
   Phenotype_G(i,g) = nanmean(strategies(:,4));
   Genotype_S(i,g) = nanmean(strategies(:,2)+strategies(:,3));
   Genotype_G(i,g) = nanmean(strategies(:,2)-strategies(:,4));

    end % generation
```

```

end % iteration

% Community resources at each generation
C_RES = mean(C_Res,1);
% Environmental resources provided at each generation
ENVIRONMENT = mean(Environment,1);
ENVIRONMENT_TOTAL = mean(Environment_total,1);
% Population composition at each generation
STRAT = nanmean(Strat,1);
% Resources gathered by each individual in each generation
I_RES = nanmean(I_Res,1);
% Resources owned at the end of the game by each individual in each generation
I_FINAL_RES = nanmean(I_Final_Res,1);
% Contribution made by each individual in each generation
I_CONT = nanmean(I_Cont,1);
% Average resources for S individuals in each generation
S_Res = nanmean(S_Res,1);
% Average resources owned at the end of the game by S individuals in each generation
S_FINAL_RES = nanmean(S_Final_Res,1);
% Average resources for G individuals in each generation
G_RES = nanmean(G_Res,1);
% Average resources owned at the end of the game by G individuals in each generation
G_FINAL_RES = nanmean(G_Final_Res,1);
% Average contribution for S individuals in each generation
S_CONT = nanmean(S_Cont,1);
% Average contribution for G individuals in each generation
G_CONT = nanmean(G_Cont,1);
% Counting variable
TOTAL_G = nanmean(Total_G,1);
TOTAL_S = nanmean(Total_S,1);
TOTAL = nanmean(Total,1);
COUNT_S = nanmean(Count_S,1);
COUNT_G = nanmean(Count_G,1);
% Cost of having S in the community at each generation
COST = nanmean(Cost,1);
% Evolution of the reproduction rates
GENOTYPE = nanmean(Genotype,1);
GENOTYPE_S = nanmean(Genotype_S,1);
GENOTYPE_G = nanmean(Genotype_G,1);
PHENOTYPE_S = nanmean(Phenotype_S,1);
PHENOTYPE_G = nanmean(Phenotype_G,1);
% Mutation rates
MUTATIONS = nanmean(Mutations,1);
```

```
% Mortality
MORTALITY = mean(Mortality,1);
% S individuals dead in the harvesting phase
S_MORTALITY = mean(S_Mortality,1);



%Save variables in a file

save('/home/OUTCOME/results.mat',...
            'C_Res',...
            'Environment',...
            'ENVIRONMENT',...
            'ENVIRONMENT_TOTAL',...
            'Strat',...
            'I_Res',...
            'I_Final_Res',...
            'I_Cont',...
            'S_Res',...
            'S_Final_Res',...
            'G_Res',...
            'G_Final_Res',...
            'S_Cont',...
            'G_Cont',...
            'Total_G',...
            'Total_S',...
            'Total',...
            'Cost',...
            'C_RES',...
            'STRAT',...
            'I_RES',...
            'I_FINAL_RES',...
            'I_CONT',...
            'S_Res',...
            'S_FINAL_RES',...
            'G_RES',...
            'G_FINAL_RES',...
            'S_CONT',...
            'G_CONT',...
            'TOTAL_G',...
            'TOTAL_S',...
            'TOTAL',...
            'COST',...
            'COUNT_S',...
            'COUNT_G',...
            'Count_S',...
            'Count_G',...
```

```matlab
                'Genotype',...
                'GENOTYPE',...
                'Genotype_S',...
                'GENOTYPE_S',...
                'Genotype_G',...
                'GENOTYPE_G',...
                'Phenotype_S',...
                'PHENOTYPE_S',...
                'Phenotype_G',...
                'PHENOTYPE_G',...
                'Mutations',...
                'MUTATIONS',...
                'MORTALITY',...
                'S_MORTALITY')

end
```

```matlab
%% INITIAL POPULATION COMPOSITION - MODEL 2 POPULATIONS

function [strategies] = initialpopulation(N,P)

strategies = zeros(N,3);

% 0 == generous risk-averse subjects
% 1 == selfish risk-seekers subjects

x=round(N*P/100);
strategies(1:x,1)=1;
strategies(x+1:N,1)=0;

reproduction_S_S = 1;
reproduction_G_G = 1;

% Assign the initial reproduction rates for the 2 phenotypes

for i=1:N

        % Reproduction rate for a H individual: (SS,SG)=(0.1,0.9)
        strategies(i,2)=reproduction_S_S;

        % Reproduction rate for a L individual: (GS,GG)=(0.03,0.97)
        strategies(i,3)=reproduction_G_G;

end

end
```

```matlab
%% INITIAL POPULATION COMPOSITION - ONE POPULATION
```

```
function [strategies] = initialpopulation(N,P)

strategies = zeros(N,4);

% 0 == generous risk-averse subjects
% 1 == selfish risk-seeking subjects

x=round(N*P/100);
strategies(1:x,1)=1;
strategies(x+1:N,1)=0;


S_phenotype = 0.01;
G_phenotype = 0.01;
reproduction_rate = 0.1;

strategies(:,2)=reproduction_rate;

% Include the external components gamma and omega

strategies(:,3)= S_phenotype;
strategies(:,4)= G_phenotype;

end
```

```
%% MORTALITY STAGE FOR S DUE TO THE RISKY ATTITUDE

function [strategies,N] = mortality(strategies,N)

% 0 == generous risk-averse subjects
% 1 == selfish risk-seekers subjects

randomnumber = rand(N,1);
mortalityrate = 0;      % parameter describing the mortality rate for S
    individuals,can take values in {0, 0.25, 0.5}
savedead=zeros(N,1);

for i=1:N
    if strategies(i,1)==1
       if randomnumber(i) <= mortalityrate
           savedead(i)=i;
       end
    end
end

savedead(savedead == 0) = [];
```

```

strategies(savedead,:) = [];

N=size(strategies,1);

end
```

```
%% HARVESTING & PUBLIC GOODS GAME

function[i_res,i_cont,...
             c_res,i_final_res,cost] = game(N,strategies,offer,
                 I_Cont_temporary,I_Res_temporary,g)

% Variables initialisation

i_res = zeros(N,2);          % individual resources (before PGG)
i_cont = zeros(N,2);         % individual contribution
i_final_res = zeros(N,2);    % individual resources (after PGG)
m = 1.5;                     % multiplier factor for the PGG
lambda = 0;                  % lambda, can take values in {0,0.5,1}
individual_cost = 0.10;      % individual cost for S individuals, set to 1/2
                             % the survival threshold

% Each individual makes a decision: first for gathering resources and then
    for contributing to the community wealth-fare

for i=1:N

        % Harvest phase

        [playerscore]=...
            harvesting(strategies(i,1),offer);

        % Report the results of the harvesting round

        i_res(i,1) = strategies(i,1);
        i_res(i,2) = playerscore;

        % sum the number of S in the previous generation

        S = mean(strategies(:,1));

        % Public Goods Game (PGG)

        [contribution]=pgg(playerscore,strategies(i,1),...
            I_Cont_temporary,I_Res_temporary,g);

```

```
        % Report the results of the PGG

        i_cont(i,1) = strategies(i,1);
        i_cont(i,2) = contribution;

end

% Sum up the community resources after every individual played the PGG

c_res = sum(i_cont(:,2))*m;

% The community pays a cost due to the presence of S in the community, which is proportional to their percentage in the population.

proportionS = (sum(strategies(:,1))/N)*100;

cost = (c_res*lambda*proportionS)/100;

cost(isnan(cost))=0;

% Subtract the cost to the community resources - final resources the community has to redistribute amongst the citizens

c_res = c_res - cost;

% Distribute the communal pot equally among the citizens, regardless their contribution - % Final resources owned by each subject not subjected to additional costs (G)

for i=1:N

    i_final_res(i,1)=strategies(i,1);

    i_final_res(i,2)=i_res(i,2)+((c_res)/N)-i_cont(i,2);

end

% INTRODUCE AN INDIVIDUAL COST FOR SELFISH INDIVIDUALS

for i=1:N

    if strategies(i,1)==1

        i_final_res(i,2)=i_final_res(i,2)-individual_cost;

    end
end
```

```


end
```

```
%% HARVESTING PHASE

function [playerscore]= harvesting(strategy,offer)

if (strategy == 1)

    % S behaviour
    playerscore = 0.8*offer;  %they gather 80% of what the environment offers

else

    % G behaviour
    playerscore = 0.5*offer; %they gather 50% of what the environment offers

end

end
```

```
%% PUBLIC GOODS GAME

% Given the total amount earned during the harvesting phase, player now have to
% decide how much to contribute to the community well-being

function [contribution] = pgg(playerscore,strategies)

% Initialisation

contribution = 0;

if (strategies == 1) % selfish risk-seekers subjects

    contribution = P_PGG(playerscore);

else % generous risk-averse subjects

    contribution = N_PGG(playerscore);

end

end
```

```
%% PUBLIC GOODS GAME - CONDITIONAL COOPERATION

% Given the total amount earned during the harvesting phase, player now have to
% decide how much to contribute to the community well-being

function [contribution] = pgg(playerscore,strategies,I_Cont,I_Res,g)

% Initialisation

contribution = 0;

if (strategies == 1) % selfish risk-seekers subjects

    contribution = P_PGG(playerscore);

else % generous risk-averse subjects - conditional cooperation

    contribution = N_PGG(playerscore,I_Cont,I_Res,g);

end

end
```

```
%% SELFISH RISK-SEEKING STRATEGY IN THE PGG

function contribution = P_PGG(playerfinalresources)

% contribution for S individuals = 20%

contribution = 20*playerfinalresources/100;

end
```

```
%% GENEROUS RISK-AVERSE STRATEGY IN THE PGG - PURE COOPERATION

function contribution = N_PGG(playerfinalresources)

% contribution for G individuals = 100%

contribution = 100*playerfinalresources/100;


end
```

```
%%GENEROUS RISK-AVERSE STRATEGY IN THE PGG - CONDITIONAL COOPERATION

function contribution = N_PGG(playerfinalresources,I_Cont,I_Res,g)
```

```

if g==1

    contribution = playerfinalresources;

else

    previous_cont = I_Cont./I_Res;
    previous_contribution = nanmean(previous_cont);
    contribution = previous_contribution*playerfinalresources;

end

end
```

```
%% REPRODUCTION RULE AND NEW POPULATION

function [newstrategies,mutations, N_new]...
        = replication(strategies , N, i_final_res)

% Initialisation

offspring = zeros(N,1);
max_offspring = 10;

% Set the survival condition for the generation

individual_threshold = 1;

% Determine the dimension of the next population according to the
% offspring of each individual


for s = 1:N

    if (i_final_res(s,2)>=individual_threshold)

        % Count the number of offspring per subject
        % proportional to their resources.

        %number_offspring = (max_offspring*(i_final_res(s,2)-
            individual_threshold))/ ...
        %                   (max_offspring*individual_threshold);

        number_offspring = i_final_res(s,2) - 1;
        offspring(s) = round(number_offspring);

```

```
    else

        offspring(s)=0;

    end
end

% Control that there are no negative number of offspring and that no
% individual has overcome the max number of offspring.

for s= 1:N

    if offspring(s)>max_offspring

        offspring(s) = max_offspring;

    end

    if offspring(s)<0

        offspring(s)=0;

    end

end

% Calculate the phenotype of the newborns and mutate the reproduction
    probabilities.

[newstrategies, mutations, N_new] = mutation(offspring, strategies, N);

end
```

```
%% MUTATION OF THE REPRODUCTION RATES OF THE TWO PHENOTYPES

% Calculate the phenotype of the newborn then mutate the reproduction
    probabilities

function [newstrategies,mutations_genotype, N_new] = mutation(offspring,
    strategies, N)

mean = 0;
variance_genotype = 0.1;
variance_phenotype_S = 0.01;
variance_phenotype_G = 0.01;

newstrategies = zeros(sum(offspring),4);
```

```

% Assign a phenotype to each new offspring according to the reproduction probabilities

for s=1:N
    if offspring(s)>0

        % new index to assign the phenotype to the correct set of offspring

        if s==1
            count = 1;
        else
            count = sum(offspring(1:s-1))+1;
        end

        randomnumber = rand(sum(offspring),1);

        for j = count:count+offspring(s)-1

            % assign the phenotype & reproduction rates

            if strategies(s,1)==1

                % S that reproduces an S

                if (randomnumber(j) <= strategies(s,2)+strategies(s,3))

                    newstrategies(j,1) = 1;
                    newstrategies(j,2) = strategies(s,2);
                    newstrategies(j,3) = strategies(s,3);
                    newstrategies(j,4) = strategies(s,4);

                else

                % S that reproduces a G
                    newstrategies(j,1) = 0;
                    newstrategies(j,2) = strategies(s,2);
                    newstrategies(j,3) = strategies(s,3);
                    newstrategies(j,4) = strategies(s,4);
                end
            else
                if (randomnumber(j) <= strategies(s,2)-strategies(s,4))

                % G that reproduces an S

                    newstrategies(j,1) = 1;
                    newstrategies(j,2) = strategies(s,2);
```

```
                    newstrategies(j,3) = strategies(s,3);
                    newstrategies(j,4) = strategies(s,4);

                else

                % G that reproduces a G
                    newstrategies(j,1) = 0;
                    newstrategies(j,2) = strategies(s,2);
                    newstrategies(j,3) = strategies(s,3);
                    newstrategies(j,4) = strategies(s,4);
                end
            end

        end

    end
end

N_new = size(newstrategies,1);

%% Now that each newborn has a phenotype, I need mutate the reproduction probabilities

mutations_genotype = normrnd(mean, variance_genotype, [N_new, 1]);
mutations_phenotype_G = normrnd(mean, variance_phenotype_G, [N_new, 1]);
mutations_phenotype_S = normrnd(mean, variance_phenotype_S, [N_new, 1]);

% Apply the mutation to the reproduction rates
% Both reproduction rates mutate for both phenotypes

for j=1:N_new

    newstrategies(j,2)=newstrategies(j,2)+mutations_genotype(j);
    newstrategies(j,3)=newstrategies(j,3)+mutations_phenotype_S(j);
    newstrategies(j,4)=newstrategies(j,4)+mutations_phenotype_G(j);

    % the reproduction rate has to stay between [0,1], hence if it exceed the limit, it will be set equal to 1 or 0.

    if newstrategies(j,2)>1
        newstrategies(j,2)=1;
    elseif(newstrategies(j,2)<0)
        newstrategies(j,2)=0;
    end

    if newstrategies(j,3)>1-newstrategies(j,2)
        newstrategies(j,3)=1-newstrategies(j,2);
```

```
    elseif(newstrategies(j,3)<0)
        newstrategies(j,3)=0;
    end

    if  newstrategies(j,4)>newstrategies(j,2)
        newstrategies(j,4)=newstrategies(j,2);
    elseif(newstrategies(j,4)<0)
        newstrategies(j,4)=0;
    end


end

end
```

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