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The role of polymorphism in the evolution and stability of cooperation

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1. Introduction

1.1. Studying positive interactions

Interactions in nature traditionally divided into three main categories in textbooks: positive, neutral, and negative (Boucher et al. 1982; Boucher 1985; Bronstein 1994a; West et al. 2006). The roots of studying and discussing negative interactions, for instance competition, are deeper in ecological and evolutionary literature, as biologists since Darwin have understood that 'struggle for survival' is the fundamental mechanism driving natural selection (Dawkins 1976; Axelrod and Hamilton 1981; Nowak et al. 1995). Positive interactions, however, have always puzzled scientists, including Darwin himself, since any individual performing a costly behavior that provides benefit for another individual faces fitness disadvantage and results in exclusion according to the laws of natural selection (Hamilton 1963, 1964; Trivers 1971; Axelrod and Hamilton 1981, Bull and Rice 1991; West et al. 2007a,b). Yet diversity of helping behavior is widespread in nature (Boucher 1985; Bronstein 1994a; Herre at al. 1999; Nowak 2012), and has been essential in shaping our biosphere (Douglas 1994; Maynard Smith & Szathmáry 1995). Thus investigating factors that promote behaviors that benefit others remains one of the main topics in evolutionary biology (Sachs et al. 2004; West et al. 2007a; Nowak 2012) since the anarchist prince Kropotkin (1902) first wrote a book about the diversity of such type of interactions in nature, partly to duel the cruel and harsh reality depicted by Darwin's theory (Nowak et al. 1995).

A behavior is termed cooperative, or altruistic, if it benefits others at the benefactor's cost, and the behavior has evolved, at least partially, because of this benefit (West et al. 2007a,b). The evolution and stability of any trait that controls such behavior is seems to be in conflict with the laws of natural selection, according to which the evolution of those traits are favored that directly and solely benefit the individual possessing them (Hamilton 1963, 1964; Sachs et al. 2004). At face value, therefore, these interactions present an evolutionary dilemma.

A great number of studies have analyzed a wide range of social interaction types, and tried to find explanations for their existence and stability (Bull & Rice 1991; Herre et al. 1999; Sachs et al. 2004; Bergstrom et al. 2003; Leimar & Connor 2003; Bshary & Bronstein 2004; Doebeli

& Hauert 2005; Lehman & Keller 2006; Nowak 2006b; West et al. 2007a,b; Archetti & Scheuring 2012; Nowak 2012). From an evolutionary perspective, a behavior is social if it has fitness consequences for both the actor individual that performs the studied behavior, and another set of individual(s), the recipient(s) (West et al. 2007b). These interactions can be considered taking place between individuals, either from the same either from different species, between populations, or between communities. We talk about cooperation, if the reciprocal interaction takes place between conspecifics (Bshary & Bronstein 2004; West et al. 2007b), meaning that partners are usually also in competition with each other, or/and share a common gene pool. When the two or more interacting individuals are from different species, and therefore competition cannot be strong between them, we term such interactions as mutualisms (Bshary & Bronstein 2004; West et al. 2007b). Mutualism is an "interaction between species that is beneficial to both", but may or may not involve physical contact between the partners. Symbiosis is an alternative expression also commonly used, and this term strongly associated with mutualisms, but generally symbiotic interactions are "the living together of two organisms in close association" (Boucher et al. 1982), and the outcome can be mutualistic, commensal, or parasitic (Bshary & Bronstein 2004).

1.2. Modeling social interactions

Social interactions are traditionally described and studied by two main approaches (Boucher et al. 1982). In a population-level consideration of positive interactions, as mutualism is generally defined, one population has a positive effect on the growth of another population. This approach monitors the population dynamics of populations, and considers an interaction positive if one population's growth is positively affected by another population's growth and/or presence. This modeling technique, while simple and elegant, is not capable of studying the evolutionary change, and evolutionary stability of interactions. In the individualistic approach, benefit is defined in terms of relative fitness' of organisms in the interacting populations, and each individual's success is determined by this fitness, which in turn depends on the strategy the individual adopts (Nowak 2006). Successful strategies will invade the population, and if these successful strategies benefit other members of the same, or other populations, we can define these strategies as cooperative, altruistic, or mutualistic. The most cooperative individuals are therefore the ones yielding the highest fitness in their partners (Bull & Rice 1991). Recently this latter approach is used more often to study cooperative interactions.

Cooperation is generally prone to exploitation by defectors. The terminology of strategies in theoretical models is usually dichotomic, and has many synonyms for the two main behavioral categories considered in social interactions. The ’good guys’ are the cooperators, investors, contributors, etc. The ’bad guys’ are termed defectors, selfish strategies, cheaters, egoists, non-investors, exploiters, etc. A dilemma derives from the fact that selfish individuals generally have an advantage over those who act cooperatively, by which we mean a costly act that can benefit others (Hamilton 1964; Sachs et al. 2004; Doebeli & Hauert 2005). In these cases selfish ’defectors’ interacting with their own kind have a lower ’payoff’ than cooperators, still defectors would eventually replace cooperators in the population (Nowak 2006). Hence, even if any cooperative behavior seems to be advantageous, its evolutionary origin and stability stands as one of the greatest questions in biology, as indicated by being involved in the top 25 scientific questions in the 125th Anniversary issue of Science in 2005. Numerous approaches and models are formulated to capture the essential features of cooperative interactions in nature, but the most commonly, and successfully, known and applied modeling framework comes from economics. It’s origins goes back to the works of John von Neumann, Oskar Morgenstern, and John Nash (Nowak 2006).

1.3. Evolutionary game theory: a tool for analysis

Evolutionary game theory has proven to be an efficient and prominent tool for the study of social interactions (Doebeli & Hauert 2005; Nowak 2006). Evolutionary game theory combines the concept of frequency dependent selection with the concept of strategic behavior of players, thus merges population ecology with economic game theory (Sigmund & Nowak 1999; Nowak 2006). In game theory, the costs and benefits of interactions are hardwired in the model, but the actual outcome solely depends on the type of actual partner(s) in the given interaction(s) of the focal individual player. The next advance in cooperation modeling was the introduction of population level thinking by John Maynard Smith and George Price (Maynard Smith & Price 1973), where players are not rational and payoff maximizing, as assumed by traditional game theory, but rather defined by their strategies and the payoffs they receive from the particular interaction(s). The costs and benefits of these interactions will thus give the net payoff, which can directly be translated into Darwinian fitness or reproductive success (Sigmund & Nowak 1999). The ’players’ are members of one population in the case of cooperation models, or members of several, different populations in the case of mutualism models, and all competing for a possibly large share of offsprings in their populations (Sigmund & Nowak 1999). Hence, players with successful strategies will receive high payoff, will have high fitness, and consequently, will reproduce faster or/and live longer. Poorly performing strategies will be outcompeted, and will vanish from the population. This presents an elegant process of natural selection of strategies, and combined with certain degree of mutational variability during reproduction or copying of these strategies, the stage is set for studying the evolution and stability of cooperation in biological situations (Sigmund & Nowak 1999; Nowak 2006).

With the development of the tools of evolutionary game theory, cooperation research boosted up. Several milestone studies were published offering explanations for the wide variety cooperative behavior that can be observed in nature (Dugatkin 1997; Bergstrom et al. 2003). The main mechanisms originate from kin selection, direct reciprocity, indirect reciprocity, group selection or multilevel selection, spatial selection, byproduct benefits, pseudoreciprocity, biological market approaches, partner choice, sanctioning, partner control mechanisms, to mention the most commonly discussed ones (Bergstrom et al. 2003; Sachs et al. 2004; West et al. 2007a, b; Nowak 2006b, 2012). All of these explanations, in one way or the other, involve mechanisms that eventually can be derived from some form of assortment, preferential or physical, between specific players or strategies (Archetti & Scheuring 2012).

In kin selection models, help is conditional, and more probably directed towards relatives, individuals that share similar genes with certain probability or in certain ratio, than towards strangers, thus cooperative genes help more their own kind (Hamilton 1963, 1964; Dawkins 1976; Sachs et al. 2004; Abbot et al. 2011; West et al. 2007a; Nowak 2012). In these models, cooperative behavior increases the player’s own inclusive fitness, which includes direct and indirect fitness components, that is its own, and every other individual’s reproductive success weighted by the relatedness (West et al. 2007a). The ongoing debate about the importance and interpretation of kin selection mechanisms, beside group selection mechanisms, have received a lot of attention recently (Nowak et al 2010; and see replies, for example Abbot et al. 2011), and stays as one of the hot topics in cooperation research.

In indirect reciprocity models (Nowak & Sigmund 1998, 2005), partner choice models (Bull & Rice 1991), biological market models (Noë & Hammerstein 1995), and models incorporating some form of choosiness (McNamara et al. 2008; Archetti et al. 2011a,b), assortment is achieved by some mechanisms or behavior that allows the individual to choose between potential partners. Preferential choice can be made according to some tags, reputation scores, past observations or past experience, signals, etc. Thus individuals can avert interaction with unwanted associates, and cooperators need not invest in non reciprocating partners.

Multilevel (or group) selection theory (Wilson 1975; West et al. 2007; Wilson & Wilson 2007) assumes that more or less closed groups can benefit from altruistic acts performed within the group. While defectors still dominate cooperators within groups, groups of cooperators can outcompete groups of defectors, as cooperator groups may achieve greater average payoff (Nowak 2012). Here selection acts not only on individuals, but also at the group level. In these models, cooperation my prevail under conditions where defectors would win without selection at the group level. The crucial point in studying such models in the precise mathematical formulation of the different selections acting at the different levels. In general, group level selection can favor the spread of cooperators, but the biological plausibility of such model is questionable, which also were published as the strongest critics on the early forms of group selection theory. Multilevel selection is assumed to have played an important role in many major evolutionary transitions, and probably also in human evolution (Maynard Smith & Szathmáry 1995; Wilson & Wilson 2007).

Reciprocal altruism (Trivers 1971), reciprocal cooperation (Axelrod & Hamilton 1981), reciprocity (Dugatkin 1998), and direct reciprocity (Sachs et al. 2004; Nowak 2006b), is considered as synchronous encounters between pairs of players, usually non-relatives, during which the social interaction takes place in one round, or in several turns. The key element of this interactions type is that the helping act, or the investment, is reciprocated by the benefactor, and specifically directed towards the donor. The most celebrated model of directed reciprocation, the famed Prisoner's Dilemma (PD) in its iterated form the Iterated Prisoner's Dilemma (IPD) game, has emerged as metaphor for cooperation (Trivers 1971; Axelrod & Hamilton 1981), and many times become the only considered metaphor for numerous empirical examples of cooperation (Archetti & Scheuring 2012). There are, however, other classical games closely related to PD, each representing different social situations in 2×2 pairwise games (Hauert 2002; Archetti & Scheuring 2012).

1.4. Pairwise cooperative interactions

Studying the phenomena of cooperation has been mostly associated with analyzing pairwise social interactions. In such models, the basic assumption is that two individuals interact, each can either Cooperate (C) or Defect (D). Cooperators pay the cost c, and may receive the benefit, or reward, bc, scaled in the unit of c. Defectors pay no cost. We assume that the benefit may depend on the number of cooperators nr, thus we get b_{nr}. Depending on the parameters c, b_1, b_2, there are four possible situations (Figure 1.1).

	COOPERATE	DEFECT
COOPERATE	$b_2 c - c$ $b_2 c - c$	$b_1 c$ $b_1 c - c$
DEFECT	$b_1 c$ $b_1 c - c$	0 0

Figure 1.1: The generalized payoff matrix of 2×2 pairwise games. Depending on the parameters c, b_1, b_2, four game theoretical situations can be distinguished. These are the *Harmony Game*, the *Prisoner's Dilemma Game*, the *Snowdrift Game*, and the *Stag Hunt Game*.

If $b_2 - b_1 > 1$ and $b_1 > 1$, cooperation (C) is the dominant strategy and the only stable equilibrium. This is often called *Harmony*, or the region of *No conflict* (Hauert 2002; Archetti & Scheuring 2012). If $b_2 - b_1 < 1$ and $b_1 < 1$, we are in the region of *Prisoner's Dilemma Game*, where defection (D) is the dominant strategy and the only stable equilibrium. In the region where $b_2 - b_1 < 1$ and $b_1 > 1$, there are two asymmetric equilibria, the CD and DC, and is called *Chicken Game*, *Hawk–Dove*, or *Snowdrift Game*. The last is a region of a coordination game, called the *Stag Hunt Game*, where $b_2 - b_1 > 1$ and $b_1 < 1$, and there are two symmetric equilibria CC and DD. These four games can be the metaphors for many different social situations (Archetti & Scheuring 2012).

Out of the four games mentioned in the previous section, Prisoner's Dilemma become the most famous and broadly studied for several reasons. First, it was the pioneering game theoretic metaphor for cooperation in biology. It also represented the hardest situation of social dilemmas, as the cooperative outcome is hopeless without additional helping mechanisms, thus the stage was set for continuing research. Its fame can also be coming from the popular tournaments that were organized at the dawn of simulating social interactions on computers. The first tournaments, organized by Axelrod, aimed to find the championship strategy, a strategy that can do best in every social situation (Axelrod 2012). Computer programs with predefined rules played in repeated interactions in a digital arena according to the parameters of the Prisoner's Dilemma Game (PD). The most successful strategies, such as "Tit-for-Tat" (TFT), "win-stay, loose-shift", or Pavlov, proved to be following the hardwired rules of conditional cooperation. The most well know and extensively studied strategy, the "Tit-for-Tat" started with cooperation and then followed a reflexive behavior by mimicking the opponent's previous move. Perhaps the extensive use of TFT-like strategies in PD games to explain all aspects of cooperation can also be due to the fact, that these strategies, in some extent and in their primitive ways, resembled the context-dependent, conditional and reflexive nature of social behaviors observed in nature. For biologists, these were the closest to real life organisms. In recent years, the significance and validity of PD and TFT like strategies is largely debated (Bergstrom et al. 2003; Bshary & Bronstein 2004; Archetti & Scheuring 2012), and the research on social interactions moved to new concepts, new game theoretic metaphors.

1.5. The aim of the study

Classical game theoretical approaches have made several assumptions for the sake of simplicity and to formulate models with relatively simple dynamics. While the results of these studies has been essential in understanding the mechanisms promoting or hindering cooperative behavior, the proposed models mostly felt too simple and artificial to explain social situations in real biological settings correctly. There are several hot topics and open questions in cooperation research nowadays (Nowak 2012), in which one or more of the simplifying assumptions are relaxed and substituted with biologically more plausible assumptions.

Among many others, one advance in theoretical research is the switch form dyadic models to multi-person, or *N*–person games (Dionisio & Gordo 2006; Hauert et al. 2006a; Pacheco et al. 2009; Archetti & Scheuring 2011, 2012). The recognition that real life social situations are rarely dyadic has paved the way for exploring and developing new model frameworks for multi-player social situations (Stanton 2003; Doebeli & Hauert 2005; Kiers & Denison 2008; Archetti et al. 2011b; Nunn & Lewis 2001; Archetti & Scheuring 2012).

Also, the emphasis of research is shifting from the long standing notion of static interactions (mainly fixed strategies and fixed investments in PD), to modeling the evolution and stability of flexible, context-dependent, and conditional strategies in cooperation (Doebeli & Knowlton 1998; Doebeli & Hauert 2005; André & Day 2007). Finally, applying game theoretic models for interspecific interactions, and also recognizing the importance of conditional reciprocal investments in mutualistic interactions came to age (Bshary & Bronstein 2004; Kiers et al. 2011).

In the next sections, we will relax one or more of the simplifying assumptions of classical models (Table 1), which mostly employed two-player games with static and random interaction topology, with fixed and unconditional investments and homogenous environment. We understood that cooperation can evolve and be stable under given conditions in classical models. But would relaxing these assumptions result in the change of their main findings as well? Can cooperation evolve and be stable on the long term if, for example, partners can choose with whom to interact with, or their investments include conditional components as well?

In particular, we will shortly overview the backgrounds and main findings of the above mentioned two paradigms, *N*–person games and conditional strategies, in cooperation research, and we will analyze specific problems which describe specific biological situations. Throughout this study we will use the formalism demonstrated in Figure 1.1, namely parameterize the studied models with the cost and the benefit of cooperation c and b, respectively. Although the proposed models will be based on only a couple of biological examples, and we will draw ideas and motivation from specific social interactions in nature, our results and conclusions will have more general validity.

	Classical cooperation models	**Replacement with biologically more realistic assumptions**
Number of interacting partners	2	2< → *N*-person games (section 2.2)
Payoff function type	Linear	Non-linear → Threshold PGGs (section 2.2)
Interaction topology	Static	Dynamic → Interaction networks (section 3.3)
Type of partner association	Random	Preferential → Partner choice models (section 3.3)
Form of cooperative investment	Fixed, static	Conditional → Reciprocal investment games (section 3.4)
Quality of the environment	Homogenous	Heterogeneous → Spatial environmental heterogeneity (section 3.4)

Table 1: Throughout this study we will shortly overview some important assumptions made in traditional cooperation studies, and then inspired by empirical observations, we will relax one or more of these assumptions.

2. Intraspecific *N*–person social dilemmas

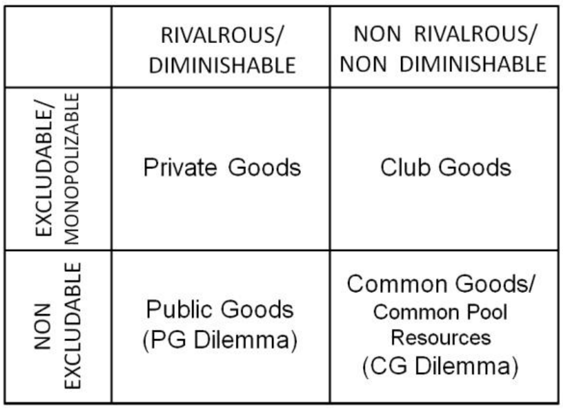
Majority of the current evolutionary game theoretical studies that shed light on the mechanism behind many cooperative phenomena in biological systems concentrated on pairwise interactions between individuals. *N*–person games have been, surprisingly, studied much less than pairwise games (Archetti & Scheuring 2012). Except for a couple of studies (see for example Boyd & Richerson 1988; Dugatkin 1990), *N*–person games not only recently have received attention, although the conceptual foundations were already established, again, originating mostly from economics and sociology (Hardin 1968; Olson 1965; Oliver et al. 1985; Heckathorn 1996). The most well-known metaphor for *N*–person social dilemmas comes from Hardin (1968).

2.1. The problem of collective actions

In the social conflict Hardin considered (1968), there is a common resource open to all–which is called the commons, or common good–which is available for everyone, and no-one controls it. He gave the example of a group of herders, who keep their cows on a common field to graze freely. Each owner's interest is to have as many cows as possible, since his or her profit increases with the number of cows grown, but at the same time costs shared equally. Hence if an owner pays the same cost as others, as has the same benefit plus one unit more, his or her profit will be the highest. This results in everyone exploiting the resource more and more, which naturally leads to over-exploitation of the common good. Without any control or institution, there is no advantage of refraining from using the resource as much as possible, and the best strategy would be over-exploitation. Thus the common will become extinct. This is called the 'tragedy of the commons' (Hardin 1968; Ostrom 1990; Kollock 1998; Dionisio & Gordo 2006).

In a second type of social dilemma, a group is supposed to achieve a common goal, or a collective action. If everyone cooperates–invests–in this collective action, the common goal can be reached easily. If a self-interested individual decides not to cooperate, the goal will probably be achieved anyway, and this individual will then pay no cost of cooperating. Therefore, each individual is tempted not to cooperate, in which way he or she pays no cost of cooperating, but receives his equal share of the benefit, thus again, will have the highest payoff. Ultimately cooperation, or investments, will diminish. This is called the public goods dilemma, or also known as provision of public goods (Olson 1965; Kollock 1998; Dionisio & Gordo 2006).

In general, in *N*–person games more than two 'players' interact with each other at the same time in the form of group actions (Marvell & Oliver 1993; Anderson & Franks 2001; Nunn & Lewis 2001; Sumpter 2006; Clutton-Brock 2009). During group interactions individuals typically invest into common goods or common goals (Bergmüller et al. 2007), or into the production of a public good (Doebeli et al. 2004; Archetti & Scheuring 2012). In most of the cases this common good is available for everyone (Figure 2.1), that is the common good is non-monopolizable (or non-excludable, non-exclusive: no one can be excluded from consuming the good, or receiving its benefits) and non-rival (synonym of joint in supply, non-diminishable: consuming by an individual does not decrease its availability to another individual) (Olson 1965; Dionisio & Gordo 2006; Nunn 2000; Kitchen & Beehner 2007; Archetti & Scheuring 2012). This raises a collective action problem, where non-cooperators, often termed as free riders, can reap the benefit of the common good without investing into it (Dugatkin 1990; Nunn 2000).



	RIVALROUS/ DIMINISHABLE	NON RIVALROUS/ NON DIMINISHABLE
EXCLUDABLE/ MONOPOLIZABLE	Private Goods	Club Goods
NON EXCLUDABLE	Public Goods (PG Dilemma)	Common Goods/ Common Pool Resources (CG Dilemma)

Figure 2.1: The classification of *N*–person games according to the type of the good. *Private good* is for example the toothbrush in someone's bathroom, or most of the personal properties. *Club goods* are owned and maintained by many, but not everyone has access to it, such as cable televisions, or private parks. *Public goods* are for example the national defense, the air quality, or the global warming. *Common goods* are the fish stocks in the seas, and grazing lands.

2.1.1. Animal collective actions with threshold effects

Arguably numerous examples of group interactions found in nature can be described as *N*–person games (Hardin 1968; Boyd & Richerson 1988; Dugatkin 1990; Kollock 1998; Dugatkin et al. 2003; Dionisio & Gordo 2006; Hauert et al. 2006a,b; Rankin et al. 2007; Boza & Számadó 2011; Archetti & Scheuring 2012). In numerous examples of a collective actions, achieving the group goal, for example capturing prey, depends on the number of encircling hunters (Stander 1992a,b). During numerous instances of cooperative hunting, several individuals simply fill the position of blocking, diverting, flushing the prey. This threshold effect is documented for cooperative hunting situations in various social carnivores including lions (*Panthera leo*) (Stander 1992a,b;), African wild dogs (*Lycaon pictus*) (Fanshawe & Fitzgibbon 1993; Creel & Creel 1995; Courchamp & MacDonald 2001), chimpanzees (*Pan troglodytes*) (Watts & Mitani 2002), Harris' Hawks (*Parabuteo inicintus*) (Bednarz 1988), Brown-Necked Raven (*Corvus rufficollis*) (Yosef & Yosef 2010), and humans (Kollock 1998; Alvard & Nolin 2002).

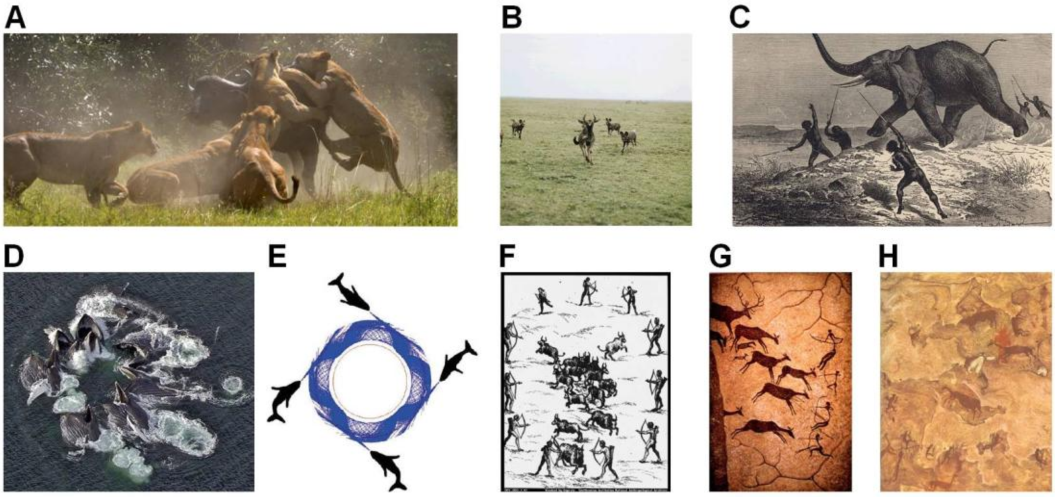


Figure 2.2: Snapshots capturing collective actions in animal and human societies. Cooperative hunting in (**A**) lions and in (**B**) African wild dogs. (**D**, **E**) Cooperative feeding in cetaceans, and the (**E**) schematics of creating a wall sound collectively with the bubble wall. (**C**, **F**, **G**, **H**) Examples of cooperative hunting in human hunter–gatherer societies. Ancient cave paintings also preserved the prehistoric hunting technique of humans, as seen in the (**G**) Lascaux caves, in French Pyrenees, originating approx. from 25,000 years ago, or the (**H**) Toquepala caves in Tacna, Peru, originating from approx. 10,000 years ago.

For example when lions are hunting small prey, each lion pursues its own animal, which is more common in wet seasons with high prey abundance (Packer et al. 1990; Stander 1992a,b). However with larger, faster, and more difficult prey (Sinclair et al. 2003), the cooperation of a group of hunters is needed to encircle, split the herd, to spot, surround and kill an animal (Figure 2.2/A) (Packer et al. 1990; Stander 1992a,b; Packer & Pusey 1997). In order to make the hunt successful several lions (about 4–7) have to work together (Stander 1992a,b; Packer et al. 1990; Funston et al. 2001), get close to the prey before starting the attack (30–50 m) and cut off its escape routes by encircling the prey from different points and filling the roles of "centers" and "wings" (Schaller 1972; Stander 1992a,b; Packer & Pusey 1997). If the number of hunters is below a threshold group size, it is not only hard to capture the prey but also to defend it against hyenas (Cooper 1991).

Chimpanzees (Boesch 1994; Watts & Mitani 2002) or wild dogs (Figure 2.2/B) (Creel & Creel 1995) sometimes use similar encircling tactics. Some predator birds, such as Harris' Hawks either perform surprise attacks on lagomorphs from different directions, or use flush–and–ambush tactics to capture hidden prey, which requires the cooperative effort of at least 4–5 hawks (Bednarz 1988). Some other bird species also hunt larger prey cooperatively, such as Brown-necked Raven (*Corvus ruficollis*) on Egyptian Mastigure (*Uromastyx aegyptius*) (Yosef & Yosef 2010), in which case two birds fill the tasks of blocking the escape routes of the prey while several others attack it from several directions, always performing the direct attack on the most exposure part of the lizard (Yosef & Yosef 2010).

Many sea mammal species, such as killer whales (*Orcinus orca*), humpback whales (*Megaptera novaengliae*), bottlenose dolphins (*Tursiops truncatus*) and spotted dolphins (*Stenella frontalis*) chase school of fish into a tight ball, sometimes driving it into a rock or to the water surface with coordinated group action, some group members performing tail slaps, creating a curtain of air around the fish ball, or performing feeding bouts (Figure 2.2/D) (Fertl & Würsig 1995; Connor 2000; Anderson & Franks 2001; Nøttestad & Simila 2001; Gazda et al. 2005). Moreover some whales may use their acoustic "trumpets" creating a "wall sound" combined with the bubble net (Figure 2.2/E), as suggested by Leighton and colleagues, to trap the fish inside the curtain (Leighton et al. 2004). These forms of cooperative feedings, naturally, requires the participation of several individuals.

Cooperative hunting in human hunter–gatherers societies has been common, as coordinated action of several hunters was necessary to chase larger preys into a natural trap and to hunt them down (Figure 2.2/C, F, G, H). Consider for example the buffalo jump sites, where supposedly several hunters chased a big herd of buffalos, or wild horses, into a cliff by making noise or scaring them with fire, and then retrieving meat safely from the dead bodies. Encircling the herd sufficiently also required several participants (Frison 1987; 1998). There are also numerous examples of threshold effects in the operation of modern human societies and in economics (van de Kragt et al. 1983). Take as an example the requirement of a minimum number of hunters on the boat during traditional whale hunting (Alvard & Nolin 2002) or the necessity of collective mass for successful employee strikes (Granovetter 1978; Macy 1991).

Finally, threshold effects in group cooperation can appear not only in human and animal hunting societies. There are well documented examples of a lower group size threshold in some cooperatively breeding species (Courchamp & MacDonald 2001; Woodroffe et al.1997; Courchamp et al. 1999). Evidence from microbial cooperation suggests, that in some cases a threshold number of cooperators, that is bacteria which produce extracellular chemical components, is crucial in producing a public good (Crespi 2001; Czárán & Hoekstra 2009). Also, at the dawn of life the first protocells were most probably composed of cooperative elements, RNA molecules, acting both as enzymes and information carriers, which could have controlled the metabolism of the protocell (Maynard Smith & Szathmáry 1995; Szathmáry 2007). The complete metabolism most probably required the cooperation of sufficient number of elements (Maynard Smith & Szathmáry 1995; Szathmáry 2007).

2.1.2. Threshold Public Good Games

Models of public goods game nicely capture the main features of all the above described cooperative phenomena (Doebeli & Hauert 2005; Archetti & Scheuring 2011, 2012). But the traditionally, and most commonly, used linear benefit return function is insufficient in capturing the threshold effect (Figure 2.3). In public good games with threshold effects, there is an optimal number of individuals necessary to perform the given group action, or there exists an optimal amount of investment into the production of the public good, or common goal. In proximity of the threshold value, joining one or few more cooperators disproportionally increases the success of the group action (Oliver et al. 1985; Kollock 1998; Ostrom 2001). So instead of the linear benefit–or return–functions, a nonlinear return paradigm is more appropriate (Figure 2.3/D, E) (Oliver et al. 1985; Heckathorn 1996; Bach et al. 2006; Pacheco et al. 2009; Archetti & Scheuring 2012).

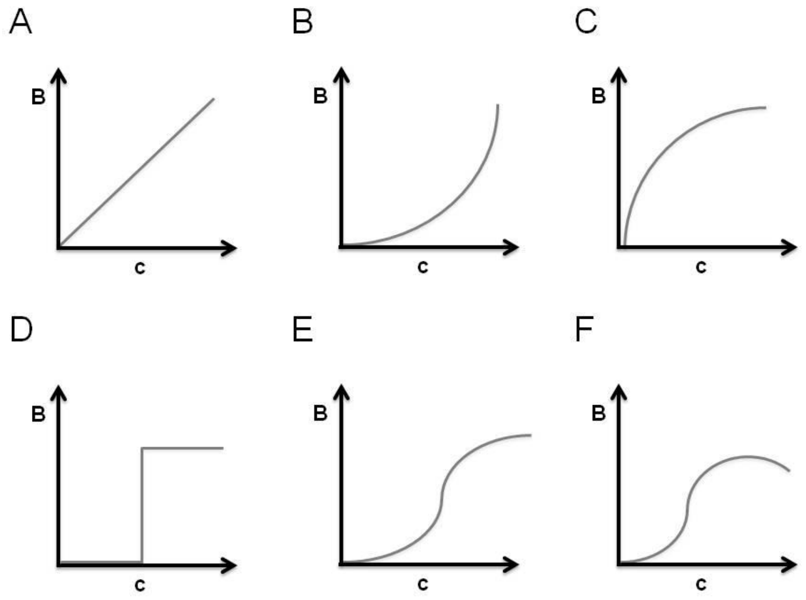


Figure 2.3: Different benefit, or return, functions in *N*–person games. The benefit of the common good, or the probability of achieving a common goal (B) depends on the number or ratio of cooperators (c). Most commonly used functions are the (**A**) linear, (**B**) accelerating, (**C**) decelerating functions. Non-linear effects can be modeled with (**D**) stepwise threshold, or (**E**) sigmoid threshold functions. (**F**) Some forms of composite functions are probably more common in biology (after Marwell & Oliver 993; Ostrom 2001; Archetti & Scheuring 2012).

There are several approaches for modelling non-linear effects in collective actions. When players invest a continuous amount into the production or maintenance of public good, the game is called the *N*–person Prisoner's Dilemma Game (Archetti & Scheuring 2011, 2012). In the n–player Threshold Public Good Game (Bach et al. 2006; Boza & Számadó 2011), in the conceptually similar Volunteer's Dilemma Game (Archetti 2009; Archetti & Scheuring 2012), or in N–person Stag Hunt Game (Pacheco et a. 2009), the successful cooperative effort is achieved only if the number of cooperating individuals reaches a given threshold. In these games different levels of cooperation can be an evolutionary stable outcome, depending on the cost of cooperation, and the proportion of initial cooperative decisions in the population (Bach et al. 2006; Pacheco et a. 2009; Boza & Számadó 2011; Archetti & Scheuring 2012). Let us now study one specific model of collective action with threshold effects in a multilevel selection model, which adequately captures the most essential features of the social situations presented in the previous section.

2.2. The coexistence of cooperators and defectors in collective actions

2.2.1. A model of Threshold Public Good Games incorporating multilevel selection

Here we study the interaction of selection acting on the level of individuals engaged in a Threshold Public Good Games (TPGG) and selection acting on these groups while competing for territories. While these situations assume that groups of individuals engage in an interaction which may or may not end in successful cooperation, these groups themselves often compete with each other (Kitchen & Beehner 2007). For example, in one of the most studied group behavioral biological systems, lioness form a pack to hunt together, yet they are in direct competition with other lion packs with which they share common borders (Packer et al. 1990; Scheel & Packer 1991; Heinsohn & Packer 1995; Grinnel 2002; Mosser & Packer 2009). The same holds for all group hunting territorial species from hyenas through whales, African wild dogs to humans (Wilson et al. 2002; Mitani & Watts 2005; Choi & Bowles 2007; Bowles 2009).

Thus, our aim here is to propose and analyze a model that integrates Threshold Public Goods Games with multilevel selection approach. We do so first by giving analytical solutions for the evolutionarily stable level of cooperators for various group sizes and threshold levels, at first assuming only individual selection; then by studying the interaction of individual and group level selection with a series of computer simulations validated by the numeric results. We study 3 basic setups in the computer simulations: (i) individual selection only, (ii) group selection only, (for comparison), and (iii) the combination of both, in which case first we assume that (iii/a) all individuals are obliged to participate in group defense, and then we relax this assumption by allowing (iii/b) voluntary participation. Individual selection in our model allows individuals to compare their success with other individuals, or compete for resources, while group selection based on the idea that stronger groups may outcompete weaker ones by overtaking their territories.

2.2.2. Models and methods

The game

The structure of the game is as follows: individuals of a group can engage in a cooperative activity (i.e. hunting, resource purchase) where every individual can follow two strategies, to cooperate with probability x or to defect with probability $1-x$. The marginal values of x are 0 and 1. The cooperative players join in the group effort (for which group size is N), and thus pay the cost of cooperation c. In contrast, defectors do not pay the fixed cost of the game. If the number of cooperators is equal or above a given threshold value T, then all of the individuals within the group can acquire the benefit b of cooperation regardless whether they cooperated or not. This derived from the non-rival, non-excludable features of the game (Dionisio & Gordo 2006), that is, no individual can be excluded from the acquired benefit of the hunt, and each consumer gains the same proportion without depleting it. However, if the number of cooperators does not reach the necessary number required for the successful achievement of the group action, then no one gets the benefit, but cooperators still pay the cost. The fitness W is calculated as the benefit (equally shared between the participants) minus the cost of the game.

Analytical solutions

We use the method described in Bach et al. (2006) to find the stable and instable equilibria of the model. According to the Bishop–Cannings theorem (Bishop & Cannings 1978), strategies supporting a mixed equilibrium need to have the same fitness. Thus, at a mixed equilibrium supported by cooperators and defectors the fitness' of both strategies should be the same. Let us denote the level of cooperativeness in the population as x, then the fitness of a mutant playing strategy y can be written for N=3, T=2 as follows (see Bach et al. 2006)

$$W(y,x) = bx^2 + y(2bx(1-x)-c) \qquad \text{Eq.2.1.}$$

where c is the cost of cooperation and b is the benefit received by all of the individuals if the number of cooperators is equal or above T. If x is a Nash equilibrium then the W should be independent of y (since any strategy be it either cooperator: y=1, or defector: y=0, or any in between should get the same payoff). This condition holds only if the second part of Eq.2.1. equals zero (Bach et al. 2006), that is

$$g(x) = 2bx(1-x) - c = 0 \,. \qquad \text{Eq. 2.2.}$$

Accordingly there are two solutions for x (Bach et al. 2006), namely

$$x_1 = \frac{1}{2} + \frac{1}{2}\sqrt{1 - 2\frac{c}{b}}, \quad x_2 = \frac{1}{2} - \frac{1}{2}\sqrt{1 - 2\frac{c}{b}} \,. \qquad \text{Eq. 2.3.}$$

Evolutionary stability further requires that $g'(x)<0$ thus x_1 is an ESS solution while x_2 is an instable equilibrium. This gives the simple bifurcation diagram shown in Fig.1. in Bach et al. (2006). The fitness of a given strategy for any group size and for any threshold number can be written up and the equation equivalent to Eq. 2.2., and can be derived accordingly. The following general formulas can be obtained:

$$x^{N-1}(b-c) - c(1 - x^{N-1}) = 0 \qquad \text{if } T = N$$

$$(b-c)\sum_{i=N-1-j}^{N-1}\binom{N-1}{i}x^i(1-x)^{N-1-i} - c\sum_{i=0}^{N-2-j}\binom{N-1}{i}x^i(1-x)^{N-1-i} - b\sum_{i=N-j}^{N-1}\binom{N-1}{i}x^i(1-x)^{N-1-i} = 0$$

$$\text{if } T \neq N, T \neq 1, \text{ where } 1<j<N-1$$

$$b(1-x)^{N-1} - c = 0 \qquad \text{if } T = 1 \qquad \text{Eq. 2.4.}$$

To verify these calculations, and to check the stability of our fixed points we used an individual based simulation of the model (details see below).

The threshold function

We also substitute the strict deterministic stepwise benefit function with a sigmoid probabilistic function (Figure 2.4), in which case

$$P = \frac{1}{1 + e^{(-s)*(cN-T)}} \qquad \text{Eq. 2.5.}$$

where P is the probability that the public goal is reached, which depends on the steepness of the function (s), the number of cooperators in the group (cN) and the threshold value (T) (Szabó & Tőke 1998; Archetti & Scheuring 2011).

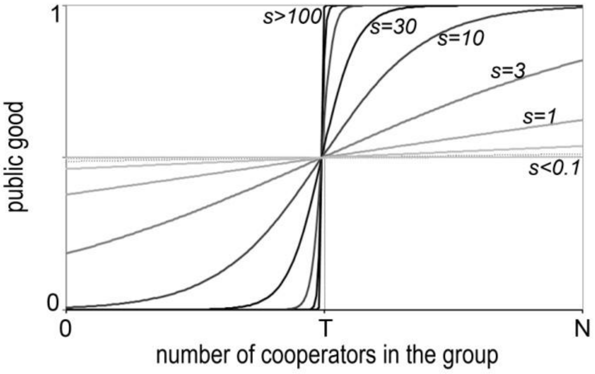


Figure 2.4: The probability of public good produced as a function of the number of cooperators for different benefit functions. The *s* parameter determines the steepness, hence the shape of the sigmoid function. When *s* approaches ∞, the probabilistic benefit function approaches to strict deterministic stepwise function, meaning that above the threshold (*T*) the public good is always achieved, while below never. With decreasing *s* the probability of public good achievement changes from strict all or nothing to a smoother function. In the later case, there is a non-zero probability of achieving the common goal even below the threshold, and also above the threshold the group can fail.

Individual based simulation of the model

We model the evolutionary dynamics in a finite size population consisting of N^2 individuals ($N^2 = 10{,}000$ individuals). We use a well-mixed population model, in which case individuals have no fixed partners. In every time step both the composition of cooperating groups and the competition neighborhood change (*N*): partners randomly chosen from the entire population, so the interaction environment of the individual is well-mixed. The neighborhood defines both the cooperating and the competing group for the focal individual (*N*), which can increase up to 50 in the well-mixed model. The simulations were run for a given number of update steps with asynchronous updating. One update step consists of a game played by the group, individual competition, group competition if occurred, and mutation.

During competition step, we consider a pairwise comparison update rule, which is the finite population analogue of the replicator dynamics (called the *imitate the better*) (Ohtsuki & Nowak

2006), in which an individual adopts the strategy of a randomly chosen neighbor with a probability proportional to the fitness difference, only if this difference is greater than zero.

$$p = \frac{W_{rival} - W_{focal}}{W_{\max} - W_{\min}} \qquad \text{Eq. 2.6.}$$

We also model territorial group behavior, in which case groups compete with each other for territories (sites). Groups composed of n individuals living in the same site, that is occupying the grid points of a regular lattice ($N_{height} \times N_{width} = N^2$), with toroidal boundary conditions, and the focal has a constant interaction environment, its immediate neighborhood. The rivals can be neighboring groups in the spatial population (Moore neighborhood, that is 8 closest sites) or groups randomly chosen from the population in the well-mixed case. Groups compared according to the average group payoffs, and the successful group entirely replaces all members of the loser one. We calculate the average payoff of the group ($\bar{W}$) as the arithmetic average of the payoffs of all group members, which means here participation in the group competition is compulsory. The chance for each group to occupy the focal site is given according to Eq.2.6, but using average group payoffs

$$\bar{W} = \frac{\sum_{j=1}^{n} W_j}{n} \qquad \text{Eq. 2.7.}$$

Next we introduce voluntary participation in both two group actions, and individuals have two continuous, evolving traits. Besides, x that defines the propensity to cooperate in the PGG, we introduce a, which describes the individual's propensity to participate in the territorial group defense action. The marginal values are also 0–1. If a is high, the individual will participate in the group competition with high probability, whereas if it is low it will participate with low probability. As the group defense is considered as an act of cooperation, it also involves a cost for those who participated. The average group payoff is now calculated as the average of the payoffs of those group members, who participate in the group competition. Groups then again compared by their average group payoffs according to the above described competition rules.

To ensure evolution, after the competition steps, mutation can occur in the traits of the focal individuals with the fixed probability (0.01). The mutant's trait is drawn from a normal distribution, with the original trait value as a mean and with a fixed variance (0.01). After individual competition, only the focal individual's traits can mutate. After group competition in all members of the focal group mutation has a chance to occur with the same probability.

To avoid confusion, in the following we denote the fixed cost of cooperation c by c_x when we talk about participation in the first collective action (the collective hunt, determined by trait x), while c_a denotes to the cost of cooperation when participating in the second collective action (the group defense, determined by the trait a).

2.2.3. Results

Effect of different threshold functions

First we study the effect of the benefit function shape on the level of cooperativeness in the population (Figure 2.5) by means of IBM simulations. For this we substitute the threshold benefit function with a sigmoid function (s-shape function), which gives the probability of achieving the group goal that is receiving the benefit for different levels of cooperative effort.

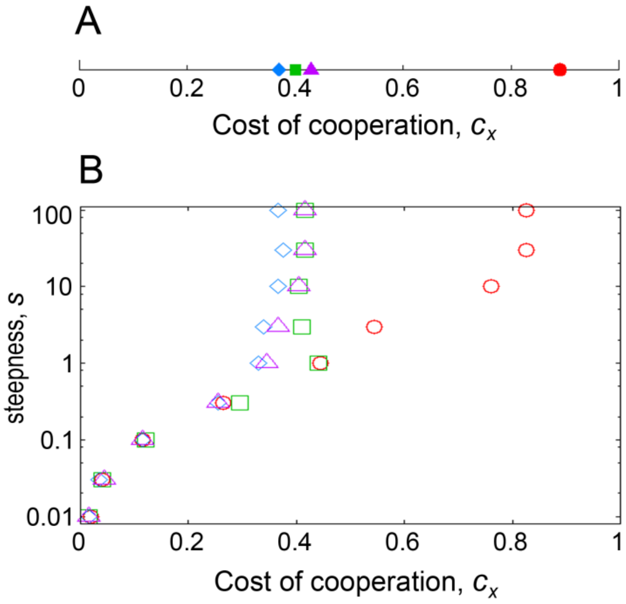


Figure 2.5: The position of the hysteresis point, with (**A**) strict deterministic stepwise benefit function, and with (**B**) sigmoid benefit functions. The effect of s (steepness of the sigmoid function) parameter on the location of the hysteresis point indicates, that for a wide range of s the sigmoid function gives qualitatively similar results as the stepwise function. The hysteresis point indicates the highest cost

value for which cooperation is still a stable outcome of the game, and even a small increase in the cost would cause the collapse of this polymorphic equilibrium to defection. Below this cost value we always find cooperative equilibria (●,○: $T = 5$; ■,□: $T = 4$; ♦,◊: $T = 3$; ▲, Δ: $T = 2$). The points on figures were calculated as the average of the last 1M update steps of 15 iterated simulation; $N = 5$. The length of the simulation was 1,000M update steps.

A good indicator of the cooperativeness in the system is the position of the hysteresis point (Bach et al. 2006), which above the proportion of cooperators drops to zero in all cases. Below the hysteresis point, we always find a stable level of cooperation, while if the cost of cooperation moves above the hysteresis point the population rapidly evolves to zero cooperativeness. The positions of the hysteresis points for different threshold values assuming sigmoid functions (Figure 2.5/A) do not change significantly for a wide range of s parameter (steepness of the benefit function). For high values of s $(1 < s < 100)$, the hysteresis point appears at the same cost values (c_x) for cases $T \neq N$ (Figure 2.5/B), as with the strict deterministic step wise function (Figure 2.5/A). For $T=N$, this parameter range is narrow ($s < 10$), and a slight change in the steepness of the benefit function results in major changes in the cooperative equilibrium. Our results indicate that the dynamics of the system remains the same for relatively steep sigmoid functions than for a stepwise function. Thus in the following, for our simulations, we will use the later one.

Results for individual level selection

Next we employ the method described in Bach et al. (2006) to find the stable and instable equilibria of the model for individual selection only (see Methods section). We also run a series of simulations in our individual based model (IBM) for comparison with the analytical model. The equilibrium level of cooperation depends both on the size of the group (*N*) and on the threshold level (*T*). Figure 2.6 depicts the resulting fixed points of the system for given group size(s) and for increasing *T*, from the analytical model (solid curves for stable and dashed curves for instable fix points), and from individual based simulations (dots), which show a close fit (Figure 2.6/A).

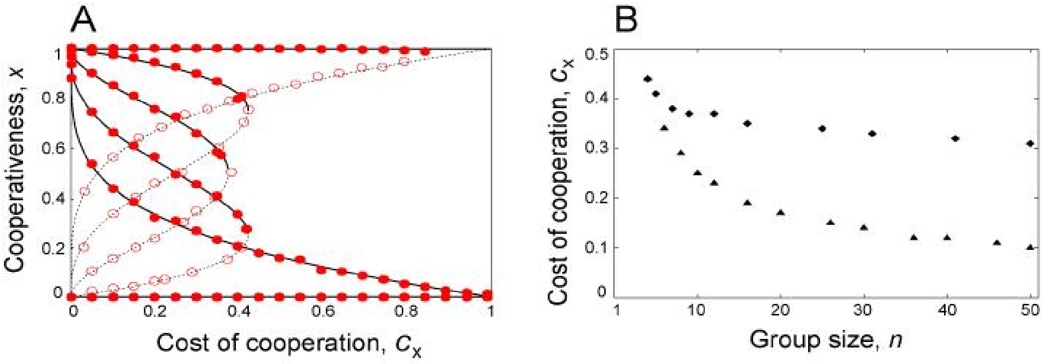


Figure 2.6: Stable and instable fix points of cooperation, and the position of the hysteresis point for different group sizes (*N*). Results from numerical and individual-based (IBM) simulations show the same results. Instable fix points (dashed line for numerical simulations, open red circles for IBM simulations) separate the interior stable fix points (thick lines for numerical and filled red circles for IBM simulations) and zero cooperativeness in the system. (**A**) Group size: $N = 5$, the threshold values are $T = 5,4,3,2,1$. (**B**) the locations of the hysteresis points (i.e. the maximal cost where cooperation is still a stable outcome), with different group sizes (*N*). (♦: $T = N - 1$; ▲: $T = N/2$). The points on the figures were calculated as the average of the last 1M update steps of 15 iterated simulation. The length of the simulation was 625M update steps.

The higher the threshold value the higher is the ratio of cooperators at a given group size. Not surprisingly the highest level of cooperation can be achieved when the threshold value equals the size of the group, and for small group sizes, the average level of cooperation is higher (Figure 2.6/B). The unstable fix points separate the attractors of the interior stable fixed points of cooperation from the attractors of zero cooperativeness (Figure 2.6/A). Above the separatrix, cooperation prevails, below this boundary, cooperation diminishes. All results from IBM model show a good fit for the predictions of the analytical model.

Introducing multilevel selection

In the following, we explore the individual based model with well-mixed and spatial population structure. In the first step, we introduce group level selection to the individual based model, assuming compulsory participation in the group defense action. Figure 2.7 depicts the cases of only group selection (A, D), and the combination of group and individual selection when group defense is compulsory (B, E).

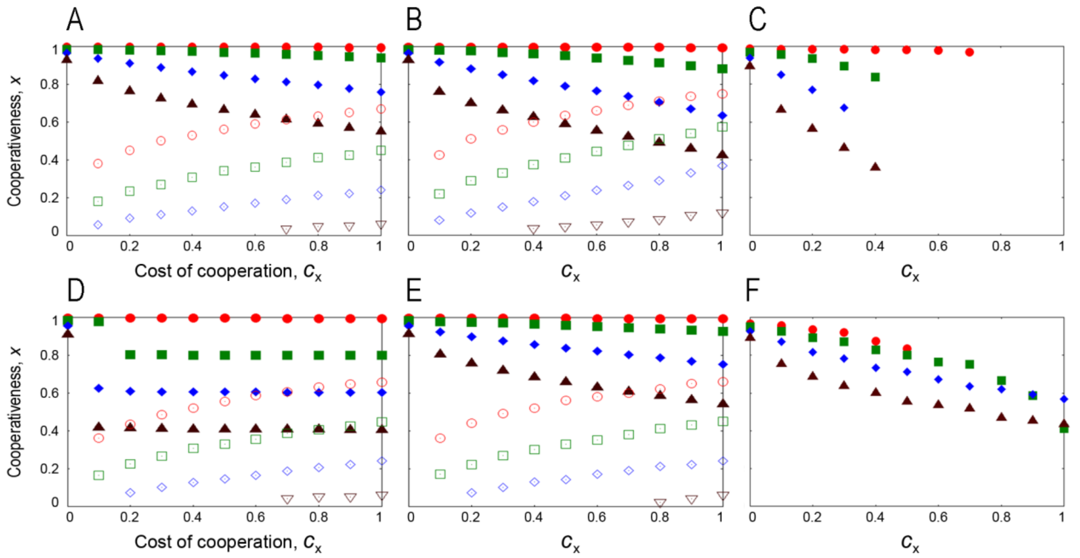


Figure 2.7: Equilibrium frequency of cooperators as a function of the cost of the Public Good Game (c_x). The panels depict the results of the individual-based simulations for non-zero stable fix points (filled marks) and instable fix points (open marks). The groups are composed of 5 individuals either picked randomly from the population (**A**, **B**, **C**), or from the local neighborhood in the model with spatial population structure (**D**, **E**, **F**). In cases depicted in panel **A**, **D** competition occurs only between groups, in the simulations of panels **B** and **E**, both individuals and groups compete with each other with compulsory participation in the group defense. Finally in the cases shown in **C** and **F**, both individual and group level selection are present and participation in the group defense is voluntary. The different marks are depicted to different threshold values (●,○: $T = 5$; ■,□: $T = 4$; ♦,◊: $T = 3$; ▲,∇: $T = 2$). The points on figures were calculated as the average of the last 1M update steps of 15 iterated simulation. The length of the simulation was 312.5M update steps

In the well-mixed case (Figure 2.7/A) the level of cooperation is higher than without group selection, however, aside from the case $T=N$, the population is still polymorphic. It means that groups with higher number of cooperators do not necessarily enjoy a competitive advantage. Groups in general respond in proportional manner to the threshold value, i.e. they optimize resource allocation. This can be best seen from the spatially explicit simulation with only group selection (Figure 2.7/D) as in this case the average equilibrium level of cooperation is exactly the threshold level. This implies that any deviation from the optimal group composition results in a disadvantage for the group, not only if the number of defectors is higher, but also if the ratio of cooperators and defectors differs from the optimal in any ways. Introducing individual level selection with compulsory participation in group defense decreases the level of cooperation in the well-mixed case (Figure 2.7/B), however, interestingly and somewhat counter intuitively it increases the level of cooperation in the spatially explicit case (Figure 2.7/E). Equilibrium populations are still polymorphic aside the case *T*=*N*.

Figure 2.7/C and Figure 2.7/F depicts the case when participation at the group competition stage is voluntary in well-mixed and in spatially structured populations, respectively. When group defense is cost-free ($c_a = 0$) the level of cooperation in the public goods game is the same as in the previous cases (not shown). When group defense is costly ($c_a = 1$) then the level of cooperation in the PGG is lower (Figure 2.7/C and Figure 2.7/F) and the hysteresis effect reappears in the well-mixed case (2.7/C). Note, however, that when cooperation is present the polymorphic nature of the equilibria is preserved (aside *T*=*N*), that is, resource allocation is still optimized, groups with higher number of cooperators do not win out by default.

Finally Figure 2.8 depicts the results as a function of the two kinds of costs, the cost of collective hunt (c_x) and the cost of group defense (c_a), and the initial number of the cooperators in the PGG when both the participation in hunt and in group defense is voluntary.

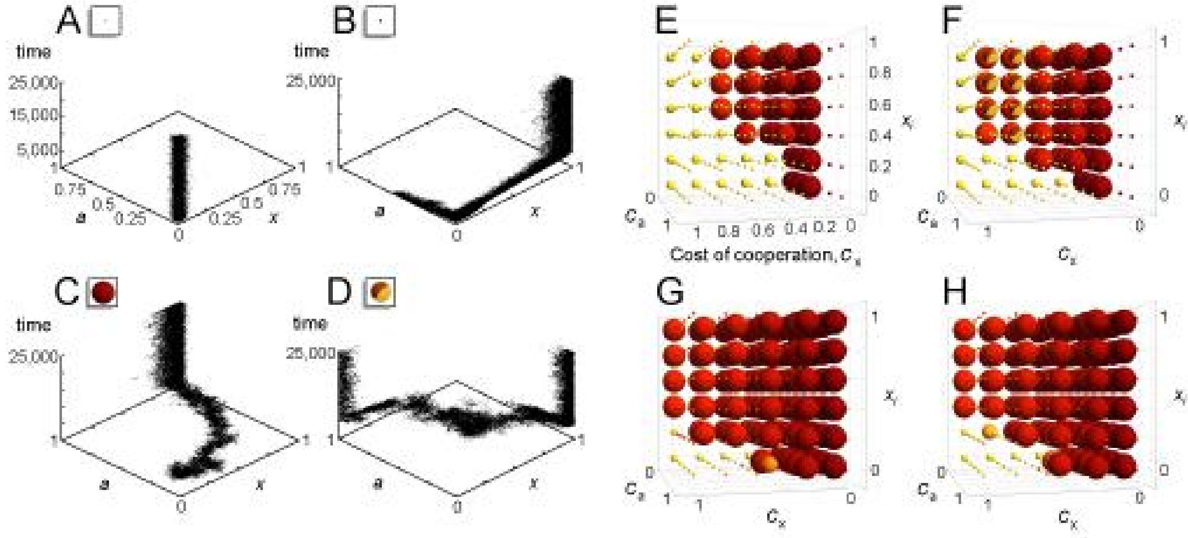


Figure 2.8: Simulation results for the multilevel selection model with voluntary participation for threshold $T = 3$ in a group of $N = 5$. The plots depict the average

tendency for cooperation for the two kinds of group actions, the public goods game and the voluntary group competition action as a function of the two costs of cooperation (c_x and c_a) and the initial ratio of cooperators (x_i) in the Public Goods Game. (**A**) For high cost values the tendency of cooperating in both of group actions is low, (**B**) or there is a full cooperation in the Public Goods Game, but full defection in the group defense action. (**C**) If the costs are not high, every individual cooperates in both of the group actions ($x \approx 1, a \approx 1$). (**D**) At the boundaries of these regions, for intermediate cost values, division of labor evolves in the population (**H**). On panels **E.**-**H**. each bubble illustrates the results of an individual based simulation, the size represents the average a in the population (large bubbles represent $a = 1$ and vice versa), and the coloring depicts the average value of x (red coloring denotes $x = 1$, while yellow coloring denotes $x = 0$). For the simulations we either used no initial incentive in the populations for participating in the group competition ($a_i = 0$) (**E**, **G**), or the simulation was started with full participation in group defense ($a_i = 1$) (**F**, **H**). The five group members were either picked randomly from the population in the well-mixed model (**A**, **B**, **C**, **D**, **E**, **F**), or from the same site in the spatially explicit model (**G**, **H**). The plotted points were calculated as the average of the last 1M (10^6) update steps of three iterated simulation results. The length of the simulation was 312.5M update steps. Graphs on panels **A**–**D** were obtained by plotting the trait distribution of the population in every 100th update step for 25,000 steps.

Other parameters: (**A**) $c_x = 0.5$, $c_a = 0.5$, $x_i = 0$, $a_i = 0$;
(**B**) $c_x = 0$, $c_a = 0.6$, $x_i = 0$, $a_i = 0.5$;
(**C**) $c_x = 0.2$, $c_a = 0.05$, $x_i = 0.05$, $a_i = 0.2$;
(**D**) $c_x = 0.6$, $c_a = 0.2$, $x_i = 0.6$, $a_i = 0.5$.

We can observe four types of dynamics in our simulations (Figure 2.8/A–D). If the costs of cooperative actions (c_x and c_a) are high, individual willingness to cooperate evolves to zero (Figure 2.8/A). Individuals willingly cooperate in group defense (i.e. large bubbles, that is high values of *a*, close to 1) only if there are high levels of cooperation with regard of group hunting (i.e. the colors of the large bubbles range from orange to red (~0.7-1) on Figure 2.8/E–H, Figure 2.8/C, and Figure 2.9). However, cooperation in the public goods game can stay at high levels even if the propensity to participate in group defense is low (i.e. there are small red bubbles when the cost of group defense is high) (Figure 2.8/B, G and H).

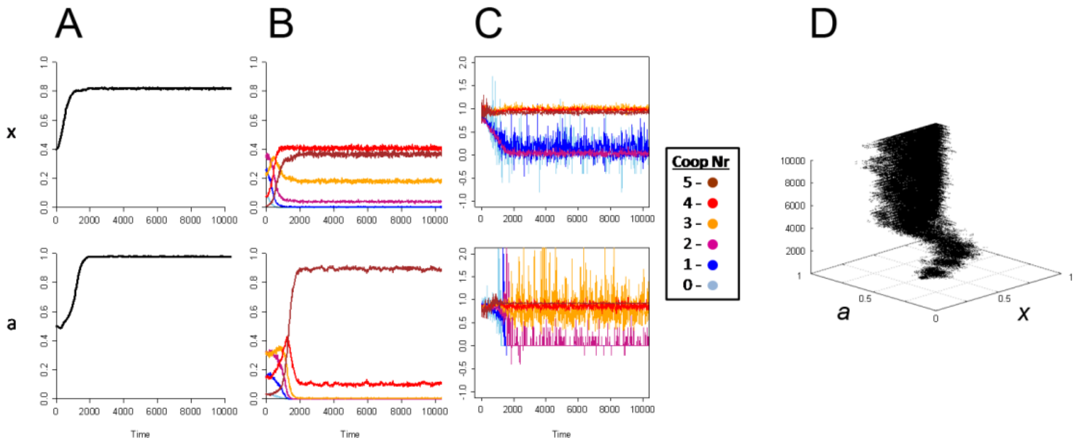


Figure 2.9: Simulation results from individual based model in well-mixed population for $T = 3$ and $N = 5$. Participation in both of the group actions is high, and groups with four or five cooperators win. The results are shown as time series graphs from 0 to 10,000 generations (that is 125 M update steps). On each panel the first row shows the attributes of trait *x* (willingness to participate in the group hunting action) and the second row shows trait *a* (willingness to participate in the group competition). The first columns on the panels show the average trait values of the population (**A**), the next row shows the frequency of groups composed of different numbers of cooperators at that update step (**B**). The group composition is coded by the colours of the lines as shown on the side panel. Colours code goes from brown to blues as the number of cooperators decrease in the group. The next column (**C**) depicts the average success of a group type. We measure the success as the difference between the number wins and loss normalized by the group type frequency. On the last panel (**D**), we show the distribution of the two traits, *x* and *a* in the trait space. Parameters: $c_x = 0.4$; $c_a = 0.2$; $x_i = 0.4$; $a_i = 0.5$.

Polymorphism of different cooperative efforts in the Public Goods Game is still present at many of the equilibria (i.e. lighter shade of red), and interestingly division of labor evolves at medium cost values in the in the well-mixed case (Figure 2.8/F red/yellow bubbles, and Figure

2.10). In these cases, polymorphism occurs at the population level, where individuals cooperate strictly in one of the collective actions, but never both (Figure 2.8/D and Figure 2.10).

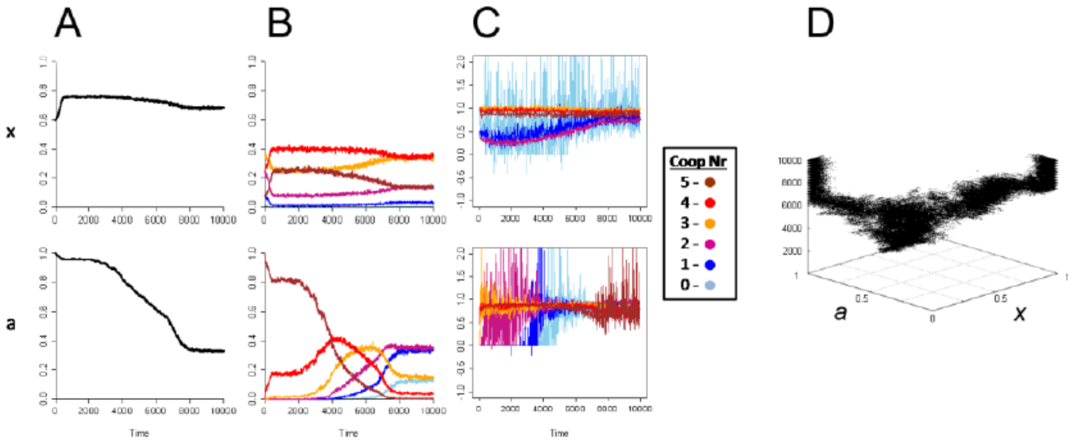


Figure 2.10: Simulation results from individual based model in well-mixed population for $T = 3$ and $N = 5$. Division of labour evolves for intermediate cost values. The results are shown as time series graphs from 0 to 10,000 generations (that is 125 M update steps). On each panel the first row shows the attributes of trait x (willingness to participate in the group hunting action) and the second row shows trait a (willingness to participate in the group competition). The first columns on the panels show the average trait values of the population (**A**), the next row shows the frequency of groups composed of different numbers of cooperators at that update step (**B**). The group composition is coded by the colours of the lines as shown on the side panel. Colours code goes from brown to blues as the number of cooperators decrease in the group. The next column (**C**) depicts the average success of a group type. We measure the success as the difference between the number of wins and losses normalized by the group type frequency. On the last panel (**D**), we show the distribution of the two traits, x and a in the trait space. Parameters: $c_x = 0.6$; $c_a = 0.2$; $x_i = 0.6$; $a_i = 1$.

Of course if the combined costs are too high then cooperation is not stable and thus division of labour cannot evolve either. Thus we can see that division of labour is expected to evolve on the boundary of cooperative vs. non-cooperative regimes when group fitness at the group competition stage is not necessarily a monotone increasing function of participation.

Our results also indicate, that spatial structure favors cooperation in the proposed model. High values of cooperation can evolve for both public actions (Figure 2.11) (hunting and group defense, see large red bubbles on Figure 2.8) even at high cost values in spatially structured populations (Figure 2.8/G and H).

Note that when $c_x > 0$, cooperation evolves only if the initial proportion of cooperation is not zero in the population with well-mixed structure (Figure 2.8/E, F, Figures 2.9 and 2.10), which indicates a separatrix in the system. However, spatial population structure promotes cooperation and it allows cooperators to invade even for higher cost values with regard of both types of costs (compare Figure 2.8/E with G and F with H, and see Figure 2.11).

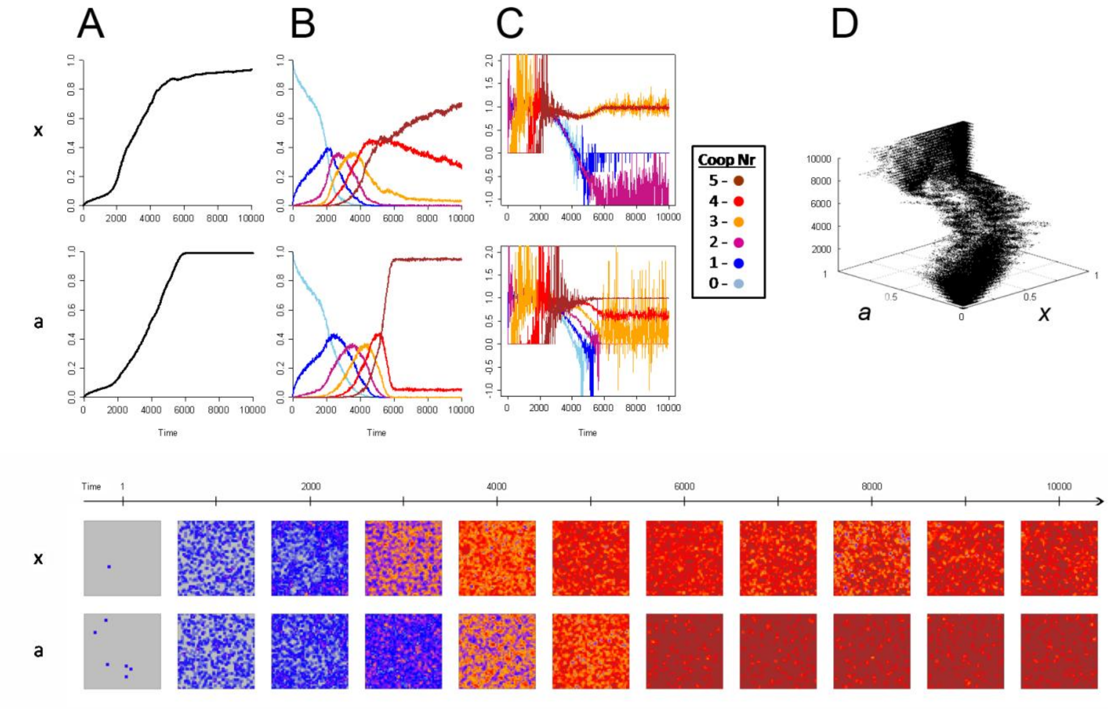


Figure 2.11: Simulation results from individual based model in spatially structured population with $T = 3$ and $N = 5$. Invasion of cooperators from an initially non-cooperating state is possible, but only for cost values close to zero. Here individual competition occurs between members of the same group (only intragroup competition). The results are shown as time series graphs from 0 to 10,000 generations (that is 125 M update steps). On each panel the first row shows the attributes of trait *x* (willingness to participate in the group hunting action) and the second row shows trait *a* (willingness to participate in the group competition). The first columns on the panels show the average trait values of the population (**A**), the

next row shows the frequency of groups composed of different numbers of cooperators at that update step (**B**). The group composition is coded by the colours of the lines as shown on the side panel. Colours code goes from brown to blues as the number of cooperators decrease in the group. The next column (**C**) depicts the average success of a group type. We measure the success as the difference between the number of wins and losses normalized by the group type frequency. On the last panel (**D**), we show the distribution of the two traits, *x* and *a* in the trait space. On the bottom of the figure, the spatial distribution of the different group types is shown as snapshots at certain time intervals. Colour coding used on the snapshots is the same as described before on the time series graphs. Each pixel represents one of the 2,500 sites on the regular 50*50 grid occupied by one group. Parameters: $c_x = 0.05$; $c_a = 0.05$; $x_i = 0$; $a_i = 0$.

Interestingly, we observe division of labor in the spatially explicit model only under given circumstances, that is when individual competition occur between randomly chosen competitors from the focal and neighboring groups (that is intra-, and intergroup competition at the individual level are both present). This means, that competition can occur between the focal and the group members, or also between individuals from the neighbouring sites. Possibly division of labor is unstable in small group sizes without limited mixing between the groups (i.e. without intergroup competition), hence it only appears in this modified model.

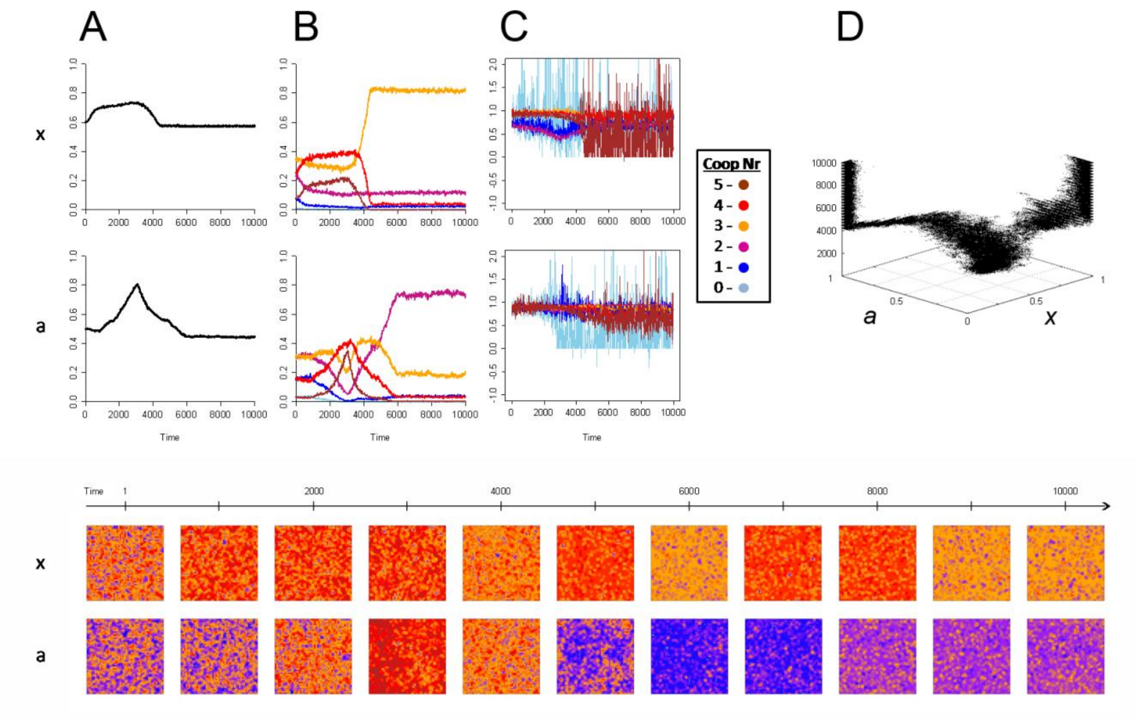


Figure 2.12: Simulation results from individual based model in spatially structured population with $T = 3$ and $N = 5$. Division of labour evolves in spatially structured population as well for medium cost values. In this scenario, the focal individual competes with a given number of randomly chosen individuals from the focal group and the closest neighbourhood (intra-, and intergroup competition). The results are shown as time series graphs from 0 to 10,000 generations (that is 125 M update steps). On each panel the first row shows the attributes of trait x (willingness to participate in the group hunting action) and the second row shows trait a (willingness to participate in the group competition). The first columns on the panels show the average trait values of the population (**A**), the next row shows the frequency of groups composed of different numbers of cooperators at that update step (**B**). The group composition is coded by the colours of the lines as shown on the side panel. Colours code goes from brown to blues as the number of cooperators decrease in the group. The next column (**C**) depicts the average success of a group type. We measure the success as the difference between the number of wins and losses normalized by the group type frequency. On the last panel (**D**), we show the distribution of the two traits, x and a in the trait space. On the bottom of the figure, the spatial distribution of the different group types is shown as snapshots at certain time intervals. Colour coding used on the snapshots is the same as described before on the time series graphs. Each pixel represents one of the 2,500

sites on the regular 50*50 grid occupied by a group. Parameters: $c_x = 0.61$; $c_a = 0.21$; $x_i = 0.6$; $a_i = 0.5$.

2.2.4. Discussions

Here we have shown that selection in Threshold PGG can maintain stable levels of polymorphism (i.e. a stable mixture of cooperators and defectors) without the need of punishment or spatially explicit population structure. We gave a demonstration that the described dynamics holds not only for stepwise benefit function (strict threshold function), but for a wide range of sigmoid curves between the stepwise and the linear benefit functions (s–shape function). Our results further indicate that polymorphism in group hunting and defense can be adaptive in case of multi-level selection, and we provided a pioneer report on the division of labor in multiple Public Good Games. We conclude that what was regarded as cheating at the individual level is in fact can play a significant part in the optimization at the group level, which optimization is provided by the described mechanisms working on behavioral polymorphism. Our results also indicate, in line with the general conclusion of previous models (Nowak & May 1992; Doebeli & Hauert 2005; Nowak 2006; Számadó et al. 2008), that spatial structure favors cooperation in Threshold Public Goods Games.

It is a common observation that humans (Fehr & Fischbacher 2004; Marlowe 2004; Gachter & Herrmann 2009) and some animal populations such as lions (Scheel & Packer 1991; Heinsohn & Packer 1995) are polymorphic. Individuals that have a high tendency to cooperate live together with those that have a high tendency to defect. The proportion of these ‘laggards’ can be high in certain societies and they are not being punished, as for example in the case of lions (Heinsohn & Packer 1995), in microbial communities (Gore et al. 2009), or in a number of human hunter–gatherer societies (Gurven 2004; Marlowe 2004). Moreover, observations suggest that the average tendency for cooperation in these populations appears to be stable in the long term. This is a perplexing set of observations, not yet fully understood, as our traditional thinking about cooperation relies on the Prisoner’s Dilemma game, in which case either cooperators, or defectors dominate. The stable coexistence of the two strategies feels somewhat controversial.

Several studies have, however, tried to provide explanations for this observation. One approach suggests that these social situations are best described by the Snowdrift game (Doebeli et al. 2004; Gore et al. 2009) with homogeneous population structure. This pairwise game, however, is not adequate to explain situations with multiple players. Punishment of non-participating individuals, or defectors (Sigmund et al. 2010), or spatially explicit population structure (Nowak & May 1992) can also results in some sort of coexistence of cooperators and defectors. None of these explanations, however, can be applied perfectly here as for example lion and human populations are neither completely well-mixed, nor spatially explicit in a sense as sedentary organisms, and punishment is also not common in these instances. Threshold effects in Public Good Games can provide an often neglected, yet powerful explanation for the observed polymorphism in the population, as an alternative to punishment (Sigmund et al. 2010), spatial structure (Nowak &May 1992), or other game structures (Doebeli et al. 2004).

Population level polymorphism is a stable outcome in *N*–person dilemmas with non-linear benefit—or return—functions, where cooperators and free riders stably live together in the population (Bach et al. 2006; Pacheco et al. 2009; Archetti & Scheuring 2011, 2012), as long as the cost of cooperation does not exceed a limit cost value, the hysteresis point. Our model predicts that for an increased group size this hysteresis, that is the point where sudden drop from cooperation to defection appears with a very small increase in the cost, appears at lower cost values, compared to smaller groups (see Figure 2.6/B). To put it in a different way, with large groups cooperation can be maintained only if the cost of cooperation is relatively low. Also for higher cost values the instable fix points move closer to the stable fix points, which means that the invasion of cooperators in a population of defectors becomes harder, while the invasion of defectors into a cooperative population becomes more likely (Archetti & Scheuring 2011).

Introducing multilevel selection into the model is a logical step towards reality, as in many biological and human examples where collective hunting occurs intergroup conflicts can also be observed (Kitchen & Beehner 2007; Wilson et al. 2002; Mitani & Watts 2005; Choi & Bowles 2007; Bowles 2009; Mosser &Packer 2009). When group level competition introduced explicitly into the model then population level polymorphism is stabilized both in the well-mixed and in the spatially explicit versions. Thus, multilevel selection need not select for the groups with the highest number of cooperators as it is often assumed. Groups that optimize the number of hunters enjoy an advantage over those groups that hunt (cooperate) on a higher, unnecessary level. Thus, defection of a given proportion of individuals during one specific cooperative group action can be an adaptive strategy for the group depending on the cost values. Because group level performance (i.e. success in the PGG) determines both individual and group level success, any deviation from the optimal group composition would cause a disadvantage in some way or other. If the number of cooperators is lower than the threshold value, then the collective action (i.e. hunting) is unsuccessful, thus neither cooperators nor defectors gain anything, and these groups are being replaced by successful groups. On the other hand, if the number of cooperators is higher than what is required for providing benefit for the whole group (in our example capturing the prey), the energy loss of unnecessary effort would cause a disadvantage when the group faces a conflict (fight for territory). Hence our novel result is that laggards, who were previously seen as exploiters of the common goods provided by cooperators (Scheel & Packer 1991; Heinsohn & Packer 1995), do actually contribute to the fitness of the group by keeping the group level allocation at the optimum level.

Our results also verify that if participation in two distinct collective actions which produce shared benefits is costly, such as hunting and territory defense, then selection pressure on cooperators can result in the evolution of certain forms of division of labor, predicting that it will evolve only for a narrow range of cost values. Interestingly, strategy polymorphism first appears at the individual level in the form of mixed strategies, that is all of the individuals participate in both collective actions with intermediate probabilities, and the strategies within the groups are identical. However, this state is not stable and evolution drives the system towards division of labor, where individuals mostly participate only in one of the collective actions, and different strategies coexist within the groups (i.e. polymorphism appears at the group level). This result is robust in our simulations at medium cost values, and turns out to be stable on the long term. Experimental support for this context dependent role specialization is poor yet (but see Arnold et al. 2005; Gazda et al. 2005), however the idea that cooperators and ‘free riders’ switch roles in different contexts is not obscure (Nunn & Lewis 2001; Nunn & Deaner 2004; Arnold et al. 2005; Gazda et al. 2005; Kitchen & Beehner 2007), as long as there is a trade off situation between two energy consuming group actions (Nunn & Deaner 2004).

While in our model individuals have only two heritable traits that describe their behavioural decisions, this two are sufficient for maintaining polymorphism in the population. Obviously, regularly many genes effect behaviour, which explains higher polymorphism, still there is evidence suggesting that some may play disproportionally important role in behavioural switches (McDermott et al. 2009). Accordingly, our model can provide a potential explanation for the observed polymorphism in lions in threshold game like situations (Stander 1992a,b; Packer & Pusey 1997) and the presence of laggards in the population (Heinsohn & Packer 1995; Packer & Heinsohn 1996).

It is more difficult to evaluate whether a threshold effect existed in hominid plio-pleistocene group hunting. The conception of hunting large preys would inevitably suggest so and the fact that hunting of medium-sized and large ungulates started long before stone-tipped and bonetipped weapons were widely used strongly suggests that cooperation amongst hunters was essential for the capture of large game (Frison 1987, 1998; Stiner 2002). If it did so, then our model applies and has the potential to explain the observed polymorphism in humans as well. Interesting implication of our results is that once human societies become larger and more fluid in composition this polymorphism was no longer necessarily adaptive and definitely was not looked upon as desirable. This, in turn could have triggered the evolution of cultural norms and institutions that attempts to obtain a universally high level of cooperation from all the members of the society regardless of their predispositions.

3. Conditional strategies in social interactions

As it was stressed in the introduction, the most extensively studied form of cooperation, reciprocal altruism, has been tightly associated to the foremost concept in game theory, the famed Prisoner's Dilemma (Trivers 1971; Axelrod & Hamilton 1981; Hauert 2002; Nowak 2006; Archetti & Scheuring 2012). This simple game theoretical concept attracted much attention, since it provides a simple platform for analysis, but still produces complex, and sometimes surprising, dynamics. To fit to the concept of PD, scientists translated all kinds of complex behaviors to primitive rules: individuals may decide to cooperate with a given probability otherwise they defect (Doebeli & Hauert 2005). Following a similar logic for continuous versions of cooperation games, individual can make continuous levels of investments $I \in [0, \infty]$ (Killingback et al. 1999). Here the level of cooperation is determined by one or more genes deterministically, without any flexibility, feedback, or response. This model framework serves most often as a basis for analyzing how cooperators can spread and can be supported, yet it neglects an important question: how do and to what extent individuals decide to cooperate? While majority of the traditional game theoretic studies focused on conditions which resulted in the spread of cooperators in the population, however, often ignore other important aspects of social interactions. Opposed to the questions related to the spread of cooperators, questions concerning the evolutionary dynamics of behavioral decision components that play role in determining an individual's level of cooperation is less pronounced in the literature. Considering conditional strategies require that cooperation is not a deterministic behavior, but players can change their behavior depending on the context, quality of the partner, or other relevant factors (Thompson 1998; Agrawal 2001).

Any potential interaction between partners can be divided into three phases: *assortative*, *interactive* and *allocative* (Dugatkin 1995). During the *assortative* phase, individuals decide with whom to interact with, during the *interactive* phase, strategies individuals follow determine how to invest, and during the *allocative* phase, individuals may decide how to divide the resource (Dugatkin 1995). Conditional behavior can evolve in each of these phases of social interactions.

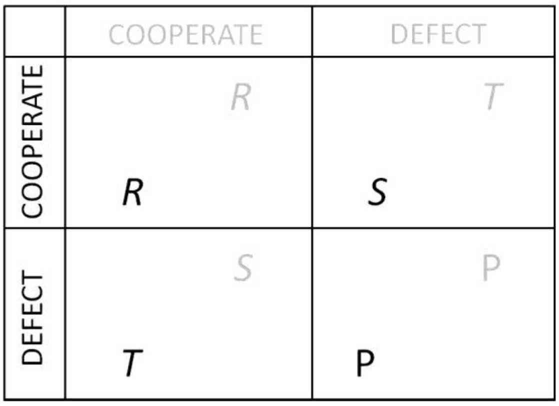
The allocative phase is assumed to be incorporated in the payoff matrix, thus in most models division is resources, goods, or spoils is already fixed before players even enter the game (Dugatkin 1995, Mesterton-Gibbons et al. 2011). Conditional strategies at the allocative phase would require switching from the traditional payoff structure of game theoretical models to a context-dependent paying off.

The assortative phase had been largely ignored for a long time, and was assumed to be random. This implies that individuals have no rules regarding who to interact with. In this case, partner choice is a random factor, and moreover the frequency of various associations is dictated by the frequency of strategies and population structure (Dugatkin 1995). Conversely, active partner choice implies that associations are the results of "decision" individuals make regarding who to interact with (Bull & Rice 1991; Dugatkin 1995).

In traditional studies of cooperation, however, only the effect of assuming conditional strategies in the interactive phase, even if in a very basic form, was studied. In these instances, conditional behavior was modeled in the interactive phase with discrete conditional strategies.

3.1. Pioneering studies of conditional strategies

In the most commonly studied approach, a strategy is composed of probabilities, which determine the chance for playing cooperatively according to the received payoff from the game (according to R, P, S, T, as the *Reward*, *Punishment*, *Sucker's payoff*, and *Temptation*, respectively) (Trivers 1971).



	COOPERATE	DEFECT
COOPERATE	*R* *R*	*T* *S*
DEFECT	*S* *T*	P P

Figure 3.1: The generalized payoff matrix of reciprocal altruism game. If both players cooperate, both get the *Reward*. If both defect, they get the *Punishment.* If the players choose dissimilar strategies, the cooperator gets the *Sucker's payoff* while the defector receives the *Temptation*. When S < P < R < T, the situation represents a dilemma. This representation served most often to formulate models

according to the four parameters, compared to the payoff matrix representation shown in Fig. 1.1, in which case three parameters suffice to cover all the possible situations.

This provided a prosperous basis for theoreticians to analyze different aspects of this form of conditionality in evolutionary game theory. Consider for example the huge share of papers analyzing the 'Tit-for-Tat' or alike strategies in the theoretical literature (Axelrod 1984; Nowak & Sigmund 1993). However clear experimental evidence on the existence of such strategies in nature is still lacking (Sigmund & Hauert 2002; Sachs et al. 2004). The reason why 'Tit-for-Tat' received wide attention comes from its logic: this strategy somehow resembles reflexive behavioral patterns of real life organisms. This strategy follows a simple, yet powerful rule: it starts an interaction with cooperation, and then picks the strategy the opponent picked in the previous round of the game. It has been proposed, that only few species, only organisms with high cognitive abilities are capable of performing the complicated task of tracking and remembering the scores from previous rounds of the interactions, and to make complicated calculations to determine the next optimal move during these interactions (Bergstrom et al. 2003). This argument assumes that the interaction eventuates on a longer time scale, with breaks in between the acts, during which participants evaluate the success of their strategies and their next moves. In certain social interactions, mainly in human societies, these assumptions can be valid. There are, however, also other forms of conditional strategies which might suit better to explain a broader range social interactions within and between species.

3.2. Studying different aspects of conditional behavior

As we have seen, models of evolutionary game mostly focused on very simple and discrete forms of conditional behavior. Also, these studies mainly considered conditional behavior at the interactive phase. Let us now focus on other aspects of conditional behavior in social interactions.

In the next sections, we will shortly overview the empirical basis of certain aspects of different forms conditional behaviors in social interactions, and we will develop and study models for their analysis. In particular, we ask how conditional strategies affect the spread and stability of cooperative behavior. In section 3.3, we will illustrate—without going into the detailed analysis of the model—conditional strategies at the associative phase, through demonstrating the effect of preferential partner choice in a very simple model, based on the work of Kun et al. (2010). In the next sections (sections 3.4–3.6), in more detail, we will develop and study a model that considers continuous conditional, and reflexive investments during the interactive phase.

3.3. Conditional partner choice

Classical studies of cooperation made the simplifying assumption of individuals interacting with the whole population (Hofbauer & Sigmund 2003), in certain studies with random partners in well-mixed models (Doebeli & Knowlton 1998; Doebeli & Hauert 2005; Mesterton-Gibbons et al. 2011), or partners from the fixed immediate neighborhood in the case of spatially explicit population models (Nowak & May 1992; Doebeli & Hauert 2005; Mesterton-Gibbons et al. 2011).

Many animals live in fission-fusion societies, such as dolphins and cetaceans (Connor 2000), hyenas (*Crocuta crocuta*) (Holekamp et al. 1997), or chimpanzee (*Pan sp.*) (Lehman et al. 2007). In these societies animals can choose partners to associate with. One intriguing example is found in bottlenose dolphins, where individuals can associate with different other individuals for different tasks (foraging, rest, social activity, travel), thus in these cases individuals can choose partners with whom they can perform certain actions best (Gero et al. 2005).

In biological market models (Noë & Hammerstein 1995), individuals can choose partners for the interaction from the ’market’ of potential partners advertising and offering services. Cleaner fish and its clients provide a commonly discussed example of biological markets (Bshary & Noë 2003). Cleaner wrasse (*Labroides dimidiatus*) form a mutualistic partnership with several reef fish, in which the cleaner fish provide cleaning service by removing ectoparasites and dead tissue from the clients’ surface, gill, or mouth, and in return the cleaner receives easy meal, and sometime even some extra bites of the clients’ healthy tissues (Bshary & Grutter 2002; Bshary & Noë 2003). As there are several clients, and also several cleaners, individuals can preferentially choose reliable partners, hence cheaters from both sides can be rejected or punished. Biological market theory thus predicts that preferential partner choice is one main factor stabilizing mutualistic relationships (Noë & Hammerstein 1995; Bshary & Grutter 2002), although the importance of partner choice or partner switching, and partner punishment is not clear yet (Bshary & Grutter 2005).

Pre-infection partner choice might play an important role in stabilizing plant-symbiont associations as well (Gubry-Rangin et al. 2010). It is assumed that nodulating plants can choose from potential bacterial partners in the rhizosphere with whom to form a nodule and initiate symbiotic association (Gubry-Rangin et al. 2010). This would require honest signals from the bacteria (Számadó 2011), based on which hosts can distinguish 'good', potential nitrogen fixing partners from 'bad', cheater partners. The relevance and process of partner choice and/or partner screening in plant-symbiont interactions is not yet clearly understood, nor from the empirical, nor from the theoretical side (Kiers & Denison 2008; Archetti et al. 2011b), but can potentially play an important role in preventing the degradation of mutualistic interactions (Archetti et al. 2011a,b).

Besides the above mentioned examples, preferential partner choice can be found in several other intraspecific and interspecific social situations (Bull & Rice 1991; Bshary & Noë 2003), for example in plant–insect, such as fig–fig-wasp, or yucca–yucca moth associations (Bull & Rice 1991). Preferential partner choice can also be found in human societies, and seems to be an important factor shaping the structure of the interaction neighborhood (Fehl et al. 2011; Rand et al. 2011; Apicella et al. 2012). It is also an important experimental observation, that cooperation decays when the social connection between participants are established randomly, or the updating of social ties is not very frequent, however frequent and preferential choice of connections can support cooperation in human societies (Fehl et al. 2011; Rand et al. 2011).

Thus, the main feature of the original games, namely the static nature of the interaction topology, with random partner associations, should be relaxed in order to study the effect of preferential partner choice and/or partner rejecting in social interactions. To formalize and analyze such models, one possibility is to represent social interactions as edges between the interacting individuals represented as nodes of a graph. In this approach, partner choice can constitute of the change of links, the edges between the nodes, of the social network.

3.3.1. A model of partner choice

Let us briefly demonstrate an example of preferential partner choice/ partner rejecting model based on the work of Kun and colleagues (Kun Á., Boza G., Scheuring I. 2010: Cooperators Unite! Assortative linking promotes cooperation particularly for medium sized associations. *BMC Evol Biol* 10: 173). Here we study how preferential association can affect the fixation probability of a single cooperator placed randomly into a population of defectors. We assume that social interaction structure is represented by a scale-free graph (Albert & Barabási 2002), and individuals have on average *k* connections to neighboring individuals ($k > 0$). A cooperator provides help to all partners to whom it is connected, thus it pays a cost (*c*) for each of these investments. Neighbors of a cooperator receive the benefit (*b*). Thus here we use a simplified formalism as presented in Figure 1.1. Generally, if a cooperator is connected to *k* other individuals and *i* of those are cooperators, then its payoff is $bi - ck$. A defector does not provide any help, and therefore pays no costs, but receives the benefit from neighboring cooperators. Thus if a defector is connected to *j* cooperators, then its payoff is bj. The fitness of a player *i* is, $1 + w + wP_i$, where *w* measures the intensity of selection (we assume weak selection $w << 1$). We employ one of the most commonly used "death-birth" updating schemes (Ohtsuki & Nowak 2006), where at each update a randomly chosen individual dies, and then its neighbors compete for the empty site in proportion to their fitnesses $P_i \Big/ \sum_{j=1}^{k} P_j$, where P_i is the fitness of the focal individual, and P_j is the fitness of the *k* neighbors.

The interaction network is changing by changing the connection between nodes (but not the degree distribution of the graph; Kun et al. 2010) according to pre-defined rule that considers only the composition of the current interaction neighborhood of the focal node. The probability of changing that link is ω_1 for a general node (basic relinking), while ω_2 is denoted to preferential linking in the case of focal cooperator-defector neighbor connections ($\omega_2 > \omega_1$).

There are several approaches to model preferential partner choice. For example in reputation based partner choice, an individual uses available information on the partner, its image score (Nowak & Sigmund 1998), which is, for example, based on its past actions, the number or ratio of cooperative decisions in the past (Fu et al. 2008). Preferential rejecting or choosing of partners can be based on the payoff received from an interaction, which can be indicative of the opponents' strategies (Santos et al. 2006).

Here we consider three different partner choice and/or partner rejection strategies (Figure 3.2): in the case of "Random choice" the focal individual can reject a random partner, and chooses a new partner randomly. The strategy of "Get rid of defectors" chooses to loose a defector as well as its new partner once a new random interaction is established. The third strategy, "The friend of my friend is my friend", is based on triadic closure, in which case individuals try to associate with associates of trustworthy partners, that is the connections of cooperative partners (Schematic representation strategies are shown on Figure 3.2).

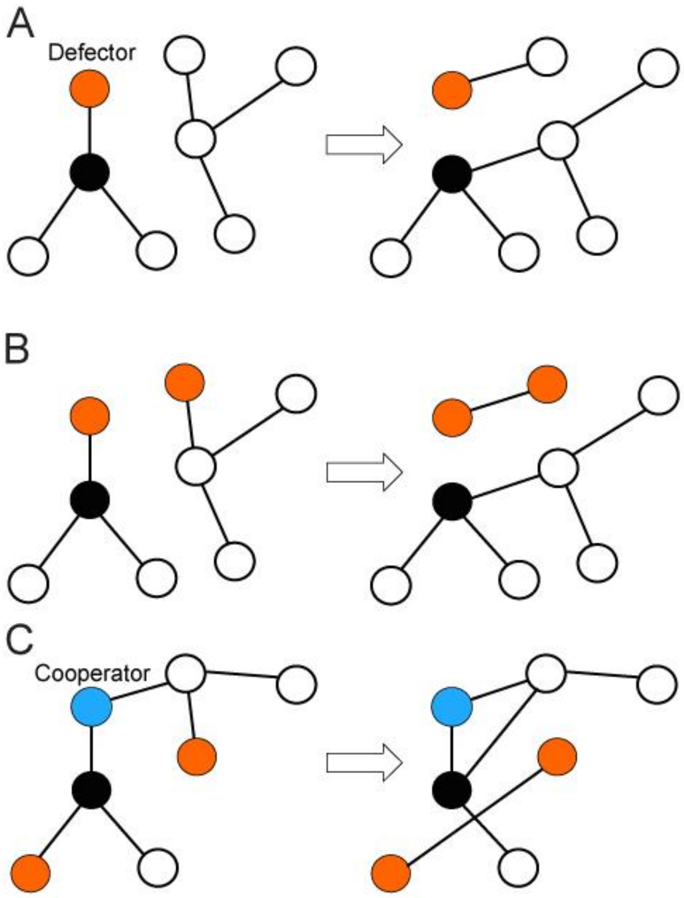


Figure 3.2: Three rules for assortative partner choice. (**A**) Random choice; (**B**) Get rid of defectors; (**C**) “The friend of my friend is my friend”. Black filled circle represents the focal individual. Red filled circles represent defectors; Blue filled circles represent cooperators; and open circle represent an individual with arbitrary strategy. Not only the focal, but also the rejected individual forms a new connection, thus the degree distribution of the graph remains unchanged.

In general, assuming dynamic networks instead of static interaction topologies effectively hinders the spread of a single cooperator, as the beneficial effect of clustering of cooperators is diluted by the random relinking (Kun & Scheuring 2009). In the case of preferential relinking of social connections, compared to the randomly relinking network topology, the fixation probability of cooperators can increase meaningfully (Figure 3.3).

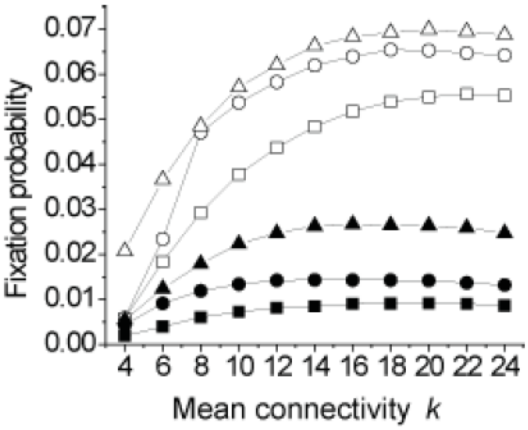


Figure 3.3: Fixation probability of cooperation with the three relinking rules as a function of mean connectivity of the interaction network (*k*), and for different benefit-to-cost ratios (filled symbols: $b = k$, and open symbols: $b = 2k$). Fixation probability shows an optimum at medium connectedness with preferential attachment rules. Squares represent random choice; circles denote to "Get rid of defectors"; and triangles represent "The friend of my friend is my friend". Other parameters $c = 1$, $\omega_1 = 0.05$, $\omega_2 = 0.95$; and w = 0.01. Each point was obtained by generating 1000 different graphs, and on each simulation on these graphs were repeated 1000 times. The simulation was run until the population consisted either of cooperators or defectors.

Interestingly, fixation probability shows a maximum as a function of average connectivity, hence the spread of cooperators is promoted best for medium sized associations in this model (Kun et al. 2010). On the one hand, is easier to get rid of defectors in larger cooperator aggregations when the connectivity is higher, as a cooperator has many other cooperating neighbors and one defector has only marginal effect on a cooperator's payoff, thus cooperators enjoy an advantage. On the other hand, the emergence of such large associations becomes less and less likely with increasing *k*. Thus these two processes shape the fixation probability function (Kun et al. 2010).

While we demonstrated that even very simple rules can increase the average level of cooperation in the population, animals, plants, or bacteria may follow even more complicated rules of preferential partner choice (Archetti et al. 2011a,b). It will be interesting to see how and to what extent empirical data confirms the stabilizing effect of conditional partner choice on cooperation within, and between species.

3.4. Conditional investments

Next we focus on relaxing the static investment behavior assumed in classical games, and thus study some aspects of the *interactive* phase of social interactions, namely conditional investments. Conditional investments are common in many species from bacteria to humans. Consider for example the reciprocal altruism observed in human societies. It has been shown, that reciprocal food sharing among Ache families is common, and the amount of food shared correlates with the amount received in previous occasions (Gurven et al. 2000; Gurven 2004a,b; Allen-Arave et al. 2008). These exchanges can occur on a daily basis, but the interval between turns can also be longer. So as in the case of reciprocal grooming behavior in some animals (Hart & Hart 1992; Gomes et al. 2009). During allogroming, impalas (*Aepyceros melampus*) takes turns, bouts, thus the interval between turns is short (Hart & Hart 1992), but in wild chimpanzees (*Pan troglodytes*) time interval between grooming can be days (Gomes et al. 2009). During these repeated interactions some short-, or long-term score keeping in necessary, so that at the next encounter the individual can choose a strategy based on the outcome of the previous interaction with the given partner, according to—for example—the rules of a Tit-for-Tat-like strategy. But consider for example symbiotic relationships. Obviously bacteria or fungi do not have memory, not in a sense that is interpreted in cognitive sciences, however, they are able to control their investments in response to environmental factors including the social environment, i.e. their symbiotic partners (Kümmerli 2009).

Take as an example further long-term or even life-long relationships, such as lichens (Honegger 1991), rhizobia (Denison 2000; Heath & Tiffin 2009), or mycorrhiza (Johnson et al. 1997; Smith & Reed 1997). Studies showed that the actual phenotype and investment rate of the symbiont significantly depends on the quality of the partner (Johnson et al. 1997; Kiers et al. 2003; Heath & Tiffin 2009). It is a straightforward assumption that increased concentration of a material provided by the cooperative act enhances the metabolism of the recipient, hence it can produce more in response as well (Resendis-Antonio 2007; Kümmerli et a. 2009). Thus such long-term (even lifelong) associations allow partners continuously to adjust their investments into these interaction (Bronstein 1994b). For example, experiments found that the volume of nitrogen-containing substances provided by the nitrogen-fixing bacteria (such as ammonium, aspartate, or alanine) is increased by the concentration of oxygen and carbohydrates (such as succinate or glutamate) provided and controlled by the host plant (Soupene et al. 1995; Resendis-Antonio et al. 2007). In turn, from the perspective of the plant, higher nitrogen supply via fixation can enhance plant metabolism (Kiers & Denison 2008; Simms & Taylor 2002), which can translate into higher carbohydrate supply to the symbiont (Denison 2000). Many studies have revealed similar mechanisms for the conditional exchange of nutrients (such as phosphates and carbohydrates) in mycorrhizal symbiosis (Johnson et al. 1997; Bago et al. 2000; Bever et al. 2001; Bever et al. 2009; Kiers et al. 2011), and other forms of symbiosis, including endosymbiosis (Maynard Smith & Szathmáry 1995). Individuals may increase or decrease rewards in response to increased or decreased services received from a partner (Leimar & Connor 2003; Denison 2000; Bever et al. 2009; Foster & Wenseleers 2006; Kiers et al. 2006; Simms et al. 2006). This iterative reciprocation throughout an interaction obviously involves phenotypic plasticity of the traits involved in the interaction (Thompson 1988; Agrawal 2001) and offers a control mechanism between the partners (Bergmüller et al. 2007).

Knowing the costs and benefits of an interactions is fundamental for understanding its ecology and evolution (Bergstrom et al. 2003; Bronstein 2001b), however, these interactions are often not described by a single discrete event, but involve the long-term, often continuous, exchange of goods (Denison 2000; Lodwig et al 2003), which also makes more complicated to specify the costs and benefits associated with these interactions. While empirical investigation is complicated, if not impossible in certain cases, modeling can offer a prosperous basis to understand the dynamics of these interaction.

3.4.1. Modeling conditional investment strategies in social interactions

There are different time scales of reciprocal interactions that could, and should be considered (Mesterton-Gibbons & Dugatkin 1997). Naturally, the operation of any feedback control loop requires that the interaction lasts more than a moment in time. This type of response to the partner's investment level can be controlled by simple rules inducing developmental and/or behavioral changes. Considering time scales equal to the life span of an individual, these rules can provide a certain form of phenotypic plasticity (West-Eberhard 1989), similar to reaction norms, which describe how the environment can affect a genotype's expression (Agrawal 2001). If we substitute abiotic environment with the biotic, that is social, environment, the rule of reciprocation can be described by an interaction norm (Thompson 1988), which thus characterizes the expression of a trait as a function of the interacting partner's strategy. Another time scale of analyzing individual responses should account for the short term changes during an interaction. These can be considered as behavioral changes, since this behavior can differ from one interaction to the other with different interacting partner qualities (assuming that one individual has multiple interactions during its lifetime). If we consider cooperative interactions with continuous exchange of investments, adjusting one's investment can result in the change of fluxes between the partners, which behavior can be performed even by simple metabolic networks (Hasty at al. 2001; Resendis-Antonio et al. 2007), and does not necessarily need high cognitive abilities (Bergstrom et al. 2003). In this case, the reproductive success of an individual thus depends on not one, but multiple interactions.

For such plasticity in investment behavior, it is straightforward to consider models with continuous, evolving traits, and assume that the rate of investment can be modified after some sort of evaluation of the current investment strategy. There are multiple approaches in the literature for modeling such continuous, conditional investment strategies. In these models, the investment behavior is either controlled by two (Lehmann & Keller 2006; Le & Boyd 2007) or three separate traits (Wahl & Nowak 1999a,b). Furthermore, the reflexive nature of these strategies can be modeled mainly in two ways. In (linear) reactive strategies the player returns a fraction of the opponents investment (Wahl & Nowak 1999a,b; Lehmann & Keller 2006; André & Day 2007; Le & Boyd 2007). In the other approach, the so called payoff based strategies do not track the investment of the partner, only monitor their own payoffs from the previous round of the game, simply calculating the difference between the benefit received from the partner and the cost incurred from its own investment, and determines the next investment according to this net gain (Doebeli & Knowlton 1998; Killingback & Doebeli 2002). These strategies are analyzed in the Continuous Iterated Prisoner's Dilemma Game (Doebeli & Knowlton 1998; Wahl & Nowak 1999a,b; Killingback & Doebeli 2002; Sherratt & Roberts 2002; André & Day 2007; Le & Boyd 2007). Similar logic is assumed in negotiation games (McNamara et al. 1999; Taylor & Day 2004), where strategies first negotiate to find the optimal investment with their partner(s), then invest this optimal amount only, thus in these models the initial negation phase does not count in the final payoff. The pioneering model for studying the evolution of conditional investment strategies was developed to study the evolution and stability of mutualisms.

3.5. Interspecific cooperation: mutualism

Although mutualisms can be simply defined as reciprocally beneficial relationships between organisms, these relationships range from multi-partner, diffuse and many times indirect interactions to coevolved obligate symbiotic, not withstanding endosymbiotic, associations between species (Herre et al. 1999). Bacterial symbioses (defined in the broad sense) include long term, persistent, intimate association between bacteria and species from all kingdoms, and date back at least to the origins of eukaryotes (Sachs et al. 2011). Parasitic bacterial species that are harmful for humanity causing diseases, health and economic problems have received intense focus from scientists during the last centuries. In contrast, except for a few early pioneers and empirical studies, bacterial mutualists, symbiotic bacteria have been largely neglected until recently (Sachs et al. 2011). Bacterial mutualists provide a variety of benefits to hosts. In symbiotic associations, bacteria can provide for the host antibiotics, bioluminescence, and most commonly, a variety of nutrients (Sachs et al. 2011).

The evolutionary maintenance of beneficial symbiotic associations is a puzzle. Why a bacteria living in a host tissue—swimming in paradise—will not switch to parasitic, and act selfishly? Putting it into other words, the basic dilemma of intraspecific cooperation (Hamilton 1964) also applies to interspecific mutualism (West et al. 2007; Boucher 1985): while both partners would be better off helping each other, a cheater that accepts help without reciprocating will have higher fitness and thus spread in the population (Bull & Rice 1991; Bronstein 2001a; Bergstrom et al. 2003; Bshary & Bronstein 2004). Several mechanisms are proposed that may promote the long term nature of these mutually beneficial relationships (Sachs et al. 2011), but how stable are these associations in reality?

Cheating by one partner can, in fact, shift a mutualistic interaction—for longer or shorter times—into parasitism (Bronstein 2003), as corroborated by observations in ant–plant mutualisms (Axén 2000; Pierce et al. 2002; Leimar & Connor 2003) or mycorrhizal mutualisms (Johnson et al. 1997; Egger & Hibbett 2004). Mutualistic interactions are known to shift along the mutualism–exploitation continuum with changes in environmental factors (Johnson et al. 1997; Herre et al. 1999; Klironomos 2003; Neuhauser & Fargione 2004). For example, many nutritional mutualisms, including mycorrhizal or rhizobial mutualisms, are highly beneficial for host plants as long as the resource provided (e.g., phosphorus, nitrogen, or copper) is absent from the environment, but can become harmful (implying that costs exceed benefits) when that resource no longer is a limiting factor (Johnson et al. 1997; Kiers & van der Heijden 2006; West et al. 2007; Lau et al. 2012). Mutualisms can also be unstable on an evolutionary timescale, and there can be a diversity of mutualistic, parasitic, and free-living variants within higher taxa. The phylogenetic analysis of mycorrhizal and free-living homobasidiomycetes suggests that there have been several transformations between symbiotic and free-living forms (Hibbett et al.

2000). The gain and loss of mutualistic traits thus seems to be relatively common on an evolutionary timescale (Sachs et al. 2011).

However, numerous mutualistic relationships appear to be persistently stable on the long term. For example coral–algal symbiosis evolved ~240 million years ago (Douglas 2008), and endosymbiotic association of eukaryotic cells with mitochondria is ~1-2 billion years old (Maynard Smith & Szathmáry1995; Douglas 2008). Mycorrhizal fungal symbiosis, which involves most of the vascular plants (Smith & Read 1997), is estimated to be existent for more than ~400 million years (Remy et al. 1994; Douglas 2008). Although sometimes mycorrhizal associations can shift into parasitism, or to free-living forms, majority of these associations are stable on the long term.

What sort of models can we use to analyze the evolutionary dynamics and stability of these complex interactions? Can we rely on the wealth information available from cooperation literature?

3.6. Understanding mutualisms with continuous conditional investment strategies

Despite the similar underlying dilemma, interspecific cooperation differs from intraspecific cooperation in several key features. In interspecific cooperation, the interaction is under the control of two separate genomes. The evolutionary success of strategies in one species depends on the strategies in its partner species (Heath & Tiffin 2007; Heath 2010); and the spread of a successful strategy in one species does not automatically result in the spread of a matching strategy in the other. Another consequence of partners belonging to different species is that one important mechanism promoting cooperation, kin selection (Sachs et al. 2004; West et al. 2007), cannot play a role. Furthermore, in many mutualisms the partners occupy different niches (Boucher 1985) and thus are not in direct competition with each other. Therefore models of intraspecific cooperation do not cover the specificities of mutualisms, so that mechanisms promoting mutualism have to be identified separately (Bshary & Bronstein 2004; Heath 2010).

In spite of the biological importance of, and the wealth of information available for, interspecific cooperation, the evolutionary dynamics of mutualism are far less understood (Bergstrom et al. 2003; Bshary & Bronstein 2004). Moreover, among models of mutualism, few concentrate on the evolutionary dynamics of interactions on the individual level when there is continuous feedback between the partners (Bergmüller et al. 2007), as captured by the concept of partner fidelity feedback (Sachs et al. 2004; Bull& Rice 1991). One of the few existing models addressing this challenge is the one proposed by Doebeli and Knowlton (1998), which is among the three most cited evolutionary models in the mutualism literature. Other well-known models of mutualistic interactions are the biological market models (Noë & Hammerstein 1995), and models of geographic mosaic theory of coevolution (Gomulkiewicz et al. 2000).

In Doebeli and Knowlton's individual-based model, each individual's strategy is characterized by two values: the so-called initial offer and the reward rate. The initial offer amounts to an unconditional or fixed investment in the mutualistic interaction, whereas the reward rate quantifies a conditional or variable component, which determines how an individual's investment depends on the payoff it gained from its current partner in the previous round. This distinction is well founded in the biology of mutualistic interactions. For example, in mutualistic interactions involving ants defending their mutualistic partners from predation, as in the case of ants and lycaenid butterfly larvae (Agrawal & Fordyce 2000) or aphids (Bshary & Bronstein 2004), both partners can adjust their investments by providing less nectar or less tending. There is also an unconditional initial investment in many interactions, which is required for establishing an interaction with a partner before evaluating its quality as a mutualist (Bshary & Bronstein 2004). Examples include honeydew droplets or volatile substances from tentacle organs to attract partners (Pierce et al. 2002) or chemical compounds released by plants in mycorrhizal or rhizobial mutualisms (Kiers & Denison 2008). Moreover, creating an interface for physical contact sometimes requires high investments from both parties before an exchange of nutrients can commence (Gage 2004).

Doebeli and Knowlton (1998) concluded that population structure or spatial confinement is essential for stabilizing these mutualisms, that is a form of assortment between the partners, and also their descendants, is the main factor stabilizing mutualisms. They demonstrated that without the facilitating effect of space, mutualistic investments vanish from the populations. Nevertheless, the specific role of spatial structure and the differences in the dynamics of mutualism in spatially structured and well-mixed populations need to be still more deeply understood. Moreover, Doebeli and Knowlton's conclusion regarding the necessity of spatial population structure was based on a single example. Reviews of the mutualism literature (Bergstrom et al. 2003; Bshary & Bronstein; Kiers & van der Heijden 2003; Verbruggen et al. 2012) have therefore debated the importance of space in stabilizing mutualism, and independent theoretical studies (Foster & Wenseleers 2006) could not corroborate the necessity of space for stabilizing mutualism. Moreover, in some cases, spatial structure was detrimental, since in mixing environment cooperator types were more successful (Verbruggen et al. 2012). What are the causes for this apparent discrepancy? Are mutualisms really unstable in the absence of spatial structure? The aim of this study is to unravel the role of space in the evolutionary dynamics of mutualism, and to provide a platform for connecting model results with experimental findings.

3.6.1. Models and methods

Throughout this study, we define mutualism as an interaction between individuals from different species, Mutualist A and Mutualist B (Doebeli & Knowlton 1998). We note here that Mutualist A and Mutualist B in our model cover mutualist guilds, which can be composed of one species or several species with the same functional relationship to mutualist partners. The fitness of an individual thus depends on the outcome of its interaction with a member of the other mutualist guild, while competition occurs only between members of the same guild. Consequently, the populations of the two mutualist guilds can be conceived as occupying two separate square lattices (Figure 3.4).

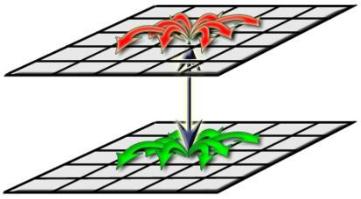


Figure 3.4: Interaction scheme in the model. Individuals cooperate with partners from the opponent population, either from the corresponding lattice point in the spatial model (grey arrow), or with a random partner in the well-mixed model. Competition takes place between, either from the local neighborhood in case of spatially structured populations conspecific (red arrows for Mutualist A and green arrows for Mutualist B), or eight random individuals from the same population in the well-mixed model.

As we assume no sexual reproduction, our use of population corresponds only to a collection of individuals belonging to the same guild. We assume that Mutualist A and B are otherwise identical, with potentially mutualistic investment described by analogous traits.

Mutualistic investments

Each individual's strategy is specified by two values (non-negative) quantitative adaptive traits: the unconditional investment (a , determining the initial offer), and the conditional investment (b , determining the reward rate). Thus, the strategy of Mutualist A is given by the pair (a_A, b_A), and the strategy of Mutualist B is given by the pair (a_B, b_B). The initial offer is an unconditional, fixed investment in the mutualistic interaction, and the reward rate determines how the investment changes depending on the last payoff gained from interaction with the current partner (Figure 3.5).

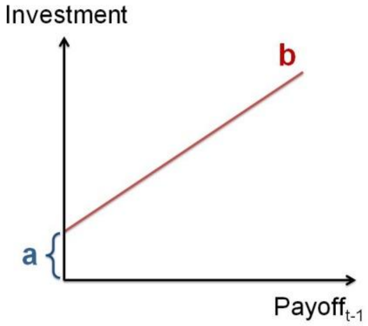


Figure 3.5: The two traits: a is the unconditional investment, while b determines the conditional investment component according to a linearly increasing function with slope b. Payoff$_{t-1}$ here represents the net gain of the individual from the previous round of the interaction.

Interactions and payoffs

Payoffs are calculated through an iterative procedure, based on a fixed number T of iterations or interaction rounds. Following Doebeli and Knowlton (1998), we use $T = 15$ rounds, but we also test other iteration numbers. Before the first iteration, the payoffs of the individuals are set to zero. In each iteration, each individual offers a certain investment to its partner, as follows.

Below we consider the investments made, costs incurred, benefits received, and payoffs accrued by a mutualist with strategy i interacting with a mutualist with strategy j. In the first iteration $t = 0$, the investment $I_{1,i,j}$ is directly given by the trait a,

$$I_{1,i,j} = a_i . \qquad \text{Eq.3.1.}$$

In every following iteration $t > 0$, the investment I_t is determined by a linear reactive strategy,

$$I_{t,i,j} = a_i + b_i p_{t-1,i,j} , \qquad \text{Eq.3.2.}$$

where $p_{t-1,i,j}$ is the net benefit, or payoff, obtained in the previous iteration $t-1$ by strategy i interacting with strategy j (see below for further details on how partners are chosen). Investments $I_{t,i,j}$ are always non-negative.

The payoffs are calculated from the investments made by the individuals of Mutualist A and Mutualist B. Each investment implies a cost for the donor and a benefit for the receiver (Figure 3.6),

$$C(I_{t,i,j}) = C_0 I_{t,i,j} , \qquad \text{Eq.3.3.}$$

$$B(I_{t,j,i}) = B_0 (1 - \exp(-B_1 I_{t,j,i})) . \qquad \text{Eq.3.4.}$$

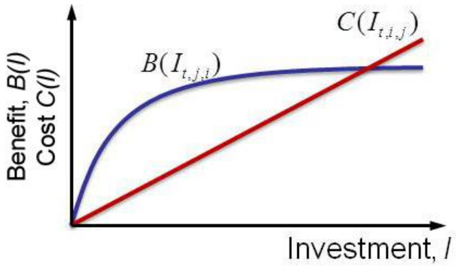


Figure 3.5: The benefit increases as a saturating function, while the cost increases linearly for higher investments.

Accordingly, the payoff from one iteration of the interaction is

$$p_{t,i,j} = B(I_{t,j,i}) - C(I_{t,i,j}) \,, \qquad \text{Eq.3.5.}$$

where $I_{t,i,j}$ and $I_{t,j,i}$, respectively, are the investments of the focal individual i and of its partner j in round t. The total payoff determining the competition between strategies from the same population (see below) is the sum of their payoffs over all rounds of the mutualistic interaction,

$$P_{i,j} = \sum_{t=1}^{T} p_{t,i,j} \,. \qquad \text{Eq.3.6.}$$

Benefit-to-cost relationship

Compared to traditional game theoretical models, where the benefit-to-cost ratio is given by b/c (benefit divided by the cost of cooperation), in the current model, it is much harder to define the benefit-to-cost relationship because of the nonlinear benefit function and the complex, iterated manner of the game. Thus we will make the following approximation: for infinitesimally small investments the benefit function can be expressed as

$$\lim_{I \to 0} B(I) \to B_0 B_1 I \,. \qquad \text{Eq.3.7.}$$

We consider the benefit-to-cost ratio written in the form of $B(I)/C(I)$, which gives

$$B_0 B_1 I / C_0 I \,. \qquad \text{Eq.3.8.}$$

From this, we arrive at

$$B_0 B_1 / C_0 \,, \qquad \text{Eq.3.9.}$$

which we will take as a simple measure of the benefit-to-cost relationship. Hence, in our case, higher benefit-to-cost ratio means bigger parameter values for the benefit function compared to parameter values of the cost function; thus, in general, larger benefit compared to the cost of investment.

Competition

In the spatial model, the focal individual and its m closest neighbors (we use the Moore neighborhood with m = 8) compete for the focal site. In the well-mixed model, we pick m random individuals from the population as competitors. We employ one or the other of two update rules. With “best takes over” updating, which was also used by Doebeli and Knowlton (1998), the individual with the highest payoff replaces the focal individual (Doebeli and Knowlton 1998; Axelrod 1984; Hauert 2002). This implies that, if no competitor has higher payoff than the focal individual, the later stays unchanged. If two individuals have the same payoffs, the winner is randomly chosen between them. With “pairwise comparison” updating, a random competitor i (interacting with individual j) replaces the focal individual k (interacting with individual l) with probability pr

$$pr = 1/(1+\exp(-w\Delta P)), \qquad \text{Eq.3.10.}$$

depending on their payoff difference

$$\Delta P = P_{i,j} - P_{k,l} \qquad \text{Eq.3.11.}$$

(Szabó & Tőke 1998; Ohtsuki & Nowak 2006); for scaling the strength of selection, we use $w = 1$. Both rules belong to the class of so-called death–birth updating processes (Ohtsuki & Nowak 2006).

Mutation

The two traits can mutate independently with probability μ per update. The mutant trait value is drawn from a normal distribution, with a mean equaling the current trait value and a given variance. Doebeli and Knowlton (1998) assumed that the standard deviation σ of this normal distribution is a given percentage (5%) of the current trait value. This assumption implies that the coefficient of variation (CV) is constant; thus, for smaller trait values the resultant variance is much smaller than for larger trait values. Accordingly, when a trait value approaches 0, its mutational variance also approaches 0. This means that trait values can essentially get “stuck” close to 0. To evaluate the consequences of this effect, we also consider models in which the mutational standard deviation is kept fixed ($\sigma = 0.05$).

Updating

In our model, N^2 updates occur per generation, where N^2 is the population or guild size of Mutualist A and Mutualist B. In the spatial model, N is the width and height of the square lattice (we consider values N = 10, 30, 50, and 100). For each update, we choose an interacting pair of Mutualist A and B. In the spatial model, the chosen individuals occupy corresponding sites of the two lattices, whereas in the well-mixed model, they are randomly chosen from the two lattices (Figure 3.4). With synchronous updating, all individuals are updated at once, while with asynchronous updating randomly chosen individuals are updated. Unless mentioned otherwise, we use asynchronous updating. Each update starts with an update of the payoffs of both chosen individuals, followed by competition among individuals.

We start the model dynamics with two homogeneous populations with both trait values close to 0 (0.005, unless indicated otherwise), implying that individuals are not mutualistic. We also consider different initial conditions, with one or both of the traits set to higher values (chosen from the interval $0-10$). We then run the dynamics for $100,000$ generations (unless otherwise indicated), which is a time horizon chosen to be long enough to detect the main dynamical trends for all model settings considered.

3.6.2. Results

As the dynamics of the full model are highly complex, we gradually build up understanding by analyzing model versions of increasing complexity throughout the next sections, starting with the simplest model version that still retains key dynamical features of the full model, and after five steps, eventually arriving back at the full model. Based on the payoffs defined in the Model and methods section, we start from a best-response analysis of the mutualistic investment strategies; we then examine the selection pressures on these investments for mutualists with low polymorphism, consider the individual-based model without spatial population structure but with higher degrees of polymorphism, reinstate the spatial population structure, and finally conclude our analysis of the full model by exploring the effects of different mutation schemes and update rules.

No investment as a best-response equilibrium

As a first step, we determine best-response equilibria of the mutualistic investments. The interspecific best response

$$s_j = r(s_i) \qquad \text{Eq.3.12.}$$

is defined here as the strategy s_j of mutualist *j* that has the highest payoff playing against strategy s_i in the other mutualist guild, for $i, j = \mathrm{A}, \mathrm{B}$, $i \neq j$ (Figure 3.8). Thus, investment strategies are in a best-response equilibrium $(s_\mathrm{A}, s_\mathrm{B})$, if

$$r(s_\mathrm{A}) = s_\mathrm{B} \text{ and } r(s_\mathrm{B}) = s_\mathrm{A}, \qquad \text{Eq.3.13.}$$

if, that is, these strategies are the best responses to each other. Incidentally, this implies that

$$r(r(s_\mathrm{A})) = s_\mathrm{A}, \qquad \text{Eq.3.14.}$$

which highlights a similarity with the concept of Nash equilibrium in intraspecific games; in that case a strategy simply is the best response to itself (Hofbauer & Sigmund 2003).

As an analytical derivation of the best-response function r is not possible for our model, we calculate it numerically by fixing a strategy s_A in Mutualist A, then scanning the strategy space of Mutualist B for the strategy $r(s_\mathrm{B}) = s_\mathrm{A}$ that yields the highest payoff to Mutualist B (Figure 3.7).

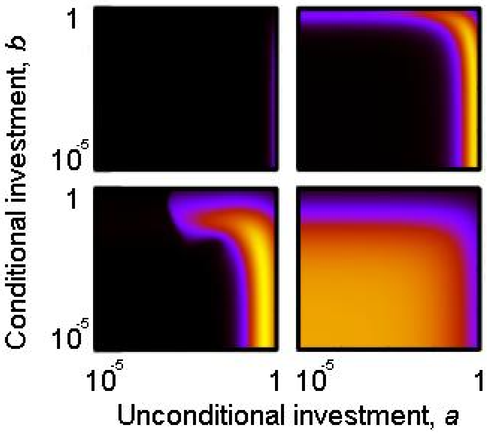


Figure 3.7: The payoff of Mutualist A (a_A, b_A) playing with fixed partner strategy in Mutualist B (a_B, b_B). The assumption of non-linear benefit function and iterated (recursive) game, the payoff increases non-linearly with the increase of investment traits *a* and *b*. For low investments from the partner ($0.0001, 0.0001$: upper left panel), only no investment pays off. If partners investments are above the threshold, but *a* is still not too high ($0.05, 0.05$: upper right panel, and $0.05, 1$: lower left panel), making high investments results in the highest payoff. When *a* is high, high investments are worse than low or no investments ($5, 0.0005$: lower

right panel). In order to emphasize the main trend, we plotted $P = P^{10}$. Parameters: $T = 15$, $B_0 = 4.7$, $B_1 = 1.8$, $C_0 = 0.6$.

We find that the best response to no investment is no investment, $r(0,0) = (0,0)$, which therefore is a best-response equilibrium (Figure 3.8). The intuitive explanation is simple: when a partner does not reciprocate, the best strategy is not to invest in that partner (Figure 3.7 upper left panel). Furthermore, as our numerical investigations reveal, no investment $((0,0),(0,0))$ is the only best-response equilibrium of our model (i.e., $a_{\mathrm{A}} = 0$, $b_{\mathrm{A}} = 0$, $a_{\mathrm{B}} = 0$, and $b_{\mathrm{B}} = 0$).

Analyzing the local stability around this equilibrium, we find two types of local best-response dynamics. The equilibrium $((0,0),(0,0))$ is locally stable (Killingback & Doebeli 2002; Scheuring 2005), but strategies converge there only if they start out below a threshold level b_{T} of reciprocation (Figure 3.8, and gray lines in Figure 3.9/A and *B*). Using the same approximation as Killingback and Doebeli (2002) for small investments, we find that this threshold is determined by the slopes of the benefit and cost functions at zero investment,

$$b_{\mathrm{T}} = C'(0)/[B'(0)^2 - C'(0)^2] \qquad \text{Eq.3.15.}$$

(Scheuring 2005), for which

$$B'(0) = B_0 B_1 \text{ and } C'(0) = C_0 \qquad \text{Eq.3.16.}$$

is substituted in our case (see Models and methods section). When starting out below b_{T}, best-response strategies converge to the no-investment equilibrium, whereas when strategies start out above b_{T}, best responses lead to an increase in investment levels (Figure 3.8 black vs. colored regions).

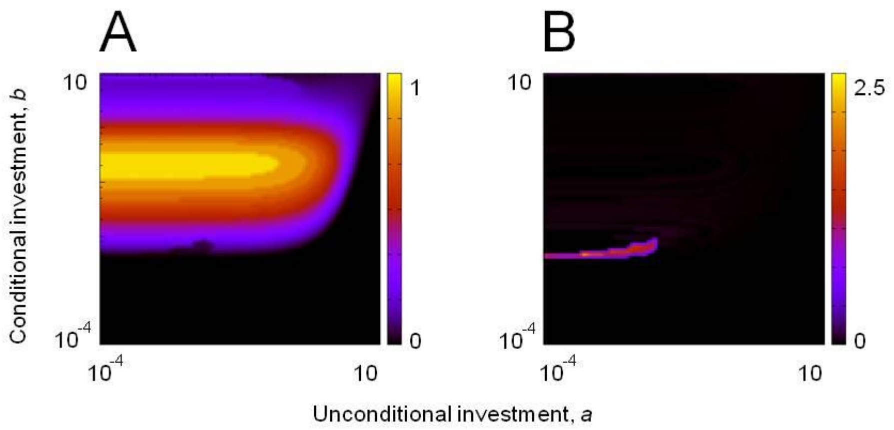


Figure 3.8: The best-response strategy of Mutualist B (a_B, b_B, on the panel **A** and **B**) playing with fixed partner strategy in Mutualist A (a_A, b_A on the axes) on logarithmic scales. Panel **A** depicts trait a_B, and panel **B** depicts trait b_B of the best-response strategy of Mutualist B. While below a threshold level of reciprocity the best response is to invest nothing (notice that for low values of *b* on the y-axis, the best strategy is 0), above this threshold increasing investments result in the highest payoffs. Parameters: $T = 15$, $B_0 = 4.7$, $B_1 = 1.8$, $C_0 = 0.6$.

To understand the latter behavior, we consider the global best-response dynamics, which gives us full information about the coevolutionary changes we must expect in mutualistic investment strategies. For this, we start from the initial strategy of one mutualist, determine the optimal strategy of its partner, then determine the optimal strategy of the first mutualist, and so on (Figure 3.9). Interestingly, this shows that the no-investment strategy is not always the best response: above the thick gray line in Figure 3.9/A, the best response differs from $(0,0)$ (Figure 3.8) and causes reciprocation to increase in a first step (Figure 3.9/A). After a few best-response steps, however, the dynamics always converge to the no-investment equilibrium, which is thus a global attractor of the best-response dynamics. In conclusion, when the best-response dynamics start out below the threshold line, these dynamics will directly lead to the no-investment equilibrium, whereas when the initial strategy lies above the threshold line, the dynamics will cause investments to increase temporarily, before bringing them down to 0 eventually (Figure 3.9/A). Throughout this study, we refer to the latter behavior as the investment cycle.

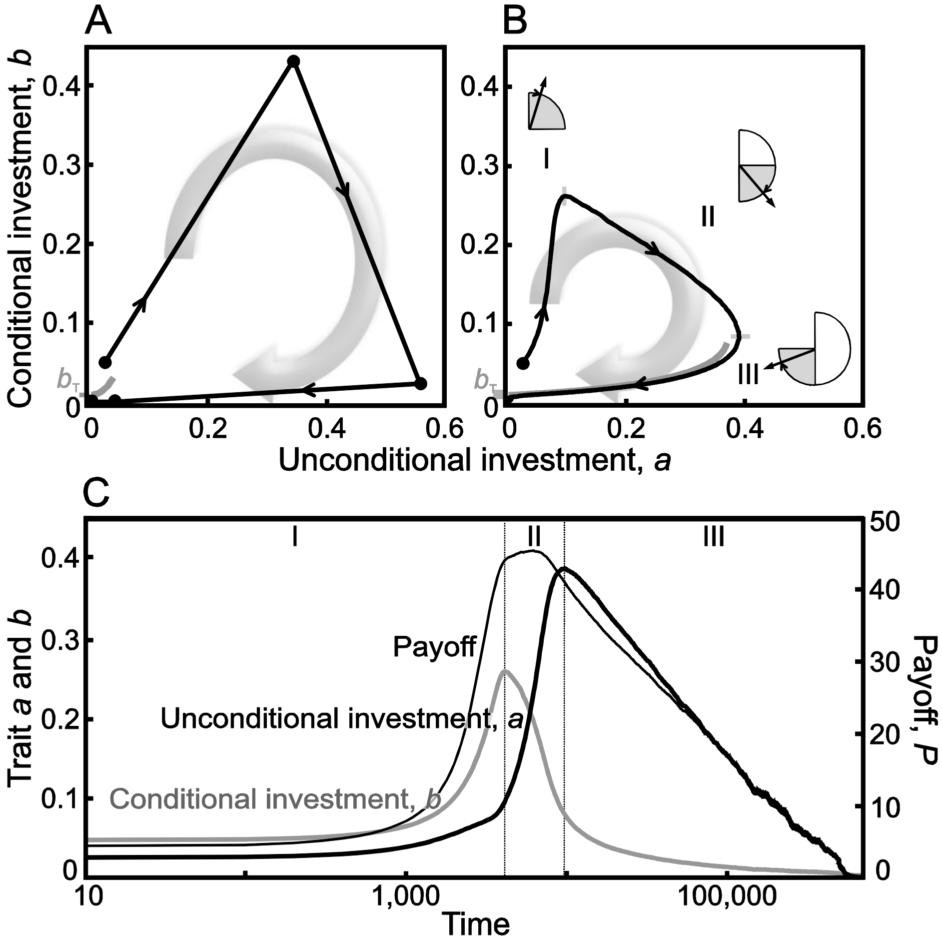


Figure 3.9: Illustration of investment cycle and reciprocation threshold in well-mixed communities. (**A**) Best-response dynamics. Arrows indicate the succession of best responses, leading to $(a,b)=(0,0)$ in just four steps. (**B**) Evolutionary dynamics in a community with low degrees of polymorphism and "pairwise comparison" updating. Arrows indicate changes of the selection gradient along the investment cycle. In A and B, representative evolutionary trajectories are shown starting above the reciprocation threshold (thick gray lines). (**C**) Resultant changes of investment traits and payoffs along the investment cycle in **B**. Results in **B** and **C** are averaged over 15 replicate model runs for the same initial condition. Above the reciprocation threshold, the best-response dynamics and the evolutionary dynamics increase the reciprocation trait b. Parameters: $T=15$, $B_0=4.7$, $B_1=1.8$, $C_0=0.6$, $\sigma=0.005$, $\mu=0.005$, and $N^2=100$.

Investment cycle and selection pressures on mutualistic investments

We now show how our insights from the best-response analysis extend to individual-based evolutionary dynamics under low degrees of polymorphism (Figure 3.9/B,C). Started below a threshold line (thick gray line in Figure 3.9/B), the evolutionary dynamics monotonically converge to no investment. Above that line, the evolutionary dynamics temporarily drive investments up (Figure 3.9/B and C). After these investments have passed a maximum, they continuously converge to zero. In other words, we again find a "boom and bust" investment cycle.

We can obtain the threshold of increasing investments (thick gray line in Figure 3.9/B) in the limit of vanishing polymorphism. In that case, the selection pressures (or gradients) on the investment traits are given by

$$g_{X,x}(x_X) = \partial P_{i,j} / \partial x'_X \Big|_{x'_X = x_X} \qquad \text{Eq.3.17.}$$

where X is the focal mutualist (A or B), Y is the other mutualist (B or A, respectively), x is the focal trait (a or b), $i = (a'_X, b'_X)$ is the strategy of a mutant in X, (a_X, b_X) is the strategy of the resident in X, and $j = (a_Y, b_Y)$ is the strategy of the resident in Y. Positive selection pressures mean that mutants with increased trait values have higher payoffs than the current resident, and therefore can spread in the population (Figure 3.10). This kind of evolutionary dynamics is still simplified compared with an individual-based model; it yields a good approximation only when population dynamics are sufficiently faster than trait dynamics ($\mu << 1$), so mutants mostly encounter monomorphic populations, and when mutational steps are sufficiently small ($\sigma << 1$). The obtained threshold line (thick gray line in Figure 3.9/B) is the unstable part of the evolutionary isocline for trait b, along which the selection pressure on b passes 0 and thus changes sign (Figure 3.10). For small investments, and thus for $a \to 0$, this isocline is located at $b = b_\mathrm{T}$.

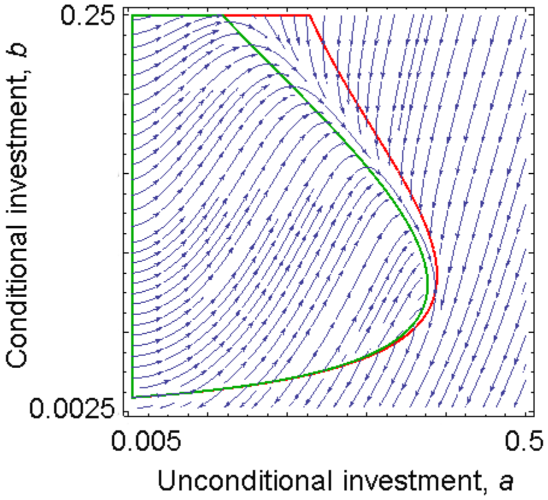


Figure 3.10: Phase portrait of the two investment traits, the unconditional (*a*) and the conditional (*b*) investment components. Isoclines, shown as solid lines for *a* (red) and *b* (green), are characterized by the change of the sign of the selection gradient (Eq. 3.17.) acting on the corresponding traits (represented by blue streamlines and arrows). Parameters: $T = 15$, $B_0 = 4.7$, $B_1 = 1.8$, $C_0 = 0.6$.

We find that our aforementioned results regarding the investment cycle are robust. First, we can approximate the underlying individual-based evolutionary dynamics by adaptive dynamics theory (Dieckmann & Law 1996), using the selection pressures $g_{X,x}$ defined above. For low mutation probabilities μ and standard deviations σ, this approximation is accurate. Second, we can consider "best takes over" updating in an individual-based model with low degrees of polymorphism, and third, we can use a modification of this updating, so that the most successful mutant is drawn from a circle around the resident traits (for this, we sample random combinations of mutants from a circle of radius $0.005\sqrt{\Delta a^2 + \Delta b^2}$, where Δa and Δb denote the trait differences between mutants and residents, and choose the one mutant with the highest payoff). All three of these variants yield results in agreement with summarized above.

The emergence of the investment cycle can best be understood by examining the gradual coevolution of the two investment traits. Evolution starts from a slightly reactive state (b exceeds the threshold b_{T}), and both the unconditional and conditional investments first increase, as selection pressures are positive on both traits. Higher reactivity (resulting from higher conditional investment b) selects for higher initial investment, because making a high initial investment yields high returns already from the first round of the interaction. Consequently, individuals obtain higher payoffs by making high investments already from the beginning of the interaction. While the initial investment increases, the selection pressure for the conditional response decreases and finally reverses, as a strategy investing a large amount in the beginning and increasing investments even further in the following rounds may end up overinvesting. Eventually, after the reactivity evolves close to zero (falling below b_{T}), initial investments also evolve to zero. In this final phase, with very little reactivity, the dynamics simply resemble those of the continuous Prisoner's Dilemma, in which no cooperative investments can be maintained without additional mechanisms.

Phases of the investment cycle

Next, we introduce a measure that helps us monitor the evolution of strategies along the investment cycle, and that suitably reduces the two-dimensional trait space, spanned by the two investment traits, to one dimension. For this purpose, we define cycle phases, φ_{A} and φ_{B} for Mutualist A and B, respectively, so that these increase along the investment cycle. As shown by the small arrows in Figure 3.9/B, these phases are determined by the direction of the selection gradients ($g_{X,a}$, $g_{X,b}$) acting on the traits (a_X, b_X) of Mutualist X with $X = \mathrm{A,B}$ (Eq. 3.17, and Figure 3.10).

Depending on the signs of $g_{X,a}$ and $g_{X,b}$, we can distinguish four quadrants of φ_X, measured clockwise relative to the positive vertical axis. In the first quadrant:

$$\varphi_X = \arctan(g_{X,a} / g_{X,b}); \qquad \text{Eq.3.18.}$$

in the second quadrant:

$$\varphi_X = -\arctan(g_{X,b} / g_{X,a}) + \pi / 2; \qquad \text{Eq.3.19.}$$

in the third quadrant:

$$\varphi_X = \arctan(g_{X,a} / g_{X,b}) + \pi; \qquad \text{Eq.3.20.}$$

and in the fourth quadrant:

$$\varphi_X = -\arctan(g_{X,b} / g_{X,a}) + 3\pi / 2. \qquad \text{Eq.3.21.}$$

The boundaries between these phases thus correspond to curves in the trait space along which the selection pressure is zero for either one of the two traits (Figure 3.10).

Phase I is characterized by positive selection pressures on a and b, so that both trait values and investment levels increase (phase I in Figure 3.9/B and C, $0 \le \varphi < \pi / 2$). In phase II, while trait a still increases, trait b declines, as the selection pressure on b is negative (phase II in Figure 3.9/B and C, $\pi/2 \leq \varphi < \pi$). In phase III, more exploitative strategies, which invest less and thus gain more, are favored by selection, so that investment levels evolve to zero, as traits a and b both decline (phase III in Figure 3.9/B and C, $\pi \leq \varphi < 3\pi/2$). For low degrees of polymorphism, selection gradients in the fourth quadrant rarely occur; here, trait b would grow while trait a would shrink ($3\pi/2 \leq \varphi < 2\pi$).

Figure 3.9 shows that the cycle phase derived from the selection gradients (Figure 3.10) acting on Mutualists A and B adequately indicates the direction of evolutionary dynamics along the investment cycle, in monomorphic populations or in populations with a low degree of polymorphism.

Phase polymorphism

In the next step of our analysis, we allow higher degrees of polymorphisms. As shown in the previous section, when mutation probability and/or mutation variance are low, the polymorphic spread among strategies remains narrow, as the two mutualist communities evolve along the investment cycle (Figure 3.11/A, left-hand side). However, there is a sharp transition in the outcome as the variety of mutants increases. Above a critical supply of strategy diversity, the two polymorphic populations can perpetually maintain strategies that on average are mutualistic and that lead to a high and stable level of average payoff (Figure 3.11/A, right-hand side). This stable community-level mutualism still implies cyclic behavior, as the averages of both investment traits continuously evolve along the investment cycle in populations with higher degrees of polymorphism (Figure 3.11/B–D). Importantly, with the increase of mutational variability, this cyclic behavior becomes perpetual, as the evolutionary dynamics no longer collapse to zero investments at the end of phase III. The increase of mutational variance not only affects the polymorphic spread of strategies along the investment cycle, but also its shape and amplitude (observe the decrease of cycle amplitude with the increase of σ in Figure 3.11/B–D). To understand these effects of mutational variability, we need to appreciate, first, how and why polymorphism arises, and second, what it implies for the community-level stability of mutualistic interactions. For this, it is helpful again to consider phases and selection gradients along the investment cycle.

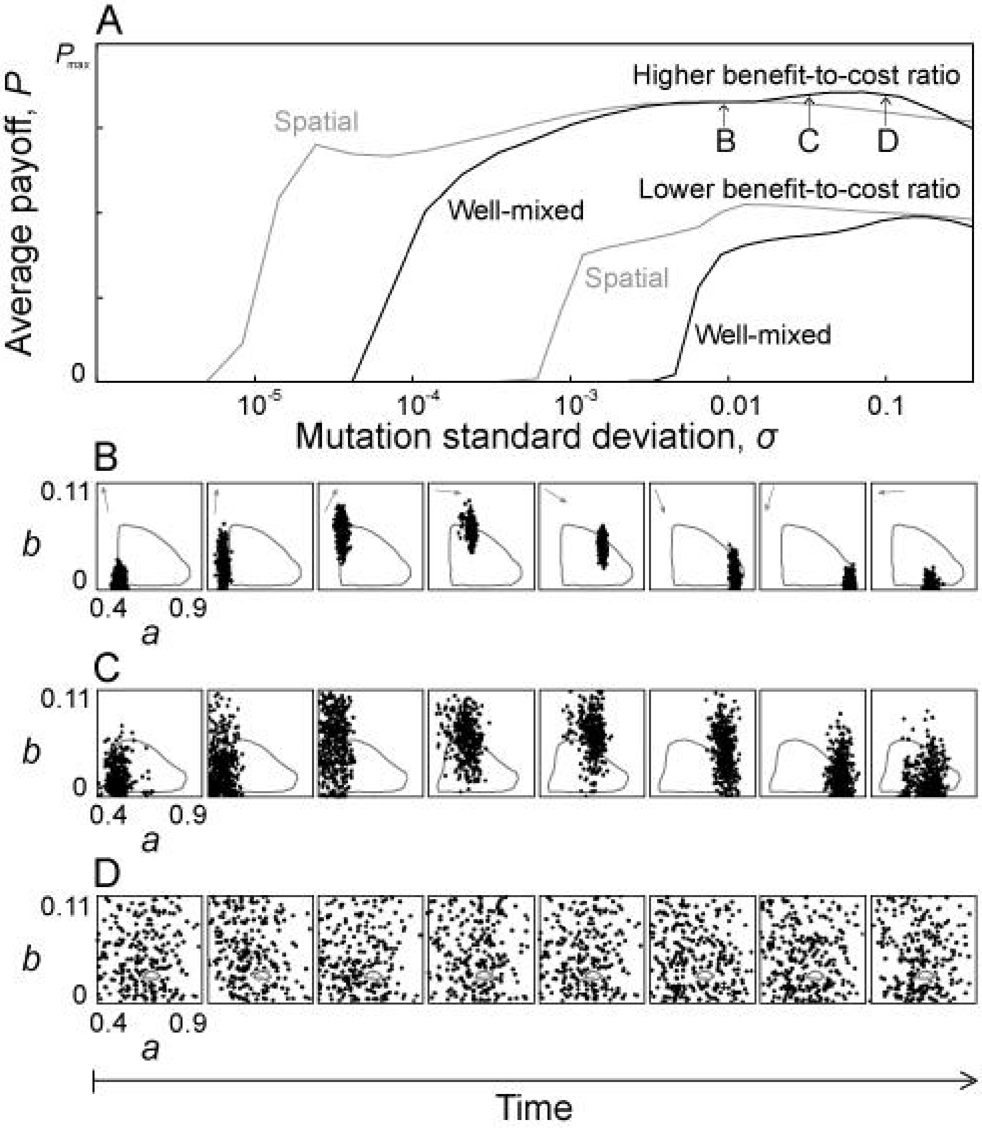


Figure 3.11: Evolution and stability of mutualistic investments in communities with higher degrees of polymorphism. (**A**) Diversity thresholds revealed by the effect of mutation variability on the average payoff in the community. For lower mutational standard deviations σ, there is no mutualism (left-hand side), while stable community-level mutualism evolves abruptly once mutational variability is high enough (right-hand side). Results are averaged over the two mutualists and 15 replicate model runs. Payoffs can range between 0 and the maximal potential payoff $P_{\text{Max}} = TB_0$. (**B**, **C**, **D**) Polymorphic spread of strategies in well-mixed communities, and their evolution along the investment cycle, with low, medium, or high mutation standard deviations $\sigma : \sigma = 0.0075$ in **B**, $\sigma = 0.025$ in **C**, and $\sigma = 0.1$ in **D**. As the averages of the traits a and b (shown as gray circular line)

move along the investment cycle, they trace out the shown circular lines, corresponding to cyclic oscillations whose amplitudes decrease as σ increases. Parameters: $N^2 = 10,000$ in **A** and $N^2 = 2,500$ in **B**, **C**, and **D**; lower benefit-to-cost ratio of 14.1 in **A**: $B_0 = 4.7$, $B_1 = 1.8$, $C_0 = 0.6$; higher benefit-to-cost ratio of 175 in **A**, **B**, **C**, and **D**: $B_0 = 7$, $B_1 = 2.5$, $C_0 = 0.1$; $T = 15$, $\mu = 0.02$.

Individuals in polymorphic populations encounter a diverse set of strategies, so the selection gradients they experience need to be determined accordingly:

$$g_{i,x}(x_i) = \partial\left(\frac{1}{J}\sum_{j=1}^{J} P_{i,j}\right)\Big/\partial x_i'\Big|_{x_i'=x_i}, \qquad \text{Eq.3.22.}$$

where i is the focal individual, the sum extends over all individuals J of the other mutualist, and the parenthesis encloses the expected payoff of a mutant offspring of individual i with strategy (a_i', b_i'). These selection gradients, shown as arrows in Figure 3.12/A, help us understand the emergence of cyclic dynamics and phase polymorphism. At the beginning of the investment cycle (phase I), mutations will typically cause some symmetry breaking between the investment strategies of the two mutualists, while the polymorphic spread among strategies still remains narrow (Figure 3.12/A, Panel 1). Once a trajectory reaches phase II, the selection pressures on the two b traits approach 0, making them especially susceptible to neutral drift and thus enhancing the symmetry breaking and polymorphic spread (observe the diversity of gradient angles in Figure 3.12/A, Panel 2). Similar mechanisms operate at the boundary of phases II and III, where selection pressures become weak on the a traits (Figure 3.12/A, Panels 3 and 4). Finally, when a trajectory reaches phase III (Figure 3.12/A, Panel 5), the strongest effect occurs: when traits evolve close to the boundary that separates trait combinations corresponding to phases III and I (see the partially overlapping black and thick gray lines in Figure 3.9/B), mutations can take the two traits across the boundary, from phase III to I and back. Such a jump across the boundary changes the sign of the selection gradient for both of the traits for at least one of the mutualists (Figure 3.12/A, Panels 6 and 1). This causes recurrent transitions across the boundary, so trajectories linger at this boundary, which naturally increases their polymorphic spread. Once a sufficient proportion of the population has thus traversed the boundary, the investment cycle is retriggered (Figure 3.12/A, Panel 1). Notice that the degree of phase polymorphism varies along the investment cycle. It typically decreases in the middle of phases I and III (observe how all gradients are pointing essentially just in one direction in Figure 3.12/A, Panels 1 and 5), and increases at the boundaries of the phases (observe the diversity of gradient angles in Figure 3.12/A, Panels 2, 3, 4, 6).

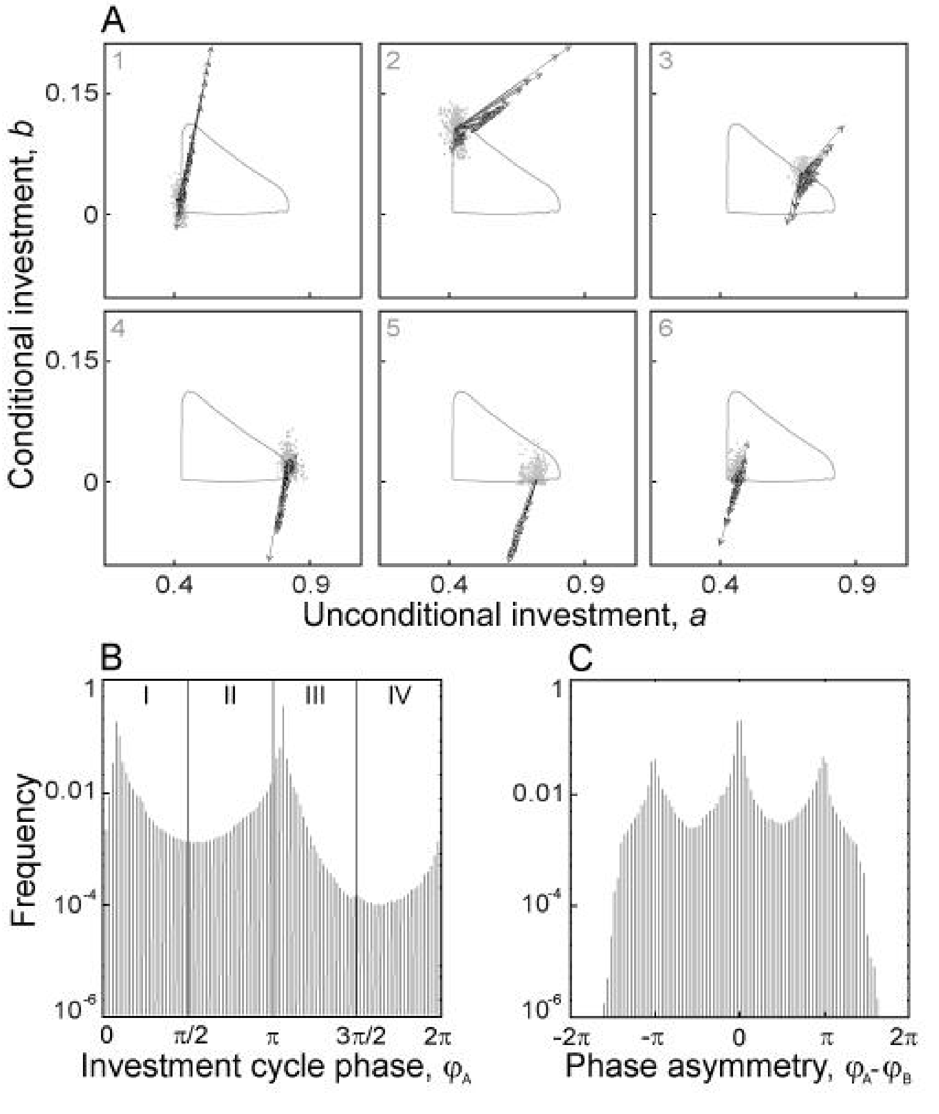


Figure 3.12: Selection gradients along the investment cycle and resultant phase distribution in a well-mixed polymorphic community. (**A**) Arrows indicate the selection gradients on a random subsample of individuals of Mutualist A as that mutualist's trait distribution (gray dots) moves along the investment cycle (gray circular lines). Average long-term polymorphic distribution of (**B**) phases along the investment cycle and (**C**) corresponding phase asymmetries during the evolution of mutualistic investments, averaged over three replicate model runs and shown on logarithmic scales. The phase asymmetry in pairs of interacting individuals of

Mutualist A and B is measured as the difference of their phases, $\varphi_{\mathrm{A}} - \varphi_{\mathrm{B}}$. The peaks at 0 and π in B correspond, respectively, to the vertical and horizontal edges of the investment cycle. Parameters: $N^2 = 900$ in **A** and $N^2 = 2{,}500$ in **B** and **C**; $\sigma = 0.025$ in **A** and $\sigma = 0.05$ in **B** and **C** ; $T = 15$, $B_0 = 7$, $B_1 = 2.5$, $C_0 = 0.1$, $\mu = 0.02$.

With further increases of mutational variability, even higher levels of polymorphism develop, so strategies diffuse across all phases of the investment cycle. In highly polymorphic populations, as a consequence of this phase spread, selection pressures become widely different for different parts of the populations; hence, a wide variety of strategies becomes established, ranging all the way from phase I to phase IV (Figure 3.12/B, 3.13). Competition between strategies and strategy pairs shapes the phase distribution of the community (Figure 3.12/B and *C*), as individuals or pairs with a competitive disadvantage fade out from the community. These losing strategies are typically those at the beginning of phase I or at the end of phase III ($\varphi \approx 0$ or $\varphi \approx 3\pi/2$), as well as strategy pairs with an extreme asymmetry or exploitation (at the tails of the distribution in Figure 3.12/C). The two most successful, and hence most frequent strategies, are conditional cooperators (akin to Tit-for-Tat strategies, with high b and low a; Figure 3.12/B, peak close to 0) and unconditional cooperators (akin to All-C strategies, with high a and low b; Figure 3.12/B, peak close to π). The result of competition within the polymorphic populations is thus a diverse cast of interactions, types ranging from strongly mutualistic (central peak in Figure 3.12/C, corresponding to both mutualists being in the same phase) to exploitative (two lateral peaks in Figure 3.12/C, corresponding to one mutualist being in phase I and the other in phase III, or vice versa). The phase asymmetry of the two populations also changes with time (Figure 3.13), during which some phases become more frequent in the populations, others fade out, and then vice versa. The snapshots of the phase distributions in the two populations regularly indicate high asymmetries (Figure 3.13). Nevertheless, as shown in Figure 2.12/C, the distribution of phase asymmetries between the two mutualists is in general symmetric, as these fluctuations produce a balanced distribution over time in the two mutualists.

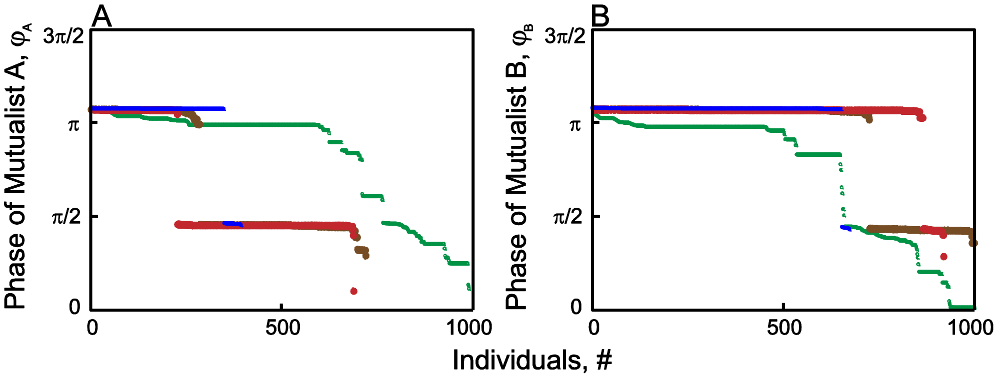


Figure 3.13: The phases distributions of the two mutualists (Mutualist A and B, on panels **A** and **B**, respectively) on snapshots taken at given intervals (colors code the generations when the snapshots are taken: blue (1000)→ red (1005)→ brown (1010)→ green (1025)). The individuals are ranked by their phases on the plot. Asymmetries are noticeable in the phase distributions of the two mutualists, and these also change over time. It is also apparent, that certain phases are more represented in the populations than others. Parameters: $N^2 = 1000$; $T = 15$, $B_0 = 7$, $B_1 = 2.5$, $C_0 = 0.1$, $\sigma = 0.05$, $\mu = 0.02$.

We highlight that our results for the diversity thresholds depicted in Figure 3.11/A are essentially invariant for lower mutation rates (Figure 3.14). The intuitive explanation is that such lower mutation rates have two effects. First, there are fewer mutations occurring in any given time window, which by itself would hinder the retriggering of the investment cycle. Second, the pace of directional evolution slows down for such lower rates, so the trait distribution “lingers” for longer periods at the phase boundaries, which by itself would facilitate the retriggering of the investment cycle. These two effects essentially cancel, leaving the critical levels of mutational variability needed for retriggering the investment cycle largely independent of the considered mutation rates. As the Figure 3.14 demonstrates, lowering the mutation rate even by two orders of magnitude has little effect on the qualitative outcome of our model. Mean payoff actually becomes higher as the mutation rate decreases: the reason is that a lower mutation rate reduces the amplitude of the investment cycle, because it allows it to be retriggered earlier. In other words, having the mutation rate beyond the value examined previously, and thus making it more realistic, only amplifies the effect of the diversity thresholds.

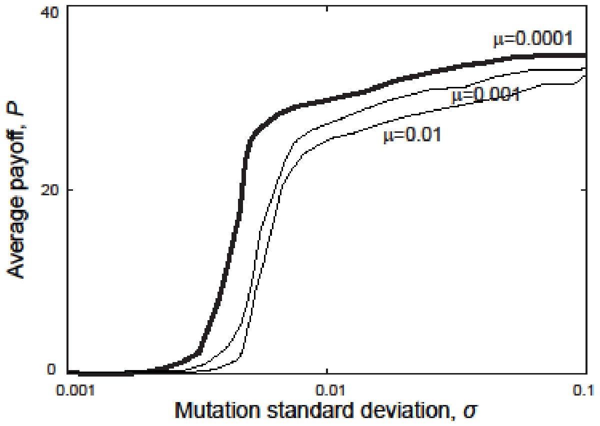


Figure 3.14: Lowering the mutation rates (μ) does not change our results qualitatively. The diversity threshold appears approximately at the same mutational variability, and the average payoff can be slightly higher for lower mutation rates. Parameters: $N^2 = 2500$, $T = 15$, $B_0 = 4.7$, $B_1 = 1.8$, $C_0 = 0.6$.

By contrast, this retriggering is strongly affected by the benefit-to-cost ratio. When the benefit-to-cost ratio is large, a smaller amount of mutational variability suffices to maintain strategy polymorphism and thus community-level mutualism (Figure 3.11/A, compare upper and lower pairs of curves). Moreover, localized interactions and limited dispersal promote strategy polymorphism, by creating a spatial mosaic structure (Figure 3.15), as we will describe in more detail in the next section. Accordingly, the transition to stable community-level mutualism appears for lower mutational variability in spatially structured populations (Figure 3.11/A, compare gray to black pairs of curves).

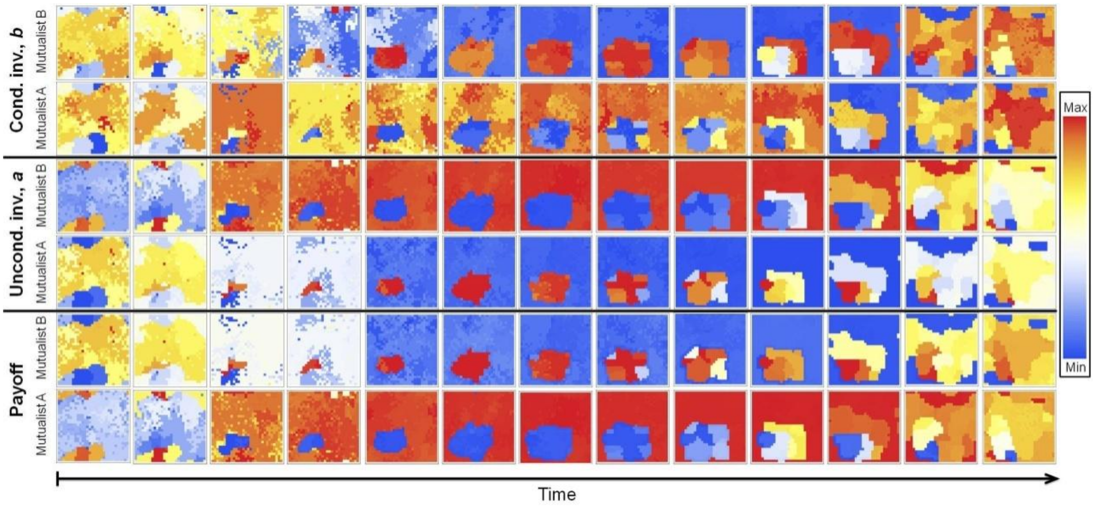


Figure 3.15: Dynamic spatial mosaics structure. Spatial mosaics are composed of bubbles, that is strategies with similar strait compositions. As we can see, the bubble structure is evident considering either the payoffs, or the trait values of the composing strategies. There is a strong correlation between the mosaic structure in the two mutualist populations. Each pixel represents an individual, colored according to its payoff, trait *a* and *b* between the minimal (blue) and the maximal value (red). The snapshots are taken at approx. every 100th generation. Parameters: $N^2 = 2500$, $T = 15$, $B_0 = 7$, $B_1 = 2.5$, $C_0 = 0.1$, $CV = 0.05$, and $\mu = 0.02$.

Spatial bubbles and polymorphism

In spatially structured mutualistic communities with local interactions and limited dispersal, strategy polymorphism occurs together with a dynamic spatial mosaic structure of spatially abutting "bubbles" (Figure 3.15, 3.16).

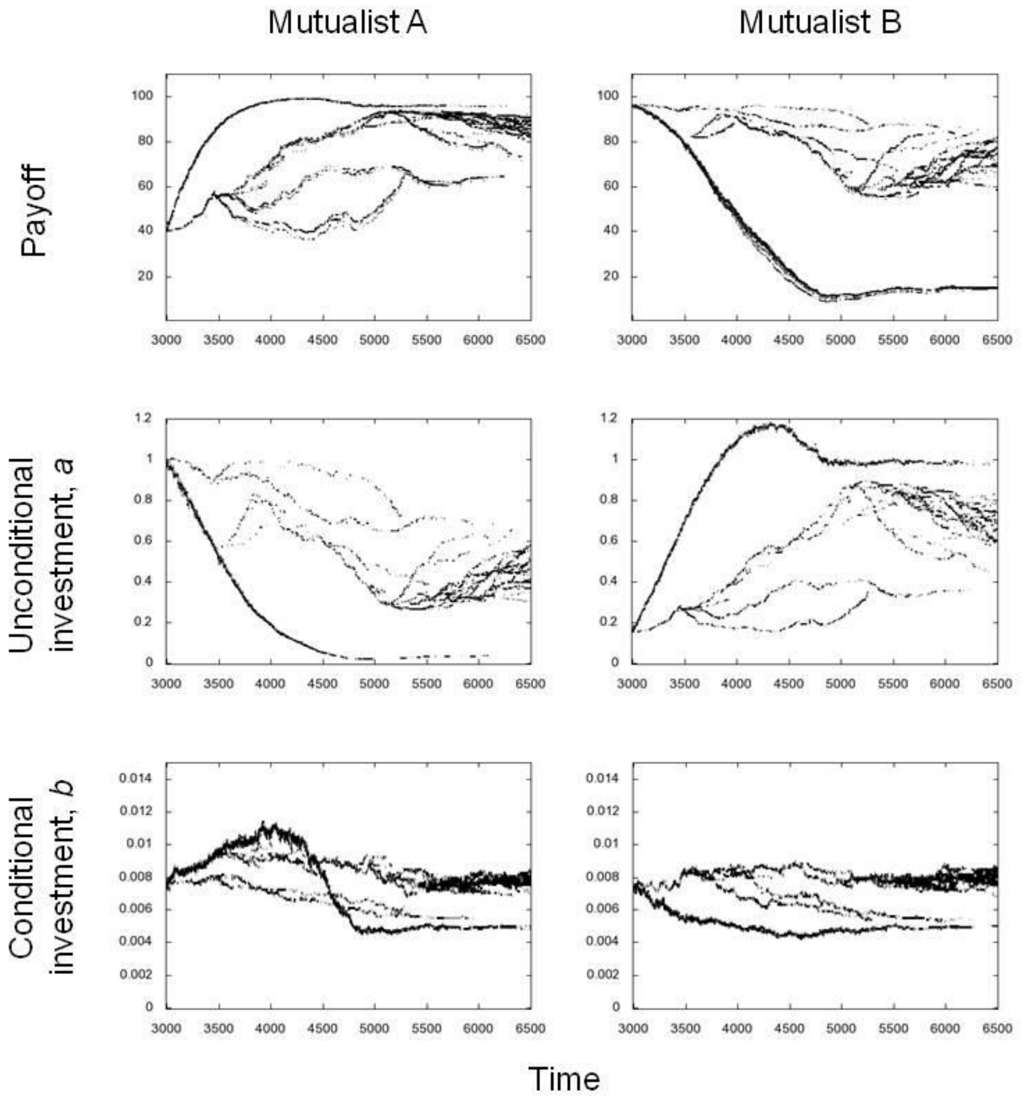


Figure 3.16: The change of payoff and trait distribution in spatially structured populations. Dynamic spatial bubbles are composed of similar strategies, which show up as separate lines in the plot, each line representing a cluster of strategies (or several dissociated cluster with similar strategy types) with their respective trait values and payoffs. As bubbles split or vanish, lines representing strategy clusters likewise split or vanish. For example, at the beginning of the time series (at time 3000), the populations splits into—at least two—large bubbles. The one with the lower payoff continuous to split (around approximately 3500), diverge, while the other (the thicker line) remains intact and dominant for a long period, but this bubble also fades away in the end (at 6200). Parameters: $N^2 = 900$, $T = 15$, $B_0 = 7$, $B_1 = 2.5$, $C_0 = 0.1$, $CV = 0.05$, and $\mu = 0.02$.

Here we use the term “bubble” to describe spatial clusters that are compact and contiguous, contain similar strategies on the inside and different ones on the outside (Figure 3.17/B), and grow gradually in size from a small core before disappearing through a sudden collapse (Figure 3.15 and Figure 3.17/D). For the most part, there is a strong correspondence between Mutualist A and Mutualist B with regard to the position and extent of spatial bubbles, and typically the corresponding strategies are asymmetric, giving one species a higher payoff than the other (compare the shading and coloring of corresponding sites in Figure 3.15 and Figure 3.17/A, and Figure 3.18). To fully understand the role of spatial population structure in stabilizing mutualism, we thus have to understand the composition of, and the ongoing dynamics among and within, these bubbles.

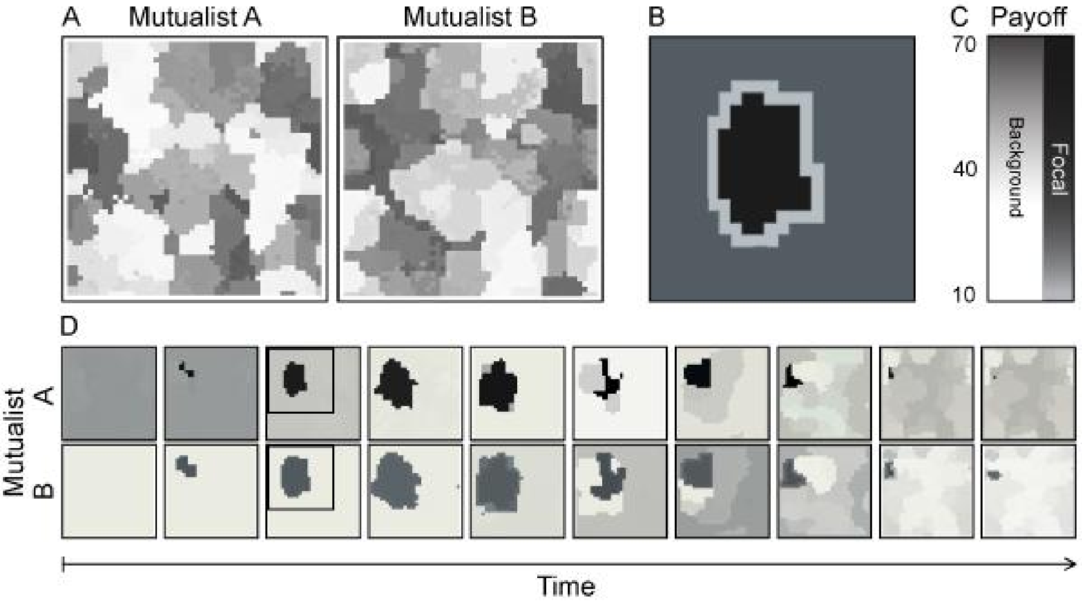


Figure 3.17: Spatial bubble dynamics and appearance of the insulating boundary layer. (**A**) Typical snapshot of the spatial mosaic structure, indicating a high degree of polymorphism and spatial bubbles comprising different strategies. Each pixel represents an individual, rendered according to its payoff between zero (light gray) and the maximal value (black). (**B**) Enlargement of a bubble with its surrounding insulating boundary layer. Notice that individuals inside and outside the bubble both have higher payoffs than the individuals forming the boundary layer. This panel is obtained as an overlay of Mutualist A and B from the third column in **D**

according to their average payoff values. (**C**) Shading of background strategies ranges from white to mid-gray, while shading for the focal bubble ranges from dark-gray to black, as the payoffs of individuals increase. (**D**) Time series of snapshots for a spatial bubble (black to dark-gray shading) that first expands and then vanishes, illustrating a spatial "boom and bust" cycle (snapshots are taken in generations 3013, 3040, 3260, 3399, 3493, 3625, 5165, 5620, 6400, and 6408). Parameters: $N^2 = 2{,}500$ in **A** and $N^2 = 900$ in **D**; $T = 15$, $B_0 = 7$, $B_1 = 2.5$, $C_0 = 0.1$, $CV = 0.05$, and $\mu = 0.02$.

As we saw in the previous section, symmetry breaking and phase polymorphism along the investment cycle can lead to asymmetry between the mutualistic partners. This emerging asymmetry is strongly exaggerated by the spatial bubble structure (Figure 3.18), as competitively inferior strategies vanish quickly, while exploiting strategies are likely to attempt an invasion of adjacent bubbles, supported by their high payoffs. Hence, spatial bubbles are often composed of exploiting strategies and their exploited partners. The degree of asymmetry and its trend among bubbles can vary, and this diversity of asymmetries provides the stage for bubbles expanding, splitting, or collapsing in various ways (Figure 3.18).

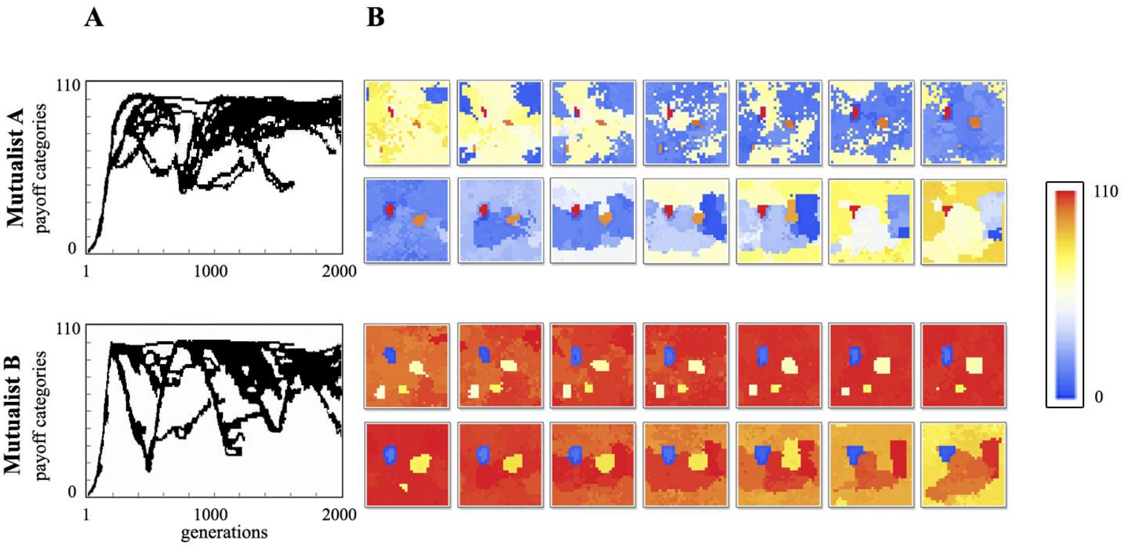


Figure 3.18: The change of payoff distribution and the dynamic spatial mosaic structure in spatially structured populations. (**A**) While the strategy compositions evolve along the investment cycle in multiple distinguishable clusters, (**B**) spatial

bubbles emerge, evolve (notice the color change without any major replacement dynamics), and vanish (time elapses from the left to the right, and from the firsts to the second rows for both mutualist populations). Notice that while coloring of the dominant proportion of the population indicates increase of payoffs in Mutualist B, it indicates decreasing payoffs in Mutualist A. However, multiple clusters are present in both of the populations (see multiple lines on panel **A**, and multiple spatial clusters on panel **B**), ranging from highly profitable to less successful strategies. Each pixel represents an individual, colored according to its payoff between zero (blue) and the maximal value (red). Parameters: $N^2 = 2500$, $T = 15$, $B_0 = 7$, $B_1 = 2.5$, $C_0 = 0.1$, $CV = 0.05$, and $\mu = 0.02$.

If a strategy can outcompete that of a neighboring strategy, its successful invasion further depends on it maintaining its competitive superiority in the invaded patch. Hence, invasion success can be determined by considering the relative payoff of the invader before and after invasion. To demonstrate this, we consider the interface between two bubbles as the site where strategy pairs can meet. We can then analyze all possible dynamics at this interface. We label the two bubbles so that Mutualist A has a higher payoff (>) in bubble 1 than in bubble 2. We can neglect cases with equal payoffs in the two bubbles, as these do not change the configuration of strategies, and thus do not contribute to the bubble dynamics. Relations between the payoffs in bubble 1, at the interface, and in bubble 2 (Figure 3.19) can thus be represented as $\underset{\cdot\ \cdot\ \cdot}{<<}$, $\underset{\cdot\ \cdot\ \cdot}{>>}$, $\underset{\cdot\ \cdot\ \cdot}{<>}$, or $\underset{\cdot\ \cdot\ \cdot}{><}$ for Mutualist A, and by $\overset{\cdot\ \cdot\ \cdot}{<<}$, $\overset{\cdot\ \cdot\ \cdot}{>>}$, $\overset{\cdot\ \cdot\ \cdot}{<>}$, or $\overset{\cdot\ \cdot\ \cdot}{><}$ for Mutualist B, yielding seven distinct situations: $\begin{smallmatrix}>>\\>>\end{smallmatrix}$, $\begin{smallmatrix}>>\\<<\end{smallmatrix}$, $\begin{smallmatrix}>>\\><\end{smallmatrix}$, $\begin{smallmatrix}><\\><\end{smallmatrix}$, $\begin{smallmatrix}<>\\<>\end{smallmatrix}$, $\begin{smallmatrix}<>\\><\end{smallmatrix}$, $\begin{smallmatrix}<>\\>>\end{smallmatrix}$.

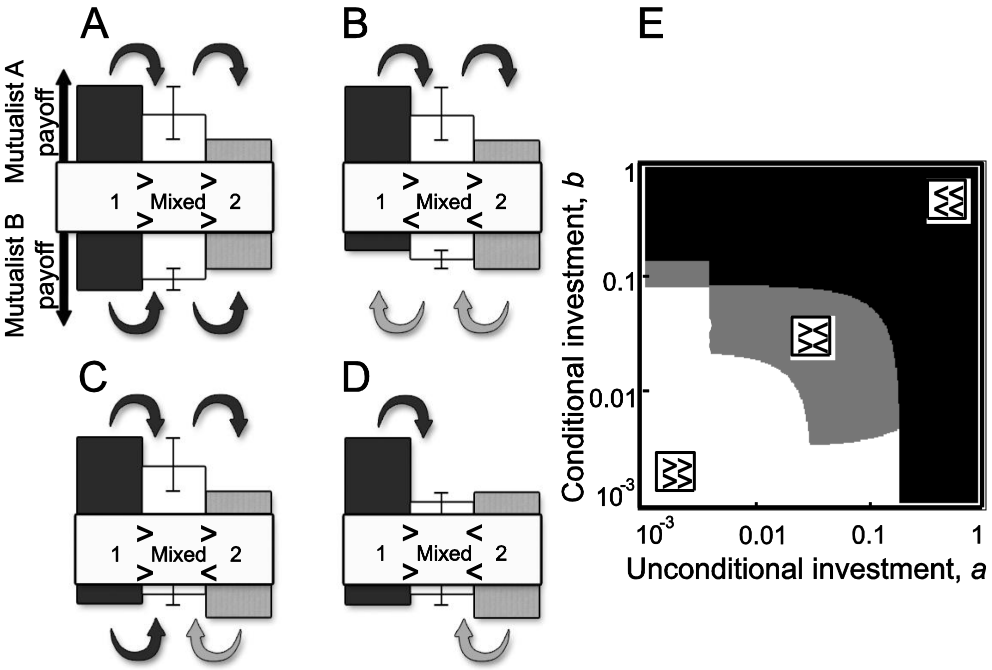


Figure 3.19: Possible replacement dynamics at the interface between two spatial bubbles. We presume that strategy pairs meet at the interface (white columns) of bubble 1 (dark-gray columns) and bubble 2 (light-gray columns). Here, the following cases can occur:

- (**A**) Unidirectional invasion: both mutualists from bubble 1 invade the other bubble, as both A1 and B1 have a higher payoff than A2 and B2.
- (**B**) Partner swapping: A1 has a higher payoff and outcompetes A2, but B2 has a higher payoff and outcompetes B1, hence A1 pairs up with B2.
- (**C**) Catalyzed invasion: only A1 is able to outcompete its competitor from bubble 2, but as it spreads, it makes it possible for B1 to follow. This is feasible because B2 fares worse with A1 than with A2, so as A1 spreads, the payoff of B2 decreases with its new partner, and hence B1 can now invade.
- (**D**) Insulating boundary layer: at the interface of two spatial bubbles, the originally competitively superior strategies A1 and B2 enter the interface, but as both then have a lower payoff than with their original partners, neither can spread further. Column heights depict the payoffs of strategies. For the described dynamics, the payoffs of a strategy with its two possible partners (i.e., from either bubble 1 or 2) at the interface must lie within the interval indicated by the two whiskers in the middle column.

(**E**) Invasion dynamics depend on the strategy compositions of the mutualist pairs. Formation of an insulating boundary layer is the result of the encounter of two strategy pairs ($\text{A1\&B1}, \text{A2\&B2}$) that are mutually unable to invade each other (gray area). Otherwise, one bubble invades and replaces the other (in the white area, the strategy pair of bubble 1 wins, whereas in the black area, the strategy pair of bubble 2 wins). We evaluate these outcomes in the absence of evolution (no mutations) and for one strategy pair (A1&B1) initially occupying one half of the lattice and the other strategy pair (A2&B2) occupying the other half. Parameters: A1 and B1, $a = 0.1$ and $b = 0.01$; A2, $a = 0.1$ and $b = 0.1$; B2, $a \in [0.001,1]$ and $b \in [0.001,1]$; $T = 15$, $N^2 = 900$, $B_0 = 7$, $B_1 = 2.5$, and $C_0 = 0.1$.

Corresponding to Figure 3.19, the upper row refers to Mutualist A and the lower row to Mutualist B, while the first column refers to the payoff comparison between bubble 1 and the interface, and the second column to the interface and bubble 2. The first four cases, in which Mutualist A in bubble 1 always has a higher fitness than Mutualist A at the interface ($\underset{\cdot\;\cdot}{\boldsymbol{>>}}$), correspond to replacement dynamics (Figure 3.19/A–D) involving unidirectional invasion (Figure 3.19/A), partner swapping (Figure 3.19/B), catalyzed invasion (Figure 3.19/C), and coexistence of the two bubbles (Figure 3.19/C). In the last three cases, Mutualist A has a higher payoff at the interface than in either bubble ($\underset{\cdot\;\cdot}{\boldsymbol{<>}}$). We can interpret these situations as having a bubble, with a strategy pair formed at the interface, that can spread in both directions. The resultant new pairs of adjacent bubbles will then behave in one of the ways covered by the first four cases above. Thus, those four cases shown in Figure 3.19/A–D and discussed in more detail in that figure's caption, cover all possible dynamics between the two bubbles.

The most relevant case for preserving phase polymorphism occurs when the two exploiting strategies of two adjacent bubbles, having high payoffs within their bubble, can both enter the intervening interface, but their exploited partners cannot (Figure 3.19/D). Then, these exploiting strategies meet at the interface, but are mismatched: by interacting with each other, they experience lower payoffs compared to when they interact with their original partners. Consequently, neither bubble can invade the other (under deterministic updating), and an insulating boundary layer forms between them (Figure 3.17/B and Figure 3.19/D). These effects yield a relatively static mosaic structure, in which most bubbles are separated by insulating boundary layers, which in turn fosters the long-term coexistence of a diverse set of strategies in both mutualist guilds. Nevertheless, the resulting mosaics are eventually not immune to the degradation of mutualism within bubbles, as strategy pairs evolve along the investment cycle, making the mosaic structure (if only slowly) dynamic.

The dynamics of the spatial mosaic are governed by evolutionary processes that maintain a balance between the expansion or emergence and the contraction or collapse of bubbles. First of all, inside a bubble, evolution drives strategies through the investment cycle (Figure 3.9, 3.16, 3.18). Sooner or later, this stochastic evolution changes the strategy pairs of two neighboring bubbles so that their boundary layer (Figure 3.19/E, gray area) loses its insulating property, thus enabling invasion from one bubble to the other (Figure 3.19/E, white or black areas). Although this invasion itself is a rapid process, the evolutionary time that is required for the insulating boundary layer to break down is usually long. Counteracting mechanisms can restore the loss of diversity resulting from bubble collapse: this happens through the emergence of new bubbles as a result of successfully established mutations (if such a mutant conquers only part of a bubble) or through the fragmentation of existing bubbles (see for example Figure 3.15 and 3.18). In the latter case, mutants occurring within the insulating boundary layer are able to invade either one of the adjacent bubbles. Through this invasion, the mutant opens up the boundary and can catalyze the invasion of strategies from the neighboring bubble (similar to how Mutualist A1 catalyzes the invasion of B1, as in Figure 3.19/C). Thus, while the two neighboring bubbles could originally not invade each other, this becomes possible through the mutant serving as a “third party.”The resultant expansion of the invading bubble can then split the invaded bubble (Figure 3.17/D, from fifth the column onwards, and Figure 3.18 lower rows of Mutualists A and B), and the two splits can then take separate evolutionary paths.

In summary, strategy diversity, and thus, community-level mutualism, is efficiently stabilized through the formation of an insulating boundary layer between bubbles of strategies. This would result in a static mosaic structure, which, however, becomes dynamic as strategies evolve along the investment cycle. The invasions resulting from these stochastic evolutionary processes establish a balance between the emergence and collapse of bubbles that maintains a level of polymorphism in a more efficient way than the corresponding well-mixed mutualistic community. The diversity threshold for community-level mutualism is thus more easily passed in spatially structured communities (Figure 3.11/A).

Environmental heterogeneity and strategy polymorphism

In spatially structured mutualistic populations of natural communities with local interactions and limited dispersal, strategy polymorphism can often occur together with an environmental heterogeneity. To investigate the effect of spatial heterogeneity on the evolution of mutualism, we model this heterogeneity by assuming that the cost of cooperative investments can differ between localities. We do it by changing the parameter C_0, and hence the cost varies, from place to place. Consequently, investments are more costly at some grid points, while other local habitats are more favorable for mutualism. For the sake of simplicity, we assume that there are only two types of points, high cost (C_0^H) and low cost (C_0^L) grid points.

Interestingly, environmental heterogeneity stabilizes interspecific investment levels. Importantly, this stabilization of mutualism even occurs when the heterogeneous environment is on average less profitable for the mutualists than the homogeneous environment. Intuition would dictate, that introducing high-cost patches leads to the decrease, or even loss of mutualisms, as the average cost of cooperative investments is higher in the population. Our results are, however, in contrast with this intuition.

If the ratio of high-cost patches is low or moderate in the spatial populations (below 50%), mutualism becomes more stable even for parameter ranges where mutualism can disappear in the homogeneous case. It is also noteworthy that only a single heterogeneous grid point is sufficient for causing changes in the outcomes of the simulations and can, under special circumstances, maintain mutualisms. The main feature of the mechanisms promoting mutualism in our model is an increase of phenotypic diversity. As we have seen, in spatial populations, a mosaic structure emerges, where insulating boundary layers form between many of the bubbles, resulting in a relatively static mosaics for certain time periods (Figure 3.17, 3.18 and 3.19). These insulating boundary layers thus promote strategy polymorphism by hindering invasion. Strategies entering the boundary layer cannot continue further, as their payoff will be lower than those of the neighbors'. In the case of spatial environmental heterogeneity, high-cost patches result in similar dynamics (Figure 3.20). Successful strategies are able to invade the high-cost patch, however as the cost of investment is higher in the patch, their payoff will be lower than those of the neighbors', and hence invasion stops at the patch (Figure 3.20).

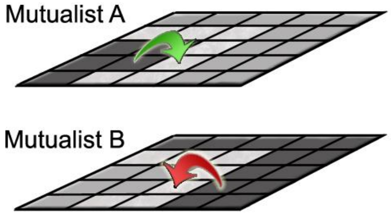


Figure 3.20: Spatial bubbles (darker shadings) with a high-cost patch (light gray layer) between them. While invasion of the patch is possible from either one of the bubbles (green arrow in Mutualist A and red arrow in Mutualist B), strategies cannot invade further. Thus high-cost patches affect bubble dynamics similarly as in the case of insulating boundary layer.

Environmental heterogeneity is thus increases and/or underpins strategy polymorphism by interacting with the boundaries of the spatial bubbles. Acting themselves as insulating boundary layers, high-cost patches hinder invasion, and further catalyze the formation of insulating boundary layers, which—at least for some regions—will be located at these high-cost patches (Figure 3.21). High-cost patches thus act like barriers that effectively separate different strategies, and thus promote and stabilize interspecific investment levels by increasing and supporting strategy polymorphism.

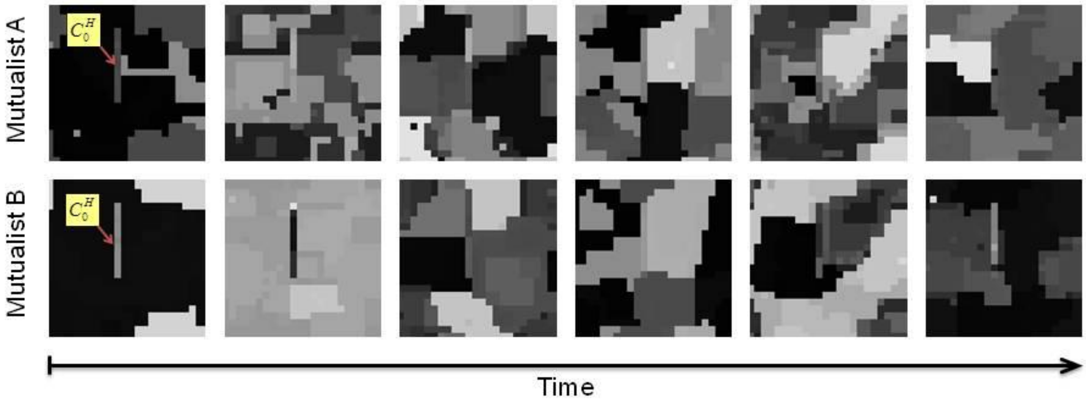


Figure 3.21: Spatial bubble dynamics with environmental heterogeneity. Here we model environmental heterogeneity as a single continuous high cost barrier in the middle of the rectangular grid (the line approx. half of the size of the field in the

middle, denoted by C_0^H). The boundaries of dynamical spatial mosaics strongly correlate with this barrier.

Extended analysis of the model

In the light of our understanding of the evolution and stability of interspecific cooperative investments established in the previous sections, we can present a more comprehensive and systematic overview of the evolution of interspecific cooperative investments under various relevant conditions (Figure 3.22 and 3.23).

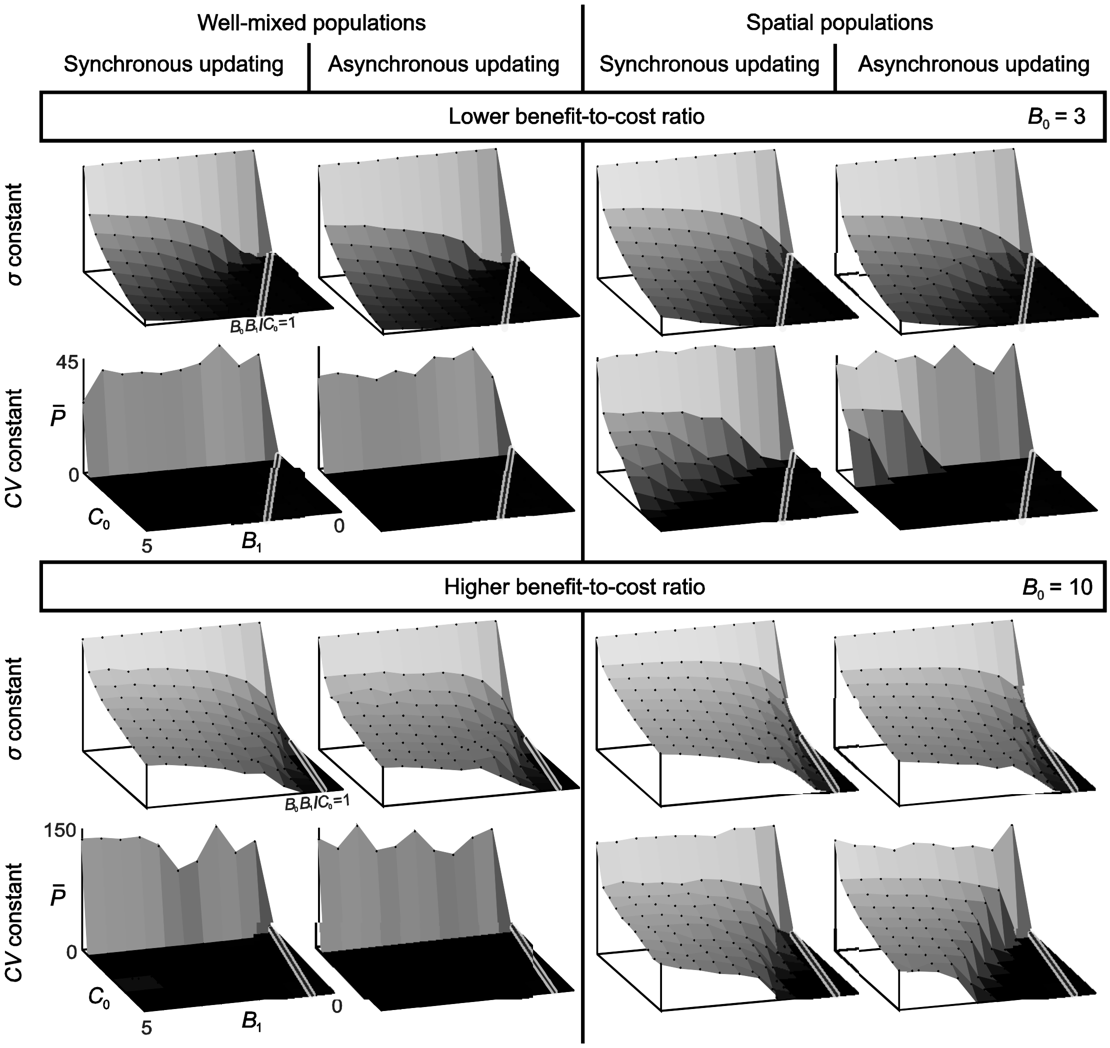


Figure 3.22: Average payoff as a function of the parameters of the cost and benefit functions, spatial structure, and update rules. Each individual panel shows the average payoff of Mutualist A and Mutualist B, calculated as the arithmetic mean of their payoffs over the last $1,000$ generations, out of the total of $100,000$ generations, and averaged over five replicate model runs. The three parameters of the benefit and cost functions are varied as follows: B_1 and C_0 along the axes and

B_0 between the upper ($B_0 = 3$) and lower ($B_0 = 10$) eight panels. The black line on white background indicates the $B_0 B_1 / C_0 = 1$ threshold, below which no investments can evolve. Results for well-mixed populations are shown in the eight panels on the left, while we employed spatial population structure for the eight panels on the right. Odd and even columns correspond to synchronous and asynchronous updating, respectively. Rows show results for a constant standard deviation $\sigma = 0.05$ (first and third rows) and a constant coefficient of variation $CV = 0.05$ (second and fourth rows). Other parameters: $T = 15$, $N^2 = 2{,}500$, and $\mu = 0.02$.

First, we present the necessary condition that no mutualistic investments can evolve below $B_0 B_1 / C_0 < 1$, that is, when the benefit-to-cost ratio falls below 1 and mutualism is thus not advantageous (see thin black lines with white background in Figure 3.22), which in general holds under all conditions. Also, the transition to high stable levels of mutualistic investments is sharper for higher benefit-to-cost ratio ($B_0 = 10$ rows in Figure 3.22). Second, besides the synchronous updating method, we also considered asynchronous updating, and found that mutualism is unstable for a wider range of benefit-to-cost ratios (compare third and fourth columns in Figure 3.22). Third, we also tested different competition rules under asynchronous updating, such as the pairwise comparison rule instead of the best-takes-over rule, and we can conclude that outcomes are essentially unaffected by these different rules (not shown). Fourth, we consider two methods for generating mutant traits. In one version, as in the original DK model (Doebeli & Knowlton 1998), we draw the trait values of mutants with constant coefficient of variation, so that mutational standard deviation linearly increases with the current trait value (“CV constant” rows in Figure 3.22). With this approach, mutational variance for small trait values becomes very low, and at 0 variance is 0. We also introduce a different assumption, in which mutational variance is constant for all trait values (“σ constant” rows in Figure 3.22). Comparing the results, we arrive at an important conclusion, namely, that the original report of “gradual evolutionary decay of cooperation” in the well-mixed model but “long term persistence of mutualism” in spatially structured population by DK (Doebeli & Knowlton 1998) is restricted to the assumption that mutations have a constant coefficient of variation (“CV constant” rows in Figure 3.22). Notably, our investigation reveals that relaxing this assumption, by assuming constant and medium values for mutation variance, mutualism robustly evolves for all kinds of populations structures and update rules (compare "CV constant" vs. "σ constant" rows in Figure 3.22). We note here that our results are qualitatively robust to changes of the number T of iterations during the mutualistic interaction, which we have confirmed by examining shorter ($T = 3$) and longer ($T = 50$) interactions instead of $T = 15$ (Figure 3.23). Fifth, we demonstrate that below a threshold level of mutational variability no stable levels of mutualistic investments evolve in the community, and this threshold is considerably lower for higher benefit-to-cost ratios and for spatially structured populations (Figure 3.11/A). We have also demonstrated, that assuming heterogeneous spatial environment instead of the homogeneous used throughout this study, strategy polymorphism is further promoted resulting in more stable levels of high mutualistic investments. In summary, we conclude that spatial population structure has a beneficial effect on the evolution of stable high interspecific investment levels, but this effect is only apparent for constant CV, for small mutational variability, and for small benefit-to-cost ratios. By changing these conditions, mutualism can be stable both in well-mixed and spatially structured communities.

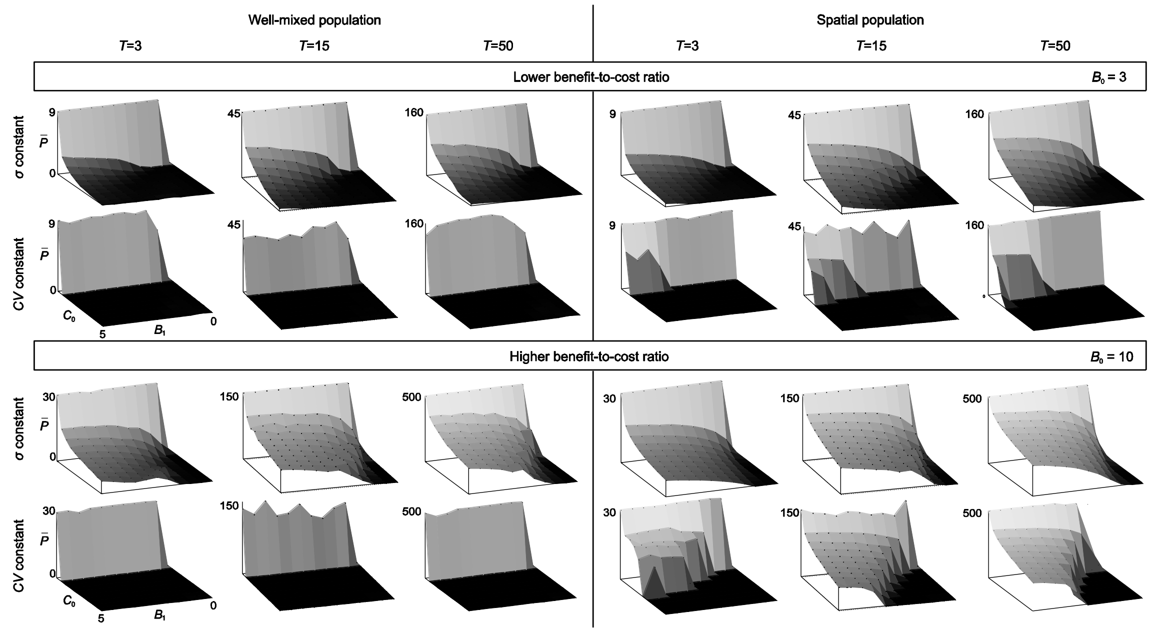


Figure 3.23: Average payoff as a function of the parameters of the cost and benefit functions, spatial structure, and iteration number. Each individual panel shows the average payoff of Mutualist A and Mutualist B, calculated as the arithmetic mean of their payoffs over the last 1,000 generations, out of the total of 100,000 generations, and averaged over five replicate model runs. The three parameters of

the benefit and cost functions are varied as follows: B_1 and C_0 along the axes and B_0 between the upper ($B_0 = 3$) and lower ($B_0 = 10$) eight panels. Results for well-mixed populations are shown in the eight panels on the left, while we employed spatial population structure for the eight panels on the right. The three columns correspond to increasing interaction length, that is $T = 3$, $T = 15$, and $T = 50$ in an increasing order from the left to the right. Rows show results for a constant standard deviation $\sigma = 0.05$ (first and third rows) and a constant coefficient of variation $CV = 0.05$ (second and fourth rows). Other parameters: $N^2 = 2{,}500$, and $\mu = 0.02$.

3.6.3. Discussion

Here we have revealed several fundamentally new mechanisms for the maintenance of interspecific cooperation. We show that pairs of strategies evolve through investment cycles (Figure 3.9), which drives the main coevolutionary dynamics of traits, and underlies the evolution of cooperative investments levels in mutualist communities, and which on their own always result in full defection. Our analyses demonstrate, however, that in both well-mixed and spatially structured communities mutualisms can be perpetually stable if a strategy-diversity threshold is exceeded and sufficient polymorphism is generated and maintained in the community. In other words, such a polymorphism of investment strategies is the main factor stabilizing mutualism. We have demonstrated the spreading of the investment cycle phases, the corresponding strategies, and have revealed the diverse ways strategies interact when they are in different phases, both within and between mutualist guilds (see Figure 3.11, 3.12, and Figure 3.19). The emerging phase polymorphism and underlying strategy diversity recurrently retrigger evolutionarily increasing levels of cooperative investments in some portion of the community (phase I in Figure 3.12/A,B), a process that is essential for maintaining high investment levels. In addition, we can provide an explanation for the differences in the stability of mutualism under constant CV vs. constant σ, as well as under low σ vs. high σ. These differences derive from the fact that if phase polymorphism is largely lost, it is much harder to retrigger the investment cycle (by attaining trait combinations above b_T) once the population has reached the last phase of the investment cycle (or in other words, once phase I has vanished from the community). For similar reasons, any mechanism that prevents or counteracts the generation of phase polymorphism will increase the chances of losing mutualism.

Strategy diversity and phase polymorphism along the investment cycle are responsible for maintaining high investment levels and the key effect of spatial structure, and also environmental heterogeneity, is to enhance this polymorphism. Thus, compared to the well-mixed case, a lower amount of variation suffices to maintain mutualism in spatially structured populations. We have studied spatial mosaic dynamics by analyzing replacement dynamics in the mutualist populations to understand why spatial structure increases polymorphism (Figure 3.15–3.19). Our investigation reveals the complex dynamics among bubbles and the key role of the insulating boundary layer in preserving polymorphism in spatially structured populations. We can now also understand why asynchronous updating makes mutualism less stable, as it more easily shatters insulating boundaries, promotes asymmetric and uncoupled invasion of the two mutualists among bubbles, and hence makes the homogenization of bubbles more likely. Finally, while our results explain why spatial structure is helpful in maintaining mutualism, they also demonstrate that space itself does not always suffice, and neither always is necessary, to maintain community-level mutualism.

Our findings underscore that mutualism is not always a stationary outcome, but may involve a polymorphism of investment levels that vary both in space and in time (Figure 3.24). Environmental heterogeneity can support this polymorphism, and can further promote the emergence of spatial mosaic structure. High-cost patches can act as barriers between spatial bubbles, can catalyze the emergence of insulating boundary layers between bubbles, and hence hinders the invasion of strategies to adjacent bubbles. Spatial environmental heterogeneity is, however, nor a necessary, nor a sufficient condition to maintain high mutualistic investment levels without sufficiently high mutational variability producing strategy diversity.

We note here that, based on our model assumptions, the two mutualist populations may correspond not only to single species interacting pairwise, but also to two interacting mutualist guilds (Stanton 2003), that is, a collection of species with the same function in mutually beneficial ecological interactions.

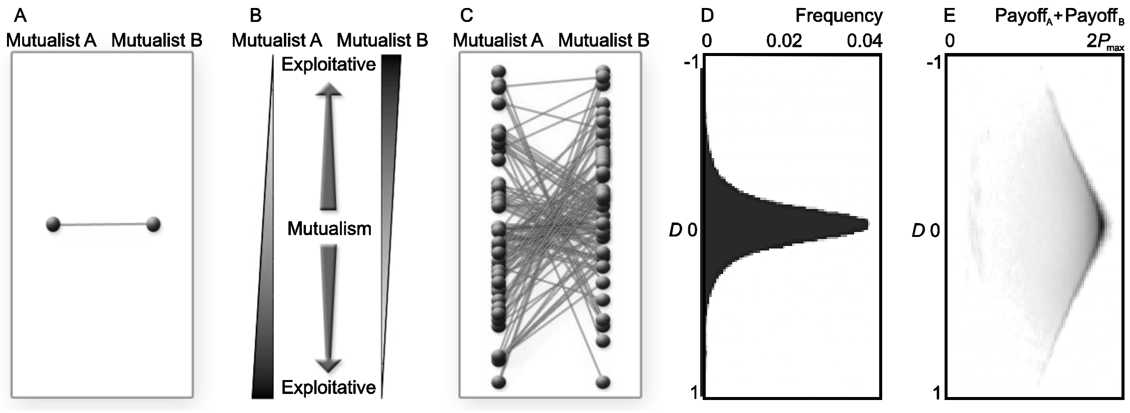


Figure 3.24: Schematic representation of mutualistic interactions in (**A**) monomorphic and (**C**) polymorphic mutualist communities. Spheres depict strategies, and the links between spheres represent the interactions between the corresponding strategies from the two mutualist populations. (**B**) According to its own and its partner's strategy, an individual receives a payoff (schematically illustrated by triangles that become darker and wider the higher the received payoff). Comparison of payoffs between partners shows whether their interaction is more mutualistic (middle) or more exploitative (bottom and top). (**D**) Average distribution of interaction types in our model, showing that small relative differences D between the payoffs of interacting individuals are more common or longer-lasting than extreme exploitations. (**E**) Average distribution of the payoff sums and relative payoff differences for interacting individuals of Mutualist A and Mutualist B, demonstrating that, on average, returns in asymmetric, or exploitative, interactions are lower than in symmetric, or more mutualistic, interactions. The distributions in **D** and **E** are based on sampling all individuals in every 100th generation for 100,000 generations and for five replicate model runs. Relative differences between the payoffs, $P_{i,j}$ and $P_{j,i}$ of individuals i and j are given by $D=(P_{i,j}-P_{j,i})/(P_{i,j}+P_{j,i})$, and $2P_{\mathrm{Max}}$ is given by $2TB_0$. Parameters: $N^2=2{,}500$, $T=15$, $B_0=7$, $B_1=2.5$, $C_0=0.1$, $CV=0.05$, and $\mu=0.02$.

Importance of polymorphism

Our analysis has shown that when the community exhibits a stable mean level of mutualism in our model, it is invariably characterized by a high degree of polymorphism and that mutualism persists only if this polymorphism is maintained. Without strategy polymorphism, the evolutionarily stable state of the system is a community consisting only of full defectors (no-investments). This is because full defection is the best response to itself (Figure 3.8), and no mutant investing more can spread in either species (Scheuring 2005). No other strategy pairs are best responses to each other, so there are no other evolutionary stable states. However, there are many pairs of strategies that can spread in initially non-mutualistic populations (Figure 3.9); above a threshold of reciprocating investments, evolution guides these strategies through an investment cycle, which eventually always results in no-investment. Hence, mutualistic investments in our model are fundamentally unstable (Bendor & Swistak 1997), never reaching finite stable levels even though they may initially be increasing. Thus in our model, without strategy polymorphism, evolution can only temporarily lead to high mutualistic investments before these eventually collapse again.

Similar dynamics have been observed in studies investigating the evolution of intraspecific cooperative investments in different game-theoretical models. For example, in the Prisoner's Dilemma Game with discrete reactive strategies (Axelrod & Hamilton 1981; Nowak 2006), the Tit-for-Tat strategy (TFT) can oust the always-defective strategy (All-D), but the always-cooperating strategy (All-C) can spread in a population adopting TFT, which in turn enables invasion by All-D. As mentioned in Results section, TFT is similar to strategies with high conditional investments b in our model, whereas All-C is similar to strategies with dominating unconditional investments a. Without the continuous reestablishment of strategies by mutations, models with discrete strategies may also end up in a fully defective state (Axelrod & Hamilton 1981; Nowak 2006).

In contrast to these results for populations with low degrees of polymorphism, when sufficient polymorphism is generated, community-level mutualism becomes stable. For this to happen, the degree of polymorphism needs to exceed a threshold (Figure 3.11/A). Even in well-mixed populations, stochastic symmetry breaking in the interactions, combined with phase polymorphism along the investment cycle, leads to the emergence of a high variety of strategy pairings and payoffs (Figure 3.12/B,C, and Figure 3.25). While evolution drives individual strategy pairs toward exploitation (and, ultimately, to zero investment), the exploited partner has a fitness disadvantage: consequently, the highly exploitative pairs are replaced by more mutualistic pairs, which show less asymmetry in their payoffs (Figure 3.12/C). These pairs are typically composed of strategies from phase I of the investment cycle (Figure 3.12). Our findings thus indicate that the interspecific interactions exist in a state of permanent flux, fluctuating between different investment levels and payoffs at the individual level (Figure 3.25). The average difference between the partners' payoffs, the payoff variance within the population, and their aggregated structure depends on the population structure (i.e. well-mixed or spatial) and the rate of strategy polymorphism (Figure 3.25).

The mean level of mutualistic investment, in contrast, remains positive (and for high degrees of polymorphism becomes stable), shaped by a balance between two components of selection: strategy evolution along the investment cycle and replacement of overly exploited strategies and of mismatched strategy pairs.

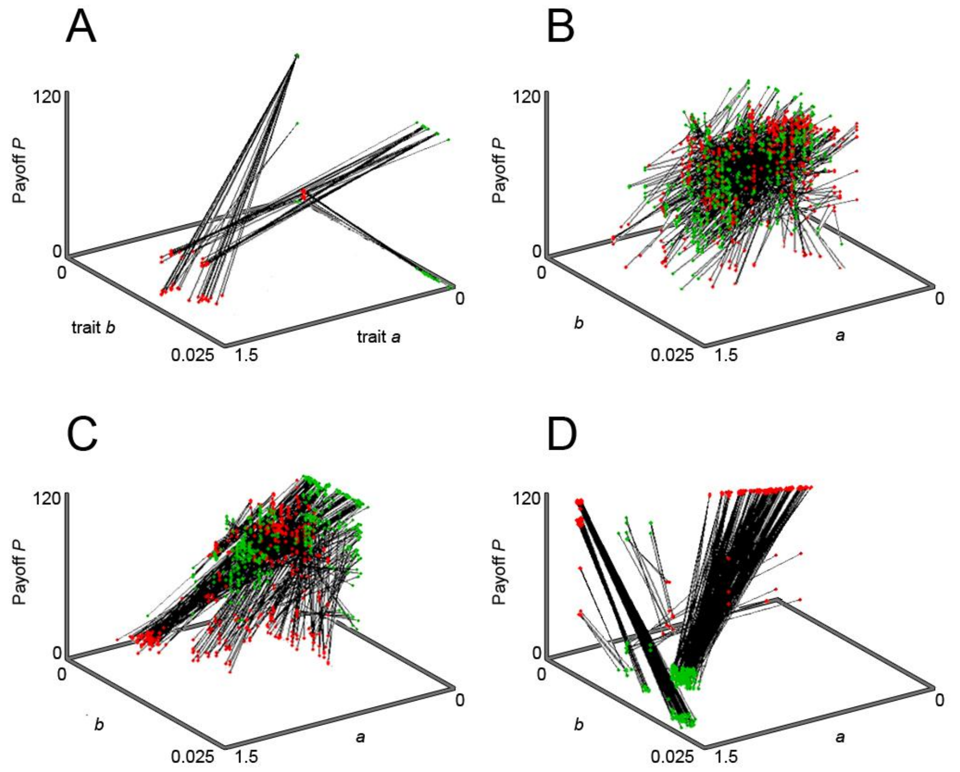


Figure 3.25: Snapshots of the distributions of outcomes and corresponding strategy combinations in different model scenarios for the mutualist pairs. Dots represent the strategies composed of the unconditional investment (trait *a*) and the conditional investment (trait *b*) components, from the populations of Mutualist A

(red) and Mutualist B (green). The black line represents the interaction between the corresponding strategies. (**A**) In well-mixed populations with low levels of polymorphism, payoffs can increase only temporarily, and during this increase usually one mutualist benefits much more from the interaction than the other (notice that all the green dots have higher payoff than the red ones which are connected to them). Here Mutualist B exploits Mutualist A. (**B**) In well-mixed populations with high degrees of polymorphism numerous combinations are established, and on average both mutualists have individuals gaining higher and lower payoffs. (**C**) In spatially explicit populations the high degree of polymorphism is combined with a spatial mosaic dynamic. Here, besides the 'cloud' of diverse combinations, correlating large clusters in the two mutualists can also emerge (notice the bundle of connections ranging between alike strategy pairs). (**D**) In spatially explicit populations, in an extreme case, the population can be composed of only a few strategies inhabiting only a few spatial clusters. Parameters: $N^2 = 2500$; $\sigma =$ 0.05 in **B** and CV = 0.05 in **A, C** and **D** ; T = 15, $B_0 = 7$, $B_1 = 2.5$, $C_0 = 0.1$, $\mu = 0.02$.

Spatial population structure further facilitates the stability of mutualism by playing a key role in supporting polymorphism (Figure 3.15–3.19). However, limited dispersal and localized interaction alone do not maintain mutualism, but only when they work together with mutational variance that is high enough to sustain a critical level of polymorphism (Figure 3.11/A). In spatially structured populations, the interaction among emerging, invading, and collapsing spatial bubbles of strategy pairs creates a dynamic spatial mosaic, by means of which different phases of the investment cycle are distributed among bubbles. As a result of this phase spread, the evolutionary dynamics of mutualistic investments become decoherent among the different bubbles. This is called phase diffusion, which in general occurs when stochastic drift reduces correlations among the cycle phases of subsystems (here the spatial bubbles) comprising a system (here the full community). Consequently, among bubbles, the community shows a wide but stable range of interaction types along the mutualism–exploitation continuum (Figure 3.24/D). We have shown how mechanisms operating at the interface of these bubbles effectively prevent the spatial homogenization of strategies across the community by creating insulating boundary layers that in turn sustain the spatial mosaic structure of bubbles together with the implied strategy polymorphism (Figure 3.25). We emphasize here that the mechanism of spatial population dynamics and interaction between neighboring bubbles described here fundamentally differs from previously described roles of spatial structure in models of intraspecific cooperation, in which case cooperation is maintained by the clustering of cooperators and by their spatial segregation from defectors (Hauert 2002).

Environmental heterogeneity is argued to be responsible for the varying outcomes in mutualistic interactions. Here we have shown that in certain cases, environmental heterogeneity serves as a catalyst for the emergence and establishment of strategy polymorphism. Spatial mosaic structure emerges in homogeneous populations as well, but if the environment is heterogeneous, high-cost patches serve as natural barriers, that hinder the invasion of strategies. As invasion beyond these high-cost patches is difficult, the barriers themselves catalyze the emergence of insulating boundary layers. Hence, similarly to the role of spatial populations structure, environmental heterogeneity enhances strategy polymorphism, thus supports the stability of interspecific investment levels at the population level. These results offer an explanation for the spatial mosaic structures that involve different genotypes observed in mutualistic communities, as well as the different local coevolutionary states shaped by different local selective forces (Thompson 1999; Gomulkiewicz et al. 2000; Thompson et al. 2002; Hoeksema et al. 2009). Our findings, however, highlight that spatial environmental heterogeneity is not required for the creation of such mosaics, as the mechanisms unraveled here provide a testable alternative explanation of these, even in the complete absence of spatial environmental heterogeneity.

This study has an additional interesting consequence. As we have seen, mismatched strategies play an important role in stabilizing mutualisms in our model, but not only particular strategy combinations can be mismatched. Our results demonstrate that any strategy picked from the population at equilibrium could have a diverse set of outcomes ranging from more beneficial to less beneficial, or even antagonistic. We can demonstrate this in a simple experiment depicted on Figure 3.26, where a randomly chosen strategy interacts with each and every member of the other mutualist population in a random generation. As it is illustrated, the majority of these interactions are in general mutualistic, but considerable proportion also results in significantly higher or lower payoffs than the average (see leftmost and rightmost part of the graph in Figure 3.26). These results seem to be in a good agreement with recent empirical observations, that compatible mutualists from different locations can be mismatched, and can result in different outcomes (Heath & Tiffin 2007; Heath 2010). The current model can thus provide a possible explanation for the observed phenomena.

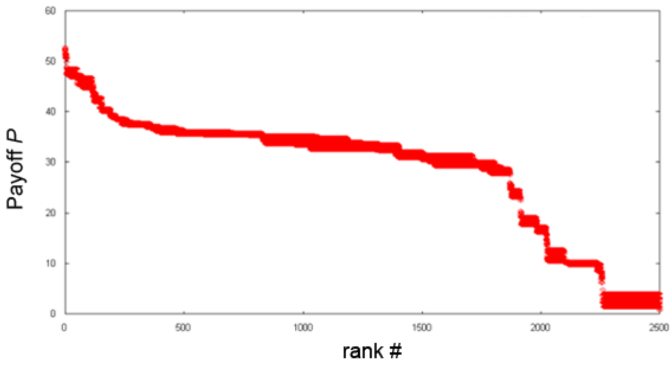


Figure 3.26: The distribution of outcomes for a randomly chosen strategy from Mutualist A having interactions with all the members of the population of Mutualist B. Associations are ranked according to the payoff the chosen individual received. Outcomes range from highly beneficial to neutral, or even negative. Parameters: $N^2 = 2500$; $CV = 0.05$; $T = 15$, $B_0 = 4.7$, $B_1 = 1.8$, $C_0 = 0.6$, $\mu = 0.02$.

3.6.4. Limitations

The model by Doebeli and Knowlton (1998) has been criticized for being applicable only to organisms with high cognitive abilities (Bergstom et al. 2003). Yet it has been demonstrated that even the simplest unicellular organisms are capable of complex reactive behavior. For example, it has been shown that, in response to the concentration of received nutrients and synthesized products, hosts and symbionts can control their exchange of material simply by controlling fluxes through their various metabolic pathways (Resendis-Antonio et al. 2007), regulating and operating proteins (Dixon & Kahn 2004; Lodwig et al. 2003), or inducing structural changes at the host–symbiont interface (Denison 2000; Provorov et al. 2002). Such adjustments closely resemble the reactive, conditional nature of interspecific cooperative investments, as captured by the model we analyzed here.

However, there are assumptions in the current model that can and should be relaxed and modified in subsequent studies. For example, in the model studied here, one individual always interacts with only one partner. Yet, in the majority of examples in nature, one host can interact with several symbionts at the same time, and vice versa (Bronstein 2001a; Bergstrom et al. 2003). The regular square grid we have considered here might be suitable if both mutualists have limited dispersal and are thus spatially confined. But one or both partners can be more motile, without well-mixed populations being the immediate result. Moreover, different interaction topologies could be considered, such as small-world or scale-free networks. Finally, partners in the current model have similar life cycles, which might apply only to a very limited number of biological examples; thus, assuming life-cycle asymmetries could be an important extension of the current model (Doebeli & Knowlton 1998).

3.6.5. Outlook

Our study has shown that the community-level picture of mutualism can be quite different from that at the individual level. As the mean outcome can provide misleading or poor information, a full understanding of the ecological and evolutionary dynamics involved requires an appreciation of the distribution of outcomes (Thompson 1988). In line with various recent studies, we have demonstrated that mutually beneficial interspecific interactions should not be conceived only as $(+,+)$ interactions, but as a continuous range of symmetrically beneficial $(+,+)$, asymmetrically beneficial $(+,0)$, and explicitly exploitative or parasitic $(+,-)$ interactions (Bronstein 1994b) (Figure 3.24). Our results thus suggest that it is not enough to monitor average fitness advantages, as localized individual interactions may be situated at different points along the mutualism–parasitism continuum (Figure 3.24, 3.25, and 3.26), and may also shift in time. The long-standing notion of mutualistic interactions being static is thus becoming extended as new findings, both experimental and theoretical, broaden our understanding. Consequently, exploitation and mutualism are not always strictly separate types of interactions, but in many instances may serve as boundaries of a continuous distribution of interactions between two mutualist guilds. This distribution embodies not only population or guild-level variation, but also dynamical changes of interactions occurring on ecological and evolutionary time scales.

4. Summary and general conclusions

In the current study we focused on specific aspects of cooperation which, in general, result in the polymorphism of different strategies in cooperative communities. Majority of traditional cooperation studies predicted that either cooperators win out, or defectors/cheater spread in the population. The coexistence of the two types was rarely considered as a stable equilibrium state of any cooperating systems. Empirical data and observations, however, hardly ever supported the idea of monomorphic populations, as in natural communities, all or nothing situations, here full cooperation or full defection, can barely be find. Relaxing some of the simplifying assumptions of the traditional models, which were mainly relying on the Prisoner's Dilemma Game to explain the diversity of cooperative associations, we have showed that polymorphic outcomes can very well be stable, and that strategies with different levels of cooperativity can very well coexist under various conditions.

First, we have overviewed the pioneering models developed and analyzed in order to explain the conundrum of cooperation. After, we have concluded that new game theoretical approaches might be needed for a more precise description of specific types of social interactions. We focused on two aspects of cooperation, non-linear *N*-person games, and conditional strategies in mutualistic interactions.

We presented a multilevel selection model of interdependence in group living species, where collective action is modeled as an *N*-player Threshold Public Good Game and where selection acts both at the individual and on the group level. We have found that the population can evolve into stable levels of cooperative polymorphism, where cooperators and free riders–laggards–can stably live together. Our results indicate: (i) that the described dynamics holds for a wide range of sigmoid benefit functions, not only for strict deterministic stepwise function; (ii) that multilevel selection need not select for the highest number of cooperators within groups but instead it may select for polymorphism depending on the details of the TPGG; (iii) that defectors contribute to the group fitness as much as they help the group to achieve the optimal amount of investment at the group level; (iv) that division of labor might evolve with regard of the participation in the two collective actions for medium cost values of cooperation; (v) and that spatial population structure promotes cooperation in TPGGs.

We also demonstrated that conditional strategies might prove more appropriate to describe cooperative behavior in many types of social interactions. We introduced conditional strategies in the process of choosing the right partners, and showed that even simple rules can promote cooperation. We also introduced conditional strategies in the investment behavior. In particular, we presented a comprehensive analysis of a continuous reciprocal investment game between mutualists, both in well-mixed and spatially structured populations, and we demonstrated a series of novel mechanisms for maintaining interspecific mutualism. We demonstrated that (i) mutualistic partners invariably follow investment cycles, during which mutualism first increases, before both partners eventually reduce their investments to zero, so that these cycles always conclude with full defection. We showed that the key mechanism for stabilizing mutualism is (ii) phase polymorphism along the investment cycle. Although mutualistic partners perpetually change their strategies, the community-level distribution of investment levels becomes stationary. In spatially structured populations, the maintenance of polymorphism is further facilitated by (iii) dynamic mosaic structures, in which mutualistic partners form expanding and collapsing spatial bubbles or clusters. We showed that (iv) insulating boundary layers between adjacent spatial bubbles, sometimes (v) catalyzed by spatial environmental heterogeneity, can have a significant effect on invasion of strategies, and hence facilitate high levels of strategy polymorphism. Additionally, we revealed (vi) strategy-diversity thresholds, both for well-mixed and spatially structured mutualistic communities, and discuss factors for meeting these thresholds, and thus maintaining mutualism. Our results demonstrate that interspecific mutualism, when considered as plastic investment behavior, can be unstable, and, in agreement with empirical observations, may involve a (vii) polymorphism of investment levels, varying both in space and in time. Identifying the mechanisms maintaining such polymorphism, and hence mutualism in natural communities, provides a significant step towards understanding the coevolution and population dynamics of mutualistic interactions.

The model proposed here can provide a potential explanation for the observed polymorphism in natural societies in threshold game like situations. As we demonstrated in the case of lions, cooperators and defectors can coexist (Stander 1992a,b; Packer & Pusey 1997) and the presence of laggards in the population (Heinsohn & Packer 1995; Packer & Heinsohn 1996) may be a natural outcome of non-linear game dynamics and the resultant division of labour emerging in such societies. Free-riders, cheaters, or defectors are frequently present in many other societies as well. For example non-producing bacteria are considered as defectors in the case of extracellular enzyme production as a cooperative act (Crespi 2001; Foster et al. 2007). Cheaters should spread and exclude cooperators from the population, yet there is a steady-state coexistence between the two strains, the wild-type cooperator and the cheater, in well-mixed cultures (Gore et al. 2009). Our model of this, and similar, social interactions incorporating nonlinear benefits can provide explanation for the origin of this coexistence and the division of labour considering multiple collective actions.

Furthermore, growing empirical evidence suggests that polymorphisms of mutualistic investment strategies are common in nature (Johnson et al. 1997; Burdon et al. 1999; Offenberg 2001; Bever 2002; Stanton 2003; Cheney & Coté 2005; Stadler & Dixon 2005; Reynolds et al. 2006; Heath & Tiffin 2007; Kiers & Denison 2008; Piculell et al. 2008; Bever et al. 2009; Hoeksema et al. 2009; Heath 2010), even on small spatial scales (Gherbi et al. 1999; Wolfe et al. 2007). Many studies suggest that microbial populations and communities are often structurally and genetically more diverse (Gherbi et al. 1999; McInnes et al. 2004), considering both type or strain richness and/or genetic diversity (Wolfe et al. 2007), than what can be explained by local host diversity (Mutch & Young 2004). Also, the effectiveness of rhizobia, such as their ability to form nodules and their capacity to fix nitrogen, varies greatly within species, and naturally, between species (Parker 1995; Kiers & Denison 2008; Thrall et al. 2011); similar conclusions hold for the performance of mycorrhizal interactions (Bever et al. 2001; Klironomos 2003; Hoeksema et al. 2009). This diversity amounts to a high variety of investment strategies; in other words, less mutualistic types coexist with more beneficial mutualists in natural communities (Bronstein 1994a,b; Parker 1995; Johnson et al. 1997; Kiers & Denison 2008; Bever et al. 2009;).

Our models analyzed in the current study thus are in a good agreement with the various empirical observations, and may change the way we think of the social dynamics in natural communities. An important implication of our study is that the diversity of different strategies of cooperation in natural communities may be high not only because of mutation and recombination, or inherent species diversity, but also as a product of selection pressures resulting from the complex dynamics of social interactions occurring within these polymorphic populations. Besides, the long lasting view that either cooperation or defection can be the stable states of any social systems, is being challenged by results that demonstrate that cooperative and defective behaviors can coexist, or even can fluctuate between different levels of cooperation. If we accept, that the Prisoner's Dilemma, and its *N*-person analog, is not the only type, and perhaps not the most relevant type, of social dilemmas, new horizons can open up in cooperation research.

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6. Abstract

A typical social dilemma develops when the benefits of cooperation can be exploited by cheaters, that is by individuals who enjoy the benefits without reciprocating. Cooperation research has offered various explanations, and has proposed several mechanisms that may promote the evolution and stability of cooperative behavior despite its disadvantage against cheaters. Here we propose novel mechanisms that can prove to be more adequate in describing the discussed biological situations. In particular, we study cooperation in collective actions as *N*-person dilemmas, and the evolution of mutualisms with conditional strategies. Several collective actions are best described as *N*-person dilemmas with non-linear effects, where a threshold number of cooperators (or investors) is necessary to achieve a group goal. We present and analyze a model of Threshold Public Good Games with multilevel selection employing an individual-based model. We find that the coexistence of cooperators and defectors is a stable outcome in this model. Furthermore, division of labor can evolve in such games, when multiple collective actions are considered, and laggards, that is cheaters, in one action are allowed to switch roles, and to become cooperators in another collective action. We also show that spatial population structure promotes cooperation in Threshold Public Good Games. Furthermore, we demonstrate that conditional strategies, such as conditional partner choice, or conditional investment strategies, can promote the evolution and stability of cooperative behavior. Mutualistic interactions between species are often best understood as a continuous reciprocal investment game, where participants iteratively adjust their investments plastically in response to their mutualistic partner's most recent investment. Our comprehensive analysis reveals that the coevolution of such investment strategies will typically induce investment cycles, that after initial increase of investments, conclude in full defection. We identify factors that can prevent this decay. First, mutualisms can be stably maintained if the investment strategies of the participants are sufficiently diverse. Second, if participants are limited in their movements, the emergence of dynamic spatial mosaic structures promotes strategy diversity and thereby facilitates the maintenance of mutualism. These ecological and evolutionary dynamics result in communities with a diversity of interaction types, ranging from mutually beneficial to exploitative, and varying both in space and in time. In general, our results and conclusions highlight that polymorphism of different cooperator types can be a natural outcome, and the models proposed here can provide a potential explanation for the observed polymorphism in natural communities.

7. Összefoglaló

A segítségnyújtás kizsákmányolása tipikusan társas konfliktushelyzetekhez vezethet, melyben a kizsákmányolt fél befektetését nem viszonozza a csaló partner. Számos tanulmány látott napvilágot, mely a segítségnyújtás evolúciójára és fennmaradására szolgál magyarázattal. Jelen munka két fő biológiai jelenség leírására mutat be modelleket és vizsgálja azokat. Egyrészről a sok-résztvevős közjó játék egy verzióját mutatjuk be, melyben a csapat együttműködésének egy küszöbértéket kell elérnie a siker érdekében. Megmutatjuk, hogy ezen modellek jóslatai alapján az együttműködők és a csalók egymás mellett élhetnek amennyiben a csapatban az együttműködők száma elégséges a küszöb eléréséhez. Továbbá megmutatjuk, hogy azokban az esetekben, melyben a csapatnak több feladatot is meg kell oldania, munkamegosztás alakulhat ki, ahol az egyikfajta szituációban csalóként viselkedő egyed egy másik szituációban már együttműködőként jelenhet meg. Kutatásaink arra is rámutatnak, hogy a térbeliségnek a vizsgált modellben is fontos stabilizáló szerepe van. Megmutattuk továbbá, hogy a feltételes stratégiák segíthetik az együttműködés elterjedését bizonyos esetekben. Ezek a stratégiák egyrészről a megfelelő partnerek kiválasztása révén, másrészről a befektetés mértékének meghatározásával befolyásolhatják az együttműködő viselkedést. A fajok közötti kölcsönösen előnyös kapcsolatok egyes típusai legjobban egy ismételt, folytonos, reciprok befektetési játékként írhatóak le. Ezekben a játékokban az egyed befektetésére hatással lehet a partner egyed befektetése is. A dolgozat második felében megmutatjuk, hogy ezen játékokban az egyedek befektetési viselkedése egy befektetési körön keresztül végül mindig az együttműködés eltűnéséhez vezet. Azonban számos folyamat segíthet a befektetés fennmaradásában, mint például a befektetési viselkedések sokfélesége, a térbeliség, vagy a térbeli heterogenitás. Ez utóbbi két esetben egy dinamikus térbeli mozaik struktúra alakul ki, mely igen hatékonyan képes a befektetési diverzitást megőrizni. Vizsgálataink rámutatnak, hogy a fajok közti kölcsönösen előnyös kapcsolatok nem feltétlenül stabilak, és gyakran térben és időben változhat a befektetési viselkedés minősége, a kölcsönösen előnyöstől a kizsákmányolásig. Összefoglalva, a dolgozatban felvetett és vizsgált modellek magyarázattal szolgálhatnak az együttműködő és csaló típusú egyedek stabil együttélésére különféle szociális helyzetekben, mely jelenséget számos megfigyelés is alátámasztani látszik.

8. Publication list

RELEVANT PUBLICATIONS

Boza, G., Kun, Á., Scheuring, I. & Dieckmann, U. (2012) Strategy diversity stabilizes mutualism through investment cycles, phase diffusion, and spatial bubbles. *PLoS Computational Biology,* 8: e1002660.

Boza, G. & Számadó, Sz. (2010) Beneficial laggards: multilevel selection, cooperative polymorphism and division of labour in Threshold Public Good Games. *BMC Evolutionary Biology* 10: 336.

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RELEVANT CONFERENCE AND WORKSHOP PRESENTATIONS

Boza, G. & Számadó, Sz. (2010) Cooperation and multilevel selection in *n*-player Threshold Public Goods Games.

> Presentation at INCORE Conference "Cooperation: an Interdisciplinary Dialogue", 2010 September 17-18, Collegium Budapest, Budapest, Hungary.

Boza, G., Kun, Á., Scheuring, I. & Dieckmann, U. (2010) Stabilizing mutualisms through investment cycles, phase diffusion, and spatial bubbles.

> Presentation at TECT Final Conference "Cooperators since life began", 2010 September 15-17, Collegium Budapest, Budapest, Hungary.

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> Plenary presentation at the TECT-INCORE summer school "Tools of the trade in cooperation research", August 30 -September 6 2008, Obernai, France.

Boza, G., Könnyű, B. & Számadó, Sz. (2008) The effect of group size and cooperation threshold on the level of cooperation in n-player prisoner's dilemma threshold game.

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Boza, G., Kun, Á., Scheuring, I. & Dieckmann, U. (2008) Evolution of mutualism in a multi-player game theoretical model.

> Poster at the Third European PhD Complexity School, "Evolution in biological systems: from molecules to life and language", February 4-8 2008, Turin, Italy (ISI Foundation, Villa Gualino).

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