

Influence of the structure of interaction among individuals
on the evolution of cooperation

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Contents

1. General introduction.....	1
1.1 Intraspecific cooperation.....	1
1.2 Definition of cooperation.....	3
1.3 Theoretical studies of intraspecific cooperation	4
1.4 Purpose of this thesis	8
2. Relationship between aggregation of rewards and the possibility of polymorphism in continuous snowdrift games	11
2.1 Introduction.....	11
2.2 Model.....	15
2.3 Results.....	23
2.4 Discussion.....	25
3. Evolution of reaction in the negotiation game with behavioural error	34
3.1 Introduction.....	34
3.2 Model.....	38
3.3 Results.....	45
3.4 Discussion.....	47
4. General discussion	59
Acknowledgements	62
Reference	63
Appendix	69

1 General introduction

1.1 *Intraspecific cooperation*

In both intra- and interspecific interactions between organisms, a trait or behaviour that promotes successes of other individuals is referred as a cooperative interaction (Sachs et al. 2004, West et al. 2007). In particular, the intraspecific cooperative interaction is an important element for considering a sociality of the species.

Intraspecific cooperation has been well studied in animals. The most remarkable cooperative interaction is a eusociality that is known in some insects and rodents, in which some individuals sacrifice their lives or reproduction for maintaining colony and helping colony mates. Cooperative interaction is also observed on the breeding process of fishes and birds, in which individuals care the non-blood related juveniles (Wong and Balshine 2011, Riehl 2013). It was reported that in chiropters, carnivores and primates individuals often share their foods with their conspecific neighbours (Wilkinson 1984, East and Hofer 1991, Hoelzel 1991, Mitani 2009). Cooperative vigilance of predators is observed in some grouping birds and mammals to detect predators (Clutton-Brock 1999, Carter et al. 2009, Pangle and Hole 2010). Information about predator is sometime shared among group members by alarm call in birds, rodents and primates (Hollén and Radford 2009, Gill et al. 2013, Fichtel and Kappeler 2002, Shelley and Blumstein 2005). Of course, human also represent various types of cooperative behaviours (Rand and Nowak 2013).

Although abundant examples have been reported in insects and vertebrates, the intraspecific cooperation is not specific property of those taxonomic groups. Social amoebas are well known to cooperate with neighbouring cells for the movement toward new resource (Kuzdzal-Fick et al. 2007) and for the fruit-body formation in reproduction (Li and Purugganan 2011). Yeast produce enzyme and obtain

decomposition products, but they often share the profit of decomposition with neighbouring cells (Greig and Trivisano 2004). Such sharing of profitable chemical materials also reported in RNA virus or bacteria in biofilms (Brown 2001, Brockhurst et al. 2008). These microbial examples can be considered as a form of cooperative interactions.

Cooperative interaction is also observed in plants. Anti-herbivore defence of a plant individual often reduces the herbivory on its neighbouring ones, so-called associational resistance, which is regarded as a type of cooperation (Olf and Ritchie 1998, Barbosa et al. 2009). Although the associational resistance was initially focused as interspecific interactions, it is recently known that it also existed in intraspecific interactions. When herbivore arthropods travel between plant individuals and graze them, an individual defence by toxic chemicals will mitigate the herbivory pressure of neighbours through reductions of the activity or survival probability of herbivores. When the herbivores disperse to the neighbouring plant individuals after the reproduction, the individual anti-herbivore defence will reduce the number of spreading herbivores (Evans 1983). In some plants, individuals attacked by herbivores produce and release specific chemical signals to attract the predators of the herbivore, in which the attracted predators could reduce the herbivory pressure of its neighbouring individuals (Sabelis and de Jong 1988, Mumm and Dicke 2010). Cooperative interactions of plants are also reported in pollination process of flowering plant. In the plants that attract pollinators by providing rewards, reward production of a certain individual can positively influence pollination success of conspecific individuals through learning process of pollinators (Giurfa 1995, Gigord et al. 2001).

According to these examples, the intraspecific cooperation is widely observed in

nature, which is often an important element for their fitness. Its evolutionary process is a significant issue to understand biological interactions. In the present thesis, I study evolutionary process of intraspecifically cooperative interaction from a theoretical point of view.

1.2 *Definition of cooperation*

The term “cooperation” has been used in various meanings in previous studies (West et al. 2007), which may potentially cause confusions. In order to investigate cooperative interactions, its definition should be clarified. According to Sachs et al. (2004), cooperation was defined as both inter- and intraspecific interactions that traits or behaviours of a focal individual (actor) increase the fitness of others (recipient). This can be regarded as a broad sense of definition of cooperation, although a narrow sense of definition has been also proposed (West et al. 2007). Before an explanation of the narrow sense of definition, we should categorize cooperation into two classes.

Based on the effects on actor, West et al. (2007) categorized cooperation into “mutual benefit” that associates with an advantage of the actor itself and “altruism” that is accompanied by a cost for the actor (West et al. 2007) (They refused to use a term “mutualism” for the former because it includes various concepts and tends to represent interspecific interactions). It is clear that the mutual benefit can evolve easily due to the actor's advantage, whereas the altruism is unlikely to evolve owing to the cost for actors. Because of the severe evolutionary condition, evolutionary biologist tends to focus on altruism in comparison to mutual benefit.

It should be noted that two types of selective pressures possibly drive evolution of cooperation, *i.e.*, a direct advantage for actor and an indirect advantage via recipients. In the altruism, the indirect advantage is only selective force due to an absence of

advantage for the actor. On the other hand, in the mutual benefit, both selective forces are possible, *i.e.*, the indirect advantage may potentially exist in addition to the direct advantage. In a narrow sense of definition of cooperation, its evolution is essentially driven by the indirect advantage (West et al. 2007). In other words, if its evolution is driven by the direct advantage on actor only, it is regarded as a selfish behaviour rather than cooperation. Some other studies have used the term “cooperation” for more restrictive cases, *i.e.*, only for altruism (*e.g.* Nowak 2006). However, it is generally difficult to separate two selective forces in empirical studies. Furthermore, the narrow sense of definition is not adequate when the trait is a continuous variable, where the property of cooperation can change continuously between mutual benefit and altruism depending on the trait value (Doebeli *et al.* 2013).

1.3 Theoretical studies of intraspecific cooperation

Theoretical study of intraspecific cooperation was initiated on the narrow sense of cooperation (Hamilton 1964ab, Williams 1966). The cooperation in the narrow sense is difficult to evolve owing to the cost for the actor itself. Even if the cooperation becomes prevalent in the population by some factors (*e.g.*, colonization or genetic drift), a less or non-cooperative individual, *i.e.* a cheater or a free rider, can invade and increase in the population by saving cost for altruism. Therefore, altruism must involve specific mechanisms that enable both evolution and maintenance in the population. In other words, the indirect advantage of altruism should be detected.

In order to find mechanisms promoting the evolution of altruism, theoretical studies have been actively investigated its mechanism by based on various frameworks. One important framework is a concept of kin selection (Hamilton 1964ab, 1972), which considers a genetic similarity, *i.e.*, relatedness, between actor and recipients. If the

relatedness between interacting individuals is larger than an average relatedness within the population, altruistic behaviour can be selected depending on its cost and benefit for actors and related recipients, respectively. Hence, when individuals can recognize their kin and choose them for the partner of the cooperation, altruism can evolve more easily (Hamilton 1964ab, 1972). Even if the individuals cannot recognize their kin, the kin selection can work conditionally. When individuals choose their partner based on a trait that genetically correlates with the cooperation, altruism tends to evolve through an enhancement of interaction between cooperative relatives (Bull and Rice 1991), so-called “green beard” mechanism (Dawkins 1976). The existence of dispersal also can increase the frequency of interaction with related individuals, which conditionally result in the evolution of altruism limitation (Nowak and May 1992).

Another important framework is the game theory (von Neumann and Morgenstern 1944, Maynard Smith and Price 1973, Maynard Smith 1982), where individual fitness is determined through interaction among players with specific traits. Studies on the cooperation using the game theory have started as a discrete game, in which individuals choose their actions from several possible choices *e.g.*, cooperation or defection. Two of the major discrete game models are prisoner's dilemma game and snowdrift game (Doebeli and Hauert 2005). Both of them consider the cooperative interaction between two individuals, although the cooperation is altruistic in the former (with a cost for actor), but mutual benefit in the latter (with a direct benefit for actor). Another major discrete game is the public goods game, in which individuals invest their effort to produce a common benefit that is eventually shared by all concerning players (Archetti and Scheuring 2012). It should be remarked that the public goods game partially involves characteristics of both the prisoner's dilemma game and the snowdrift game.

The game theoretic approach has been extended with consideration of information reference in repeated interactions. For example, a player decides own action by referring information of past plays or reputations about its opponent players (Trivers 1971, Axelrod and Hamilton 1981, Nowak and Sigmund 1998, Frank 1995, 2003). Such responding behaviour based on its opponent information under the repeated interactions is also known as a factor that makes the evolution of altruism easily.

In parallel with the extension of discrete game models, researches have also developed another class of game model, *i.e.*, the continuous game model, in which the investment for cooperation is a continuous variable rather than the discrete limited choices. In the continuous game, two models are generally used, *i.e.*, the continuous prisoner's dilemma game and the continuous snowdrift game. According to Doebeli *et al.* (2004), the cooperative investment does not influence a reward of the actor itself at all in the continuous prisoner's dilemma game, but it increases actor's reward in the continuous snowdrift game. Differently from discrete models, these definitions do not correspond with altruism and mutual benefit, which are characterized by negative and positive effects on the actor, respectively. This is because that such a categorization is meaningless in the continuous game, in which effects on actor continuously change between negative and positive depending on the investment for cooperation.

These continuous game models have been investigated by using the adaptive dynamics, which is an approach to analyse evolutionary process on continuous trait space, combining game theory and quantitative genetic model (Dieckmann and Law 1996, Metz *et al.* 1996, Geritz *et al.* 1998). In the adaptive dynamics, we consider the invasion of a rare mutant into a resident population, whose trait value is slightly different from that of resident individuals. If the fitness of the mutant is larger than that

of the residents, the mutant will increase in the population, eventually replacing the resident strain. This approach enables us to theoretically investigate the evolutionary process of the continuous cooperative trait.

Applying this approach, previous studies successfully revealed the dynamic process of the evolution of cooperative traits with continuous variable. For example, previous studies revealed dynamic process of emergence of polymorphism in cooperation level as a consequence of “evolutionary branching” (Doebeli *et al.* 2004). Even if the cooperation level is initially monomorphic in a population, it can be gradually polymorphic with multiple strains depending on a cooperation process and parameters. This process can also cause the oscillation of population size, driven by the dynamic change of a frequency of cooperative individuals in the population (Hauert *et al.* 2006, 2008). The increment of less cooperative strain can reduce an average fitness of the population, which sometimes results in an extinction of the population, so-called “evolutionary suicide” (Parvinen 2011). In the continuous game, cost and benefit of the focal player are functions of cooperative investments of all interacting players (including the focal player itself), respectively. Previous studies indicated importance of the curvatures of those functions in the evolution of cooperation (Motro 1991, Doebeli *et al.* 2004, Archetti and Scheuring 2012).

These models consider the evolutionary process of the cooperation level *per se*. However, we can also consider another class of evolutionary trait, *i.e.*, the decision-making process of the cooperation level. For example, some organisms can flexibly choose their cooperation level based on their partner’s behaviour (Wright and Cuthill 1990, Markman *et al.* 1995, Beauchamp 2009). The evolution of such response to the partner has been investigated by using some specific frameworks, *e.g.*, the

iterated version of the continuous prisoner's dilemma game or the "negotiation game," in which individuals can repeatedly observe their partner's behaviour before carrying out the investment. In both frameworks, it is assumed that individuals can choose their cooperation level based on that of their partner, in which we would investigate the evolution of the response in the cooperation. By using these frameworks, the evolution of the decision-making process of the cooperation level has been investigated. For example, it was reported evolution of the reaction to a cooperation level of the partner can cause evolutionary fluctuation of the cooperation level (Wahl and Nowak 1999ab). The realized cooperation level can differ from that with evolution of cooperation level itself (Taylor and Day 2004). However, the evolutionary pattern of the decision making process have not been revealed well compared to that of cooperation level itself because of the difficulty of the analytical investigation (see below and Chapter 3 in detail).

1.4 Purpose of this thesis

As I explained in above, previous theoretical studies can be classified into two classes regarding to the focused evolutionary trait, *i.e.*, evolution of cooperation level itself and evolution of reaction mode to decision of opponent. These studies have successfully revealed mechanisms of evolution of continuous cooperative trait, but some issues still remain to be solved in each study class. In the study class focusing on the evolution of cooperation level itself, the process of producing cooperative reward from individual contributions has not been considered in detail. In the study class focusing on the evolution of reaction mode, general property of the evolutionary process of reaction mode with continuous cooperative traits have been revealed insufficiently. In this thesis, I reveal those issues by developing theoretical models,

In Chapter 2, I investigate evolution of cooperation level, focusing on a relationship

between functions of cooperation process and condition of the emergence of polymorphism in cooperation levels within a population. Intraspecific cooperative interactions of organisms sometime involve polymorphism of investment for cooperation (see Introduction of Chapter 2 for real examples). The conditions of emergence of polymorphism in cooperation have been theoretically investigated by using continuous snowdrift games. Those studies, however, tended to consider a restricted class of interaction. In the cooperation process, individual investments are eventually aggregated to produce benefits, accompanied by costs for the actor. Previous studies were likely to assume a simple function for those benefit function (aggregation process) and cost function. In this study, I investigate the evolutionary process by considering more general functions and indicate that aggregation process in cooperation is an important determinant of coexistence of multiple strains with specific cooperation level. This finding provides a significant implication to understand the observed polymorphism in organisms.

In Chapter 3, I study the evolution of reaction mode to opponent player, focusing on effect of error in negotiation process. Organisms potentially exchange information about their decision in cooperation each other (negotiation process), by which they can decide their cooperation levels (see Introduction of Chapter 3). Some studies investigated evolution of functional form of reaction mode by using continuous snowdrift game. Despite of various approaches, those were likely to reveal only limited properties of the system due to complexity of the evolutionary dynamics of reaction. Contrary to this, I found that an existence of error in negotiation process can reduce such a complexity and enable further theoretical analysis. This analysis can contribute to understand evolutionary process of a higher level of cooperation system with

information exchange.

In Chapter 4, I summarize the influence of structure of interaction among individuals on the evolution of cooperative. I discuss the importance of our findings for considering the empirical examples of the cooperation. Finally, I discuss some unconsidered ecological factors in the present thesis, and indicate some future works which are important for more deep understanding about the evolution of cooperation.

2 Relationship between aggregation of rewards and the possibility of polymorphism in continuous snowdrift games

2.1 Introduction

Cooperative relationships have been widely observed in various taxonomic groups, involving bacteria, reptiles, mammals, and plants (Dugatkin 1997, Sachs *et al.* 2004, Melis and Semmann 2010, Raihani *et al.* 2012). Previous empirical studies on cooperation have often reported the existence of intra-population variation in cooperation level. For example, yeasts cooperate with neighbouring cells by sharing their profit in the process of resource decomposition, in which morphs with different levels of enzyme production can coexist (Greig and Travisano 2004). Animals or birds form groups and cooperate in being vigilant to approaching predators, but some individuals vary in their contributions to group vigilance (kangaroos, Carter *et al.* 2009; hyenas, Pangle and Holekamp 2010). In plants, it has been reported that anti-herbivore defence by an individual plant often reduces herbivory on its neighbouring ones (so-called “associational resistance”), under which polymorphism of defence level is also observed in some cases (Agrawal *et al.* 2002, Hare and Elle 2002).

Some previous studies theoretically tried to explain the empirical examples of the polymorphism in cooperation level. One remarkable finding in theoretical studies is that in the continuous snowdrift game evolutionary branching conditionally occurs, which result in the emergence of polymorphic cooperation levels (Doebeli *et al.* 2004). After this finding, following studies have investigated the influences of the various factors on the emergence of polymorphism (Brännström *et al.* 2011, Parvinen 2011, Wakano and Iwasa 2013). Fluctuation in group size either stabilizes or destabilizes the dimorphism of cooperative levels depending on the shape of payoff function (Brännström *et al.* 2011), the existence of metapopulation structure relaxes the condition for the emergence

of polymorphism (Parvinen 2011), and a small population size prevents evolutionary branching (Wakano and Iwasa 2013). Functional forms of reward and cost are also proposed as an important factor for the coexistence of polymorphic cooperation levels (Archetti and Scheuring 2012). Doebeli *et al.* (2004) indicated that the concavity of both reward and cost functions is a necessary and sufficient condition for the occurrence of evolutionary branching.

These previous studies, however, generally have paid less attention to the process by which rewards result from investment. In the process of producing reward on cooperation, each individual provides ‘investment’ in order to obtain some advantageous ‘effect,’ the amount of which can be represented by a function of investment (*e.g.* an investment z produces an effect $f(z)$). For example, yeast produce enzymes in order to produce decomposition products, or in the group vigilance individuals consume time in vigilance in order to detect their predators. In cooperative interactions among multiple individuals, the contributions of neighbouring individuals are aggregated, and consequently each individual obtains a resultant effect as the reward of cooperation. We can consider some types of aggregation process depending on the mechanism of the aggregation.

First, we can consider two aggregation stages depending on whether the individuals’ contributions are aggregated at investments or at effects. Here, effects refer those produced by the investments. Aggregations of investments and effects will have equivalent consequences only if the aggregation is additive and the relationship between investment and effects are linear. However, the condition is not likely to be realistic in most cases. For example, the amount of enzyme produced by yeast will not be linearly related the obtained decomposition, because the decomposition rate generally follow

Michaelis-Menten kinetics (Zaks and Klibanov 1985). The detail of the cooperation of yeast should be investigated by considering the chemical reaction-diffusion process (*e.g.* Borenstein *et al.* 2013, Archetti 2014, Scheuring 2014). However, for generality of analysis, I summarize those processes into two simple equations, which are ineffective for quantitative predictions but effective for qualitative investigation of essential mechanisms in the considered system. One is that each individual produces enzyme z , and the total of this enzyme by all group mates, Σz , is used to produce decomposed products $f(\Sigma z)$, in which aggregation occur before producing products. Alternatively, each individual invests energy z to produce decomposed products $f(z)$, the total of which, $\Sigma f(z)$, benefits the focal individual. In this case, the aggregation occurs after the producing products. I call the former “aggregation of investments” and the latter “aggregation of effects,” respectively throughout the paper.

The second issue is how the factors are associated, *i.e.*, “additive aggregation” or “multiplicative aggregation” (*e.g.* Σz or Πz). An additive aggregation often applies to material benefits such as enzyme or decomposition products in yeast, but the multiplicative aggregation is also conceivable. Consider group vigilance: if individual bouts of vigilance overlap, the probability of spotting a predator is calculated by the product of the probabilities of a single individual not finding an enemy. This is also a greatly simplified situation, and the group vigilance should be investigated by considering behavioural process in detail (*e.g.* Proctor *et al.* 2002). However, this example shows that multiplicative benefit is more appropriate in some cases.

Third, we can classify the cooperation according to the reward type, *i.e.* the reward is obtained through whether promotion of advantage or suppression of disadvantage. In the cooperation in yeast, more investments promote the advantage by producing more

decomposition products. Contrarily, in group vigilance, more investments suppress the disadvantage by reducing the risk of predator attack. This difference will appear as whether the reward term is positive and $f(z)$ is increasing, or the reward term is negative and $f(z)$ is a decreasing function.

Accordingly, we can categorize the aggregation processes of producing reward with respect to three aspects, *i.e.* (i) additive or multiplicative aggregation, (ii) aggregation of investments or effects, and (iii) promotion of advantage or suppression of disadvantage (Figure 2.1). As a component of the payoff function, previous studies are mainly focused on the functional shapes of reward and cost, but not considered effects of aggregation process. For example, most of the previous models of continuous snowdrift game (Doebeli et al. 2004, Brown and Vincent 2008, Parvinen 2010) assumed the aggregation process, which I call "additive aggregation of investments with promotion of advantage." Yet, in order to understand general properties of evolutionary processes in a continuous snowdrift game, we should analyse its evolutionary dynamics for various possible aggregation processes in rewards.

In this analysis, I investigate two properties: (i) the possibility of the occurrence of evolutionary branching leading to polymorphism and (ii) the possibility of the sustained coexistence of polymorphism. I also compare the influence of the functional shapes of effect and cost among aggregation processes. I analytically show that these possibilities are different depending on the type of aggregation process of rewards. My results show us the condition for the emergence of polymorphisms that are observed in various organisms.

2.2 Model

2.2.1 Payoff function

I consider a sufficiently large asexual population, individuals of which are categorized into morphs based on their trait values. For social interactions, it is assumed that N individuals are randomly chosen from this population to form a group, within which members interact with each other. Consider a certain individual in an interacting group, a trait value of which is represented by y . The payoff of this individual depends on the traits of its $N-1$ group mates. Those group mates can be polymorphic in trait values. In particular, I refer to the trait value and number of i -th morph in the group except for the focal individual as x_i and n_i ($n_i \geq 0$ and $\sum n_i = N-1$), respectively. When the total number of morphs in the population is m , an assemblage of group mates is represented by $\{(x_i, n_i)\}_{i=1\dots m}$, which is an assemblage of (x_i, n_i) of all morphs. In this group, the payoff of the individual with trait y given the traits of the other group members is

$$w(y | \{(x_i, n_i)\}_{i=1\dots m}) = F(y | \{(x_i, n_i)\}_{i=1\dots m}) - g(y), \quad (2.1)$$

where the first and second terms of the right-hand side are the reward and the cost of cooperation for the focal individual, respectively. I assume that the cost function $g(y)$ is a monotonically increasing function of y .

Because the group mates are randomly chosen from the population, the expected payoff of the focal individual with trait y is calculated by asking the expectation over all possible combinations of group mates. Let us represent the frequency of i -th morphs in the population as p_i ($\sum p_i = 1$). The probability of obtaining the composition of group mates $\{(x_i, n_i)\}_{i=1\dots m}$ follows a multinomial distribution, which I represent in this article as

$$\binom{N-1}{\mathbf{n}} \mathbf{p}^{\mathbf{n}} = \frac{(N-1)!}{n_1! n_2! \cdots n_m!} p_1^{n_1} p_2^{n_2} \cdots p_m^{n_m} . \quad (2.2)$$

Averaging Eq.(2.1) with this probability, the expected payoff of the focal individual with phenotypic value y is

$$W(y | \{(x_i, p_i)\}_{i=1, \dots, m}) = \sum_{\mathbf{n}} \left[\binom{N-1}{\mathbf{n}} \mathbf{p}^{\mathbf{n}} F(y | \{(x_i, n_i)\}_{i=1, \dots, m}) \right] - g(y) . \quad (2.3)$$

2.2.2 Five possible aggregation processes

In this study, I consider the difference of the aggregation process of individual contributions on the reward. For simplicity of explanation, I represent the trait values of all group members by $(z_1, z_2, \dots, z_N)$, including the focal individual's. Each individual provides investment, z_i , which results in some advantageous effect. The individual investments are translated to the reward differently depending on its aggregation process as illustrated in Figure 1. Thus, the reward function of focal individual, F , is defined by two factors, *i.e.*, the aggregation process of individual contributions, and the functional shape of effect $f(z)$ determined by investment z . I assume that the reward $F(\bullet)$ always increases as the amount of investments increases, although $f(\bullet)$ can be both increasing and decreasing functions depending on the aggregation process. I represent the effect functions in former and latter case as $f_+(\bullet)$ and $f_-(\bullet)$, respectively.

I consider aggregation processes with respect to three aspects, *i.e.* (i) additive or multiplicative, (ii) aggregation of either investments or effects, and (iii) promotion of advantage or suppression of disadvantage. By considering the every combination of these aspects, we obtain eight types of aggregation process. However, except for the combination of multiplicative aggregation of effect, aspect (iii) does not yield an essential difference, because one can always convert a monotonically decreasing

function $f_-(\bullet)$ to a monotonically increasing function $f_+(\bullet)$ simply by adding a minus sign in its front. On the other hand, in multiplicative aggregation of effects, where the “promotion of advantage”-type reward function, $\Pi f_+(z_j)$, cannot be transformed to the “suppression of disadvantage”-type reward function, $-\Pi f_-(z_j)$. This difference may seem trivial. However, the functional form of aggregation process influences the curvature of the reward function (and then payoff function), which can be a significant determinant of evolutionary dynamics. It may ultimately affect the possibility of the occurrence of polymorphism in cooperation level.

As a result, we have five types of aggregation process (Figure 2.1). The first four functions, $f(\bullet)$ and $f_+(\bullet)$, are monotonically increasing. The bottom function, $f_-(\bullet)$, is monotonically decreasing. I also assume that z is always positive in multiplicative aggregation of investments, and that f_+ and f_- are positive in multiplicative aggregation of effects.

2.2.3 Evolutionary properties

I analysed the evolution of cooperation level using adaptive dynamics theory (Dieckmann and Low 1996, Metz *et al.* 1996, Geritz *et al.* 1998). I seek for a solution satisfying the two conditions; (i) all coexisting strains have the same payoff (=feasibility) and (ii) each strain has zero selection gradient with respect to its cooperation level. The population satisfying the latter condition is called “evolutionarily singular coalition.” It is a generalization of “evolutionary singular point” for a polymorphic case. Consider a population with $\{(x_i, p_i^*)\}_{i=1\dots m}$. The former condition can be written as

$$W(x_j | \{(x_i, p_i^*)\}_{i=1\dots m}) = W(x_k | \{(x_i, p_i^*)\}_{i=1\dots m}) \quad \forall \quad j, k = 1\dots m. \quad (2.4)$$

If these simultaneous equations have no real solutions, one morph becomes extinct. Otherwise, coexistence is achieved. For coexistence, solving Eq.(2.4) provides a set of equilibrium frequencies $\{p_i^*\}_{i=1\dots m}$ that can be expressed in terms of $\{x_i\}_{i=1\dots m}$, with which we can rewrite the payoff at the coexisting state as $W(y | x_1, x_2, \dots x_m)$, excluding $\{p_i^*\}_{i=1\dots m}$. Dieckmann and Law (1996) showed that the selection gradient of x_i can be written as

$$\frac{dx_i}{dt} = \beta_i(x_1, x_2, \dots x_m) \left. \frac{\partial W(y | x_1, x_2, \dots x_m)}{\partial y} \right|_{y=x_i}, \quad (2.5)$$

where $\beta_i(x_1, x_2, \dots x_m)$ is a positive coefficient determining the rate of evolutionary change of x_i . Therefore, the condition for the evolutionary singular coalition $x_{i=1\dots m}^*$ (or the evolutionary singular point for $m = 1$) can be written as

$$\left. \frac{\partial}{\partial y} W(y | x_1^*, x_2^*, \dots x_m^*) \right|_{y=x_j^*} = 0 \quad \forall j = 1 \dots m. \quad (2.6)$$

On a solution that satisfies both Eqs. (2.4) and (2.6), I investigated two kinds of stabilities of the solution concerning their evolutionary property, *i.e.*, convergence stability and evolutionary stability. The convergence stability shows that a focal singular solution can be evolutionally reachable or not from a slightly different state from the singular solution by invasions of mutants. On the other hand, the evolutionary stability shows that a focal singular solution can be sustainably maintained under invasions of mutants whose strategy is slightly different from the solution. If the solution is both CS and ES, the solution is a continuous stable state (CSS: Eshel 1983). If the singular solution is CS but not ES, an evolutionary branching occurs and a new morph with a different cooperation level joins the population. If the singular solution is not CS, such a solution will never be reachable as a result of evolution. According to Geritz *et al.*

(1998), the solution is ES when

$$\left. \frac{\partial^2}{\partial y^2} W(y | x_1^*, x_2^*, \dots x_m^*) \right|_{y=x_j^*} < 0 \quad \forall j = 1 \dots m \quad (2.7)$$

is satisfied. The condition of CS can be investigated by examining a matrix $\mathbf{M}$ whose (i, j) -element is

$$\mathbf{M}_{ij} = \frac{\partial}{\partial x_j} \left(\beta_i(x_1^*, x_2^*, \dots x_m^*) \frac{\partial W(y | x_1^*, x_2^*, \dots x_m^*)}{\partial y} \right) \bigg|_{y=x_i^*}. \quad (2.8)$$

The solution is CS when real parts of all the eigenvalues of $\mathbf{M}$ are negative (Leimar 2009).

2.2.4 Evolutionary polymorphism and sustained polymorphism

By examining these evolutionary properties, I investigate two types of possibilities of the existence of polymorphism. First, I consider the possibility of emergence of polymorphism by successive evolutionary branching from a monomorphic state. If there is a feasible singular coalition in a population with $m = l$ morphs and an evolutionary branching is possible at the singular coalition, an evolutionary branching occurs and the number of morphs becomes $m = l+1$. By successively examining this condition from a monomorphic to polymorphic population, I investigate how many morphs can potentially appear through evolutionary branching. In the present study, I refer to this potential as the possibility of “evolutionary polymorphism.” Notice that the word “evolutionary” is a key here, because this term suggests the possibility of polymorphism through an evolutionary process. In summary, I say that an evolutionary polymorphism with l morphs is possible if (i) the singular coalitions can be CS but non-ES for states with 1, 2, ..., $l-1$ morphs, (ii) singular coalitions can be feasible for states with 1, 2, ...,

l morphs, and (iii) the singular coalition can be CS and ES for a state with l morphs.

By examining these three conditions, I investigated the possibility of evolutionary polymorphism for five types of aggregation process. The detail of the analyses is shown in Appendix 2.A. Here I show the analyses for additive aggregation of effects (AE) and additive aggregation of investment (AI) as the examples. In AE type, the payoff of a mutant with y in a monomorphic population with x can be written as

$$W(y | x) = (N - 1) f(x) + f(y) - g(y) . \quad (2.9)$$

According to Eqs. (2.7) and (2.8), the singular points x^* become CS but non-ES when

$$f'(x^*) < g''(x^*) < f''(x^*) . \quad (2.10)$$

Since left and right inequalities are never satisfied simultaneously, an evolutionary branching never occurs. Therefore, the condition (i) is never satisfied when $l > 1$, and we can conclude that the evolutionary polymorphism with two or more morphs is impossible in AE type. On the other hand, in AI type, the payoff function can be written as

$$W(y | x) = f((N-1)x + y) - g(y) . \quad (2.11)$$

The singular points x^* become CS but non-ES in a monomorphic population when

$$Nf''(Nx^*) < g''(x^*) < f''(Nx^*) . \quad (2.12)$$

This condition can be satisfied if $g(x^*) < f(Nx^*) < 0$, therefore we cannot reject the possibility that the condition (i) with $l = 2$ can be satisfied. Moreover, I can show that we cannot also reject the possibility of the existence of a solution satisfying the conditions of evolutionary polymorphism with $l \geq 2$ (Appendix 2.A). Consequently, in AI type, the evolutionary polymorphism with two or more morphs is potentially possible. I investigated the possibility of evolutionary polymorphism for the other types of aggregation process (MI, pME and sME) by using similar analysis (see Appendix 2.A

for the detail of the analysis).

Second, I consider the possibility of the sustained coexistence of multiple morphs in a polymorphic population. Even if we find the number of morphs k ($< l$) such that a singular coalition with k morphs never satisfies a branching condition (hence the emergence of polymorphism with l morphs is never possible through a successive evolutionary branching), one cannot reject the possibility of a sustained polymorphic solution when the polymorphism is already established for some historical reason. For example, when individuals immigrate from different environments, or when mutations with large effects on trait values occur, the population can be polymorphic potentially without the occurrence of evolutionary branching. Such a potential can simply be examined by studying conditions for both feasibility and evolutionary stability of an evolutionarily singular coalition with l morphs, ignoring the property of a singular solution with 1, 2, ..., $l-1$ morphs (see Appendix 2.A). In the present study, I refer to this potential as the possibility of “sustained polymorphism.” Note that the word “sustained” is a key here, because we do not a priori assume any mechanisms of how a polymorphic population with l morphs was initially built up. To summarize, I say that a sustained polymorphism with l morphs is possible if (i) a singular coalition can be feasible for states with l morphs, and (ii) this singular coalition can be CS and ES. By definition, if the evolutionary polymorphism with l morphs is possible, it automatically suggests that the sustained polymorphism with l morphs is also possible.

Here I show the examples of the analysis for the possibility of the sustained polymorphism for AE type and AI type. Please see Appendix 2.A for more details and the analyses for the other types of aggregation. In AE type, the necessary condition for the coexistence of m morphs is that the simultaneous equations

$$f(x_i^*) - g(x_i^*) = f(x_j^*) - g(x_j^*) \quad \forall \quad i, j = 1 \dots m, \quad (2.13a)$$

$$f'(x_i^*) = g'(x_i^*) \quad \forall \quad i = 1 \dots m, \quad (2.13b)$$

have a solution. Because Eqs. (2.13a) and (2.13b) yield $m-1$ and m constraints respectively, there are $2m-1$ constraints in total. The number of unknown variables in Eqs. (2.13) is, m (*i.e.*, trait value $x_{i=1 \dots m}^*$). Since the number of variables is fewer than that of constraints for $m > 1$, two or more morphs cannot coexist; the sustained polymorphism with two or more morphs is impossible in AE. On the other hand, in AI type, we already know that evolutionary branching is possible (see Eq. (2.12) and Appendix 2.A). Since the evolutionary polymorphism is a sufficient condition for the sustained polymorphism as mentioned above, the sustained polymorphism with two or more morphs is also possible in this case. By using similar analysis, I investigated the sustained polymorphism for the other types of aggregation process (*i.e.* MI, pME and sME, see Appendix 2.A).

It should be noticed that I focused on necessary conditions for evolutionary polymorphism and sustained polymorphism rather than sufficient conditions. These conditions do not ensure that a polymorphism with an appropriate number of morphs always occurs. However, it is surely ensured that when the concerning conditions are violated those phenomena never occur. My study is thus useful in elucidating evolutionary conditions for polymorphism, and it has direct implication to empirical studies.

2.3 Results

2.3.1 Influence of the aggregation process

I analytically investigate the possibilities of evolutionary and sustained

polymorphism by applying the general approach described above for five types of aggregation process (see Appendix 2.A for details of my analyses) under the condition without any restriction for the functional shapes of the effect $f(\bullet)$ and the cost $g(\bullet)$. Table 2.1 summarizes the result of the analytical investigation. According to the present analysis, both AI and MI could result in evolutionary and sustained polymorphism with more than two morphs. Even in those cases, the polymorphism with more than two morphs tends to occur under restricted conditions only. Carefully choosing adequate functional forms and parameters, we can show the emergence of polymorphism through an adaptive dynamic process by using individual-based simulations (Figure 2.2, the detail of the simulation is written in Appendix 2.B). On the other hand, AE leads to monomorphism only, resulting in neither dimorphism nor polymorphism. This is because the singular solution does not depend on the amount of investments by the other individuals (see Eq. (2.A9) and (2.A10) in Appendix 2.A). This implies that interactions among individuals are not relevant but that the efficiency of one's contribution is simply maximized through an evolutionary process. Therefore as a solution of simple optimization it results in a monomorphic state.

Interestingly, in the case of ME, the possibility of evolutionary polymorphism is different between whether cooperation is advantage-promoting or it is disadvantage-suppressing. In the sME, monomorphism and dimorphism are possible although polymorphism with more than two morphs is generally not possible except for some degenerate cases. On the other hand, for the pME, dimorphism never results from an evolutionary branching, but is sustained. This implies that in such a case, mutations with large effects or migrations from another population are needed to result in dimorphism. I also consider the situation that an individual investment either more or

less influences its own reward than those from other members. However, such inequality of the group member's contribution does not alter the general results of my analysis (see Appendix 2.A).

2.3.2 Influence of the functional shapes of effect and cost

The functional shapes also influence the possibility of the evolutionary branching. Next, I examine the influence of their functional shapes on the evolutionary process. To do so, I categorize the functional shapes simply into four types, *i.e.* linear, convex, concave, and the other functional shapes (*e.g.* sigmoid), I call the last type as complex type. I examine the condition for evolutionary branching by focusing on AI, MI and sME (see Appendix 2.A) and reveal the combination of the functional shapes of effect and cost that realizes evolutionary branching. Similarly to the above analyses of evolutionary and sustained polymorphism, I consider necessary conditions under which polymorphism occurs.

Figure 3 shows the summary of the analysis. In both AI and MI, evolutionary branching can occur only when *both* effect and cost functions have a decelerating shape at the singular solution. Therefore, both effect and cost functions must be in either a concave or complex shape for the occurrence of branching. On the other hand, in sME, evolutionary branching can occur when *either* effect *or* cost function has a decelerating shape at the singular solution, and, therefore, either effect or cost function should be either a concave or a complex type of function for evolutionary branching.

2.4 Discussion

In the present study, I show that the aggregation process of rewards significantly influences the possibilities of both evolutionary and sustained polymorphism in

cooperation level. Previous studies have reported multiple factors affecting the emergence of polymorphism in cooperation levels (Doebeli *et al.* 2004, Brännström *et al.* 2011, Parvinen 2011, Wakano and Iwasa 2013). However, they focussed on the payoff functions that conditionally enabled polymorphic cooperation level to evolve. Although some previous studies investigated the influence of the aggregation process of reward with focusing on some specific cases (*e.g.* reaction-diffusion process of yeast in Borenstein *et al.* 2013, Archetti 2014, Scheuring 2014), the general pattern of the influence of the aggregation process on the evolution of cooperation has not been revealed. By considering a wider class of payoff functions with various aggregation processes of reward effects, the present analysis significantly generalised these works to show the potential possibility of evolution of polymorphism. I indicated that polymorphism of cooperation levels never emerges from the evolutionary process unless the aggregation process is AI, MI or sME type. Consequently, I show that the type of aggregation process is an important and remarkable element of cooperation when we consider the variation of cooperation levels.

By applying my findings to the empirical examples of cooperation, I can predict the possibility of variation in cooperation levels from the information of aggregation process, or suggest the mechanism of aggregation process itself under an existence of variation of cooperation level. In the cooperation of yeasts, for example, both AI and AE types are possible depending on whether they share the decomposing enzyme or the decomposed products. According to my results, cooperation level becomes always monomorphic under AE, but can be polymorphic under AI (see Table 2.1). In reality, yeasts may share both enzyme and decomposed products probably through the chemical reaction-diffusion process, and my classification of the type of aggregation in yeast is

generally difficult to apply to realistic situations directly. However, it is possible to predict from my analysis that some level of enzyme sharing with neighbours is necessary for the coexistence of multiple morphs with different abilities of enzyme production (Greig and Travisano 2004). In addition, we can also predict that both the amount of decomposed products and the individual cost of producing enzyme should be concave functions of amounts of the total enzyme and the individual enzyme, respectively (see Figure 2.3). Indeed, an experimental study reported that the functional shape of benefit and cost are concave in an experimental system where dimorphism of the producing ability of enzyme is observed (Gore *et al.* 2009).

Polymorphism in the plant defence (Agrawal *et al.* 2002, Hare and Elle 2002) can also be caused by the cooperative interaction called associational resistance, but the aggregation process of them depends on the mechanism of the associational resistance. In order to discuss the effect of the aggregation process in the plant defence, let us consider some simplified situations. For example, one possible situation is the production of toxic chemicals against herbivores which visit plant individuals one by one and feed on them (*e.g.* grasshoppers or caterpillars). Because toxic chemicals will reduce the activity or survival probability of the feeding herbivores, the production of toxic chemicals will mitigate the herbivory pressure of neighbouring. If the toxic chemicals accumulate in the feeding herbivore and eventually result in the reduction of herbivores' survival probability, the aggregation process is categorized to AI. On the other hand, if the toxic chemicals do not accumulate in the herbivores but reduce their survival probability multiplicatively by each feeding event, the aggregation process will be sME. In these cases, we can predict that in both cases dimorphism of defensive chemical production can emerge. We can also consider other type of associational

defence in plants that is against herbivores reproducing on plant individual (*e.g.* aphids, spider mites or white flies). If the herbivores disperse to the neighbouring plant individuals after the reproduction, the individual defence will reduce the number of spreading herbivores. In this case, the number of herbivores on each plant will be a summation of remaining herbivores and dispersal from neighbours, the aggregation process of which will be categorized to AE, always resulting in monomorphism of defence.

In the analysis of the possibility of evolutionary and sustained polymorphism, I assume that the cooperative trait is determined genetically and that it evolves with small mutations. However, in the cooperation based on the flexible decision-making and behavioural action (*e.g.* group vigilance against enemy), individuals can change their cooperation level discontinuously at any time. In such a case, coexistence of multiple phenotypes can be realized by a mixed strategy with multiple tactics rather than phenotypic polymorphism; hence we cannot apply the presented analysis directly to such behavioural cooperation. However, by an adequate extension of the present analysis, the conditions for sustained polymorphism are applicable to behavioural polymorphism that is controlled by flexible decision-making by individuals (Appendix 2.C). Consequently, we can discuss behavioural cooperation based on the presented results. For example, in the group vigilance for natural enemy, individuals seem to aggregate the probabilities of finding enemies rather than the investment in the vigilance itself, which would correspond to the aggregation of effects. When every group member scans the same area, the probability of no one finding an enemy is the product of the probabilities that each individual fails to find it, which can be categorized to sME. On the other hand, when each individual scans a different area, the probability of finding an

enemy will be a summation of the probabilities of each finding an enemy, which coincides with AE. Therefore, we can predict that polymorphisms of vigilance level (Carter *et al.* 2009, Pangle and Holekamp 2010) will be observed only in the former case. However, we should consider carefully when we apply the present result to the behavioural polymorphisms. Generally speaking, behavioural polymorphism is realized not only by a mixed strategy that is evolutionarily stable, but also by condition-dependent alternative strategies. None of my "impossibility" results rejects the possibility of behavioural polymorphism realized by condition-dependent alternative strategies.

In the present analysis, the payoff function is simply formulated as reward minus cost, but another expression may be possible depending on the mechanism of considering cooperation. When we consider the situation that individuals use a common-pool resource cooperatively, consuming the resource of an individual increases its own payoff but reduces the common rewards. In such a case, an individual's cost will be a function of both own and other's investments while its reward will be a function of only its own investment, *e.g.* $f(z)-g(\Sigma z)$ (Killingback *et al.* 2010). Nevertheless by applying a translation $\hat{z} = -z$, $\hat{f}(\bullet) = -g(\bullet)$ and $\hat{g}(\bullet) = -f(\bullet)$, we can apply my results to such case, the result of which is consistent with the result of Killingback *et al.* (2010). A payoff can often be expressed as the product of reward and cost, (*e.g.* $f(\Sigma z)g(z)$ in Brännström and Dieckmann 2005), but we can simply map such cases to my framework by using the log translation of payoff (*e.g.* $\log[f(\Sigma z)] - \log[g(z)^{-1}]$).

Although I successfully revealed the importance of the aggregation processes on the evolution of polymorphic cooperation level, there are some open questions. In the present study, I categorized the aggregation processes according to the stage of

aggregation, *i.e.* the aggregation of investments or effects. However, it is also possible that individuals aggregate both their investments and effects. In reality, such an aggregation process can be considered, *e.g.* in the cooperation of yeast, they may share both enzyme and decomposed products rather than either of those. Such a multi-stage aggregation may alter the properties of the evolution of polymorphism. In addition, the studies about the aggregation process with focusing on specific empirical systems of the cooperation are also important for detecting the biological factors or parameters which determine the emergence of polymorphism.

Figures

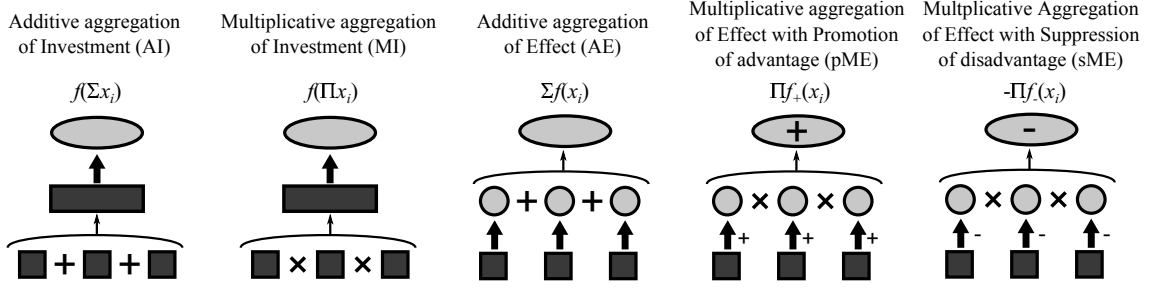


Figure 2.1

An image of the types of aggregation process of rewards obtained by considering the combination of three aspects. In the process of the cooperation, individuals' contributions are aggregated on the stage of investments (boxes) or effects (circles), which eventually yields individual reward F . The plus and multiplication signs indicate the aggregation is additive and multiplicative, respectively. The difference that the reward type is promotion of advantage (arrows with plus signs) or suppression of disadvantage (arrows with minus signs) also makes difference in the multiplicative aggregation of effect, but in other cases it yields no difference (see main text in Model). Therefore, AI, MI, and AE are represented without distinction of the difference.

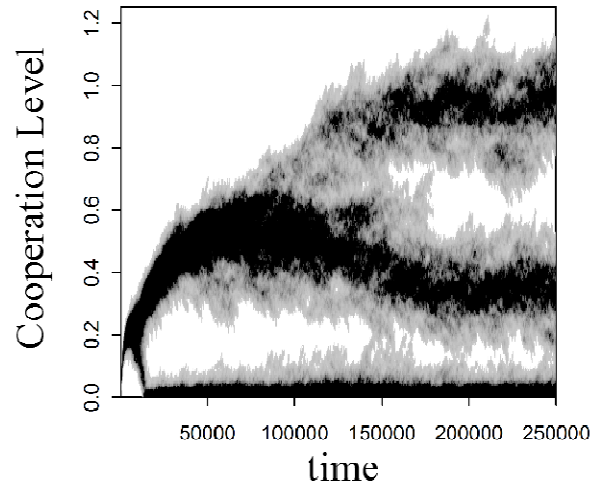


Figure 2.2

An example of individual-based simulation, resulting in evolution of polymorphism with more than two morphs. The darkness of the colour shows the density of the individuals with the cooperation level (vertical axis) in the population at the generation (horizontal axis). Under the aggregation type AI concave effect and cost functions, multiple evolutionary branchings are possible. In this case, three morphs with different cooperation levels emerge and coexist in the population evolutionarily. The detail of the simulation and the parameter values are shown in Appendix 2.B.

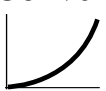
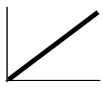
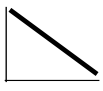
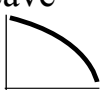
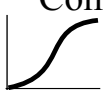
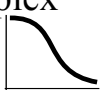
		<i>Functional shape of Cost</i>				
		Linear	Convex	Concave	Complex	
						
<i>Functional shape of Effect</i>	Linear	 	---	---	sME	sME
	Convex	 	---	---	sME	sME
	Concave	 	sME	sME	AI, MI, sME	AI, MI, sME
	Complex	 	sME	sME	AI, MI, sME	AI, MI, sME

Figure 2.3

Relationship between branching conditions of monomorphic singular solution and functional shapes of effect and cost. Rows and columns are the functional shapes of effect and cost, respectively.

Tables

Table 2.1

The possibilities of evolutionary and sustained polymorphism in each type of aggregation process from the analytical investigation (see Appendix 2.A).

Type of aggregation process		Possibility of evolutionary polymorphism	Possibility of sustained polymorphism
AI	$f(\Sigma z)$	Polymorphism	Polymorphism
MI	$f(\Pi z)$	Polymorphism	Polymorphism
AE	$\Sigma f(z)$	Monomorphism	Monomorphism
pME	$\Pi f_+(z)$	Monomorphism	Dimorphism
sME	$-\Pi f_-(z)$	Dimorphism	Dimorphism

3. Evolution of reaction in the negotiation game with behavioural error

3.1. Introduction

In studies of evolution, we should clearly denote strategies of organisms. In theoretical studies of cooperation, the amount of investment in cooperation has been considered as a strategy of organisms under which evolutionary mechanisms of cooperation have been successfully revealed (Smith and Price 1973, Doebeli *et al.* 2004, Chen *et al.* 2012). This assumption of strategy can be justified when the investment is genetically determined without any flexibility, *i.e.*, individuals cannot change their action in an interaction (McNamara *et al.* 1999).

On the other hand, an alternative situation may be also possible, where an individual flexibly determines its own investment for cooperation depending on the behaviour of interacting players. For example, if there is a time for communication among players before decision making, individuals could change their strategies following observation. Importantly, this system may effectively prevent increments of cheater and free-rider because an individual can immediately respond against an attitude of cheating (Axelrod 1984, Posch *et al.* 1999, McNamara *et al.* 1999). In this situation, a response rule to the behaviour of partner can be a strategy to evolve. In other words, the strategy can be a response function to partner's attitude, which is analogous to "reaction norm" in phenotypic plasticity.

Indeed, several studies empirically suggested existences of reactive decision making in cooperation. For example, some birds or animals form breeding pairs and take care of their offspring cooperatively. Some empirical studies reported that an individual often changes its own investment for the parental care depending on that of the partner (Wright and Cuthill 1990, Markman *et al.* 1995). In the group vigilance in gulls, an individual often monitors the vigilance behaviour of their neighbours, and

changes its own vigilance behaviour (Beauchamp 2009). In the cooperation of microbes, they share the chemical materials with their neighbours through the chemical diffusion process. Microbes generally control their production rate of enzyme depending on the concentration of chemical materials around them, some of which are produced by neighbours. As a consequence, each cell can indirectly obtain the information about the production rate of neighbouring cells and change their own production rate (Rueness *et al.* 2003, Hense *et al.* 2007, Czechowska *et al.* 2014). In plant species, anti-herbivore defence sometime involves a structure of cooperation, in which an integration of individual defences effectively reduces herbivory on them, so-called association resistance. It is often reported that a plant individual changes its phenotypic character responding to information from their neighbours through volatile substances released into the air (Karban *et al.* 2014), root exudates in soil (Semchenko *et al.* 2014) and chemical signals in hyphae of shared mycorrhizal fungi (Babikova *et al.* 2013). This suggests that plants can potentially determine their own defence level responding that of neighbours.

The evolution of reactive decision of cooperative behaviour has been theoretically investigated by extending frameworks of game theory (Maynard Smith and Price 1973, Maynard Smith 1982). One major approach is an iterated game, in which individuals repeatedly play the same game with same partner (Trivers 1971, Axelrod 1984). Each repetition is called round, in which individuals can change their action based on the information at the past rounds. Iteration of the discrete game has been well investigated, *e.g.*, iterated prisoner's dilemma game (Axelrod 1984) or iterated snowdrift game (Posch *et al.* 1999). These studies suggested that in the discrete game, evolution of the reaction based on the past round promotes establishment of more cooperative

interaction than evolution without reaction.

On the other hand, in continuous game, few studies theoretically investigated evolution of reaction by using two types of approaches. One is a continuous iterated prisoner's dilemma game (CIPD) proposed by Wahl and Nowak (1999a, b). In this model, each individual decide its own cooperation level as a function of its partner's cooperation level at previous round. By using this model, they showed that in CIPD, a cyclic evolutionary fluctuation of cooperation levels generally occurs. Therefore the cooperative interaction cannot be maintained stably under the existence of the reaction to cooperation level of partner (Wahl and Nowak 1999a, b). On the other hand, by modifying this model, some subsequent studies reported different conclusions. Killingback and Doebeli (2002) showed that when individuals react to the amount of obtained reward at the previous round rather than the partner's cooperation level, the high level of cooperation can evolve and remain in the population.

Another important approach for the evolution of reaction in continuous game is a negotiation game (McNamara, 1999). This approach assumes that individuals reciprocally observe the actions of their partners before they carry out the cooperation. It should be remarked that individuals obtain payoff of the game only once at the end of interaction in the negotiation game, but in each round in CIPD. Because of this difference, the analysis of evolutionary dynamics is relatively easier in the negotiation game than in CIPD. It should be noted that if the number of rounds of CIPD is large enough to neglect effects of earlier rounds before interaction reach to stable state, it approximately identical to the negotiation game (Andre and Day 2007). Under the negotiation game, Taylor and Day (2004) have shown that the reaction to action of partners promotes the evolution of higher cooperation level depending on the initial

state.

Despite of those attempts of simplifications, both continuous iteration and negotiation games generally result in a difficulty for analysis. In any cases, many (substantially infinite number of) forms of reaction norms can be evolutionarily stable simultaneously. According to this property, it is difficult to reveal detailed properties of evolution of reaction in continuous cooperation game (McNamara, 1999, Wahl and Nowak 1999ab, Taylor and Day 2004). Some previous studies tried to overcome this difficulty. For example, Taylor and Day (2004) investigated the evolutionary dynamics of reaction using individual based simulation, and showed that the evolutionary realized reaction represented some variation within the population. Andre and Day (2007) focused on a small population, in which a frequency of interaction between mutants is not negligible. In such a case, the optimal strategy can be a “perfect mirroring” that is an strategy imitating a cooperation level of the partner. These studies revealed evolution of reaction under restricted conditions.

In this chapter, I try to reveal evolutionary process of cooperation with reaction, focusing on the continuous negotiation game. The key factor of my study is a behavioural error. I found that in the presence of errors, a finite (not infinite) number of reaction norms can be evolutionarily stable, by which properties of the system become more transparent. The assumption of error may be sufficiently realistic because a realized behaviour of individual could be altered from its original decision by various factors, including noise in its expression processes.

In the present study, I assume that the reaction norm can be represented by a linear function of cooperation level of the partner. By using adaptive dynamics theory, I analysed the evolutionary dynamics of such linear reaction norm and investigated

factors that influence the evolution of reaction norm in the negotiation game. According to the analysis, I found that the curvature of benefit function is an important factor for the evolution of reaction. When the shape of benefit function is convex (or concave), the slope of the evolved reaction function becomes positive (or negative). Moreover, the realized cooperation level in the negotiation game can be either higher or lower than a game without negotiation depending on the curvature. This indicated that negotiation between players does not always promote cooperation evolutionarily.

3.2. *Model*

3.2.1. Basic Framework

In order to investigate evolution of decision making in response to attitudes of other players, I extend a previous two-player negotiation game (McNamara 1999). It is assumed that two individuals are randomly chosen from an infinite size of population and cooperatively interact. The process of cooperation consists of two stages, a negotiation stage and an action stage. In the negotiation stage, two players reciprocally observe an attitude of cooperation level of its partner and change its own cooperation level, a process of which is repeated until they reach an agreement. It should be noted that a cooperative action is not carried out in this stage, but is held in the subsequent action stage based on the agreement, resulting in some returns, *i.e.*, payoff.

Here, the negotiation stage is described in more detail. It is assumed that individuals linearly response to the observed cooperation level of the partner, by which the response strategy can be represented by a linear function with two values, *i.e.* the slope and the interception. Hereafter, I call this linear function as “reaction line” that are referred a set of the slope b and the interception c as (b, c) . The range of these trait values are assumed as $-1 < b < 1$ and $0 \leq c$, respectively. It should be noticed that both b

and c are individual strategies that eventually determine an individual investment for cooperation.

Consider two individuals, X and Y, whose reaction lines are represented by (b_x, c_x) and (b_y, c_y) , respectively. Two individuals observe the attitude of cooperation level each other and change their own attitude. The attitude of cooperation levels of X and Y at the i -th negotiation step are denoted by x_i and y_i , respectively. After a single negotiation step, their attitude of cooperation level change to x_{i+1} and y_{i+1} by following their own reaction functions as

$$x_{i+1} = b_x y_i + c_x + \epsilon_x, \quad (3.1a)$$

$$y_{i+1} = b_y x_i + c_y + \epsilon_y, \quad (3.1b)$$

where ϵ_x and ϵ_y are behavioural errors of X and Y that follow a normal distribution with a mean zero and a variance σ^2 . Importantly, the error is assumed a property that is constant over negotiation process over the negotiation stage of each match. After sufficient number of negotiation, the attitude of cooperation level of X and Y reach to an agreement (x, y) . The agreement is an intersection of two reaction lines Eqs.(3.1a) and (3.1b), which is a solution of simultaneous equation,

$$x = b_x y + c_x + \epsilon_x, \quad (3.2a)$$

$$y = b_y x + c_y + \epsilon_y. \quad (3.2b)$$

By solving this, we can obtain the cooperation levels at the agreement point as

$$x = \frac{1}{1 - b_x b_y} [b_x c_y + c_x + \epsilon_x + b_x \epsilon_y], \quad (3.3a)$$

$$y = \frac{1}{1 - b_x b_y} [b_y c_x + c_y + \epsilon_y + b_y \epsilon_x]. \quad (3.3b)$$

When the population is monomorphic and all individuals have an identical reaction function (*i.e.*, $(b_x, c_x) = (b_y, c_y) = (b, c)$), the mean cooperation level is $c/(1-b)$ for anyone. It should be noticed that the cooperation levels can potentially be negative depending on the values of behavioural error (*i.e.*, ϵ_x and ϵ_y), although the mean cooperation level becomes always zero or positive.

After the negotiation stage, players move to the action stage that determines a payoff of the game. Following the agreement, they invest the agreed level of investment for cooperation in this stage, and eventually receive some payoff. When two players invest x and y , respectively, the payoff of individual X is formulated as

$$W(x, y) = f(x + y) - g(x), \quad (3.4)$$

where f and g are functions that determine benefit and cost for the player, respectively. In the present study, I assume that both f and g are quadratic functions, which are represented as

$$f(x + y) = p_f \left(\frac{x + y}{2} \right)^2 + (1 - p_f) \left(\frac{x + y}{2} \right), \quad (3.5a)$$

$$g(x) = s[p_g x^2 + (1 - p_g)x]. \quad (3.5b)$$

In those equations, s determines the magnitude of cost relative to the benefit. Parameters p_f and p_g control the curvatures of benefit and cost functions, respectively. When this is negative (or positive), the function becomes concave (or convex) shape (Figure 3.1). Note that the functions with negative p_f or p_g have a part where more investment reduces the benefit or cost of cooperation (see Figure 3.1), which is not a realistic situation. However, in the result of the numerical analysis, the mean cooperation in the population never reach to such unrealistic part on the evolutionary process except for cases that the cooperation level in the population diverge to infinitely large level (see

result section in detail).

Accordingly, two individuals obtain the payoff of a single interaction represented in Eqs. (3.4). I consider that an individual interacts multiply with many individuals that are randomly chosen from the population. Thus, it should be remarked that an individual fitness should be considered as an average payoff for multiple interactions.

3.2.2. Evolutionary dynamics of cooperation with negotiation

I analysed the evolutionary dynamics of reaction line using adaptive dynamics theory (Dieckmann and Law 1996, Geritz *et al.* 1998, Doebeli *et al.* 2004). This approach focuses on an invasion process of rare mutant strain into a population comprising resident strain. In addition, it is also assumed that a focal trait is coded by quantitative gene, by which it evolves gradually. A detail of this approach was described in the model section in chapter 2.

In order to apply the adaptive dynamics theory, we have to formulate a fitness of a rare mutant in the resident population. Consider an invasion of a rare mutant with reaction line (b', c') into a monomorphic resident population with reaction line (b, c) . By considering an average payoff for multiple matches, the fitness of the mutant can be formulated by

$$H(b', c' | b, c) = W \left(\frac{b'c + c'}{1 - bb'}, \frac{bc' + c}{1 - bb'} \right) + \frac{\sigma^2}{4(1 - bb')^2} \left(p_f [(1 + b')^2 + (1 + b)^2] - 4sp_g [2b' + (1 + b)^2] \right) \quad (3.6)$$

(see Appendix 3.A). It is remarkable that the second term on the right-hand side in Eq.(3.6) involves a variance of behavioural error, σ^2 . Without the error (*i.e.* $\sigma^2 = 0$), this term disappears.

We assume that both a slope b and an intercept c of reaction line are quantitative genetic traits. If the reaction line of a rare mutant (b', c') is sufficiently close to that of resident individuals (b, c), the evolutionary rate of b and c can be represented as

$$\frac{db}{dt} = \beta_b(b, c) \frac{\partial H(b', c' | b, c)}{\partial b'} \bigg|_{\substack{b'=b \\ c'=c}}, \quad (3.7a)$$

$$\frac{dc}{dt} = \beta_c(b, c) \frac{\partial H(b', c' | b, c)}{\partial c'} \bigg|_{\substack{b'=b \\ c'=c}}, \quad (3.7b)$$

where $\beta_b(b, c)$ and $\beta_c(b, c)$ are a positive coefficient determining the rate of evolutionary change of b and c , respectively (Dieckmann and Law 1996). Those coefficients are generally functions of resident strategy b and c , although we can ignore those effects because we focus on $\partial H/\partial b'$ and $\partial H/\partial c'$ of Eqs.(3.7a,b) in the analysis. The evolution stops when $\partial H/\partial b'$ and $\partial H/\partial c'$ of Eqs.(3.7a,b) become zero at a certain set of b and c , which are represented by b^* and c^* , respectively. The set (b^*, c^*) is called “evolutionarily singular coalition” (Geritz *et al.* 1998). The evolutionary singular reaction line can be represented by using (b^*, c^*) as $x = b^*y + c^* + \epsilon_x$. Consequently, it is evolutionarily realized that an agreement of the negotiation between two players are intersection of two lines, $x=b^*y+c^*+\epsilon_x$ and $y=b^*x+c^*+\epsilon_y$. According to the analysis in Appendix 3.A, b^* and c^* simultaneously satisfy

$$\sigma^2 \left[\frac{p_f}{2} (1+b^*)^3 - 4b^*sp_g \right] = 0 \quad \text{and} \quad (3.8a)$$

$$c^* = \frac{-(1-b^{*2})(1-p_f) + 2(1-b^*)s(1-p_g)}{2(1+b^*)p_f - 4sp_g}. \quad (3.8b)$$

When $\sigma^2 = 0$, Eq. (3.8b) is an only condition because Eq. (3.8a) becomes trivial. In this case, any x values within a certain range can be singular solutions with corresponding reaction lines. This implies that infinite numbers of combination of b and c can be

singular sets. This is the reason for the appearance of infinite numbers of singular solutions in previous studies (McNamara et al. 1999, Taylor and Day 2004), resulting in difficulties of analysis. On the other hand, when $\sigma^2 > 0$, Eq. (3.8a) restricts the value of b at the singular solution, by which the number of solution becomes finite. Interestingly, the magnitude of σ^2 does not influence evolutionary singular solution itself because σ^2 is no more than a multiplier in Eq. (3.8).

Next, I examine two types of stabilities of the evolutionary singular strategy *i.e.*, convergence stability (CS) and evolutionary stability (ES) (see model section in Chapter 2 in more detail). According to Appendix 3.A, the condition for CS is

$$\frac{1}{4} [p_f(1+b^*) - 4sp_g] [3p_f(1+b^*)^2 - 8sp_g] > 0 \quad \text{and} \quad (3.9a)$$

$$\begin{aligned} & \frac{1-b^*}{1+b^{*2}} \left[\left(\frac{c^*}{1-b^*} \right)^2 + \frac{\beta_c(b^*, c^*)}{\beta_b(b^*, c^*)} \right] [p_f(1+b^*) - 4sp_g] + \frac{\sigma^2}{(1-b^{*2})^2} [3p_f(1+b^*)^2 - 8sp_g] \\ & < - \left(\frac{c^*}{1-b^*} \right) \left(2p_f \frac{c^*}{1-b^*} + (1-p_f) \right) \end{aligned} \quad (3.9b)$$

and that for ES is

$$p_f(1+b^*) - 4sp_g < 0. \quad (3.10)$$

Those conditions indicate that the magnitude of the behavioural error σ^2 influence the condition of CS (Eq.(3.9)), but not that of ES (Eq.(3.10)). The singular solution is more likely to be CS with an increasing behavioural error when it satisfies ES condition, but less likely when it is not ES (Appendix 3.A).

Based on the analytical approach, parameter dependence of evolutionary process can be analysed to some degree (Appendix 3.A). However, such an analysis is restrictive and difficult to represent exact consequences of evolution. For example,

when the system has multiple solutions that satisfy both ES and CS conditions, evolutionary dynamics ultimately reach either depending on the initial condition. In addition to this, it cannot provide sufficient information about oscillatory solution and divergence to infinity of the trait value. Therefore, I also analysed the evolutionary dynamics by using numerical method. In the numerical approach, I assumed that all resident individuals in a population initially have a reaction line (0, 0). I calculated changes of b and c at each moment by using Eqs. (3.7a,b), and pursuit evolutionary trajectory of those traits in order to detect the evolutionary consequence. It is remarkable that the results well correspond to those of supplemental analysis using analytical method (Appendix 3.B).

3.2.3. Evolutionary dynamics of cooperation without negotiation

In order to examine effects of negotiation on the evolution of cooperation, I also clarify evolutionary process of cooperation without negotiation, in which individuals cannot behaviourally respond to actions of partners. The evolution of cooperation without negotiation can be represented with a modification of the above formulations by fixing a slope of the reaction line (b) at zero, in which only intercept of the line (c) can evolves as a cooperation level itself. Using Eq. (3.6), the fitness of a mutant with (0, c') in a resident population with (0, c) can be written as

$$H(0, c' | 0, c) = W(c', c) + \frac{\sigma^2}{4} (2p_f - 4sp_g) \quad (3.11)$$

When $\sigma^2 = 0$, this model becomes same with the continuous snowdrift game (Doebeli *et al.* 2004). The evolutionary rate of c can be written as

$$\frac{dc}{dt} = \beta_c(0, c) \left. \frac{\partial H(0, c' | 0, c)}{\partial c'} \right|_{c'=c} \quad (3.12)$$

According to the analysis in Appendix 3.C, an evolutionary singular solution of c is

$$c^* = \frac{-(1-p_f) + 2s(1-p_g)}{2p_f - 4sp_g}, \quad (3.13)$$

and its CS and ES conditions are

$$p_f < 2sp_g, \quad (3.14)$$

$$p_f < 4sp_g, \quad (3.15)$$

respectively. Since Eqs.(3.13), (3.14) and (3.15) do not include σ^2 , the behavioural error never influences the evolution of cooperation in the absence of the negotiation. I can also analytically investigate the final state of evolution from an initial state $c = 0$ (see Appendix 3.C).

3.3. Results

Using both analytical and numerical approaches, I examined the finally realized reaction line that evolves from an initial state with $(b, c) = (0, 0)$ in the cooperation with negotiation. Figure 3.2 is the density plots of the mean cooperation level with changing the curvatures of benefit and cost functions (p_f and p_g). The results with and without negotiation are represented Fig.3.2a and 3.2b, respectively. In black regions in the panels, the cooperation level eventually evolves toward an infinitely large level. On the other hand, the grey and white colour shows the regions where the cooperation level evolutionally reaches to a stable state with positive value and zero, respectively. The benefit and cost functions have a decreasing part when p_f and p_g are negative, but numerically investigation showed that the reaction only within the part where both of them are increasing shape in white and grey regions.

Figure 3.2 indicates that the evolutionary branching of cooperation level occurs in

the absence of the negotiation (dotted region in Figure 3.2b), but not occurs in the presence of the negotiation. This tendency can be also confirmed by analytical approach. According to Appendix 3.A, in the presence of negotiation, evolutionary branching is possible only when more investment in cooperation by its partner decrease the benefit of the cooperation, which is unrealistic situation. Figure 3.2 also shows that the slope and intercept of the reaction line can continuously fluctuates without reaching a steady state in the presence of negotiation, which results in evolutionary oscillation of the cooperation level (in the hatched region in Figure 3.2a) as illustrated in Figure 3.3. Such evolutionary oscillation of the cooperation level never occurs in the absence of negotiation.

Next, I compared the magnitude of mean cooperation levels in the population with and without negotiation. Figure 3.4 shows differences of mean level of achieved cooperation between evolution with and without the negotiation. The white and black regions indicate parameter combinations that the negotiation promote and suppress the cooperation level, respectively, whereas the negotiation does not influence the cooperation level in the grey region. According to this figure, with $0 < p_f$, the negotiation indicates either promotional or neutral effect on evolution of cooperation level. On the other hand, with $p_f < 0$ and $p_f < p_g$, the negotiation indicates suppressive effect. This pattern is independent of a relative weight of cost to benefit s and a magnitude of error σ^2 .

The curvature of the benefit function p_f also influences a sign of slope of reaction line that are evolutionary realized. Figure 3.5 shows that when the reaction line reaches to a stable state (*i.e.*, neither fluctuate of (b, c) nor diverge to infinity), the slope is positive (white region in Figure 3.2a) with a convex benefit function ($p_f > 0$), but

negative (grey region in Figure 3.2a) with a concave benefit function ($p_f < 0$). This pattern of the slope is also independent of a relative weight of cost to benefit s and a magnitude of error σ^2 .

Although the analytical investigation shows that the magnitude of behavioural error σ^2 does not influence the singular solution itself, the condition of CS depends on the σ^2 . Therefore, the magnitude of error influence on the evolutionary realized state from a same initial condition. Indeed, when the magnitude of error is large, the parameter region with such oscillations tends to be narrower (Figure 3.6), which is also supported by an analytical approach (Appendix 3.A). The larger errors also suppress evolution of infinitely large cooperation level in $p_g < p_f < 0$ through facilitating a conversion of cooperation level toward zero.

3.4. Discussion

Decision processes of actions of players can significantly influence evolution of cooperation (McNamara 2003). In the discrete cooperation games, evolution of reaction was studied by considering a competition between reactive and non-reactive strategies, which suggested that evolution of reactions increased a realized cooperation (Axelrod 1984, Posch *et al.* 1999, well reviewed by Doebeli and Hauert 2005). On the other hand, in the continuous game, reaction modes were considered to evolve gradually. Its evolutionary process has been studied by using continuous iterated game and negotiation game, although those attempts have failed to reveal general evolutionary properties due to emergences of infinite numbers of singular solutions (McNamara 1999, Taylor and Day 2004). In the present study, I studied effects of behavioural error on evolutionary process of reaction, and successfully showed that it contributes to resolve the difficulty of analysis, which enable us to investigate general evolutionary properties.

The error is a key factor to understand the evolutionary process of reaction in cooperative interaction.

Previous studies focusing on the discrete cooperation games suggested that the reaction promotes the cooperation (Axelrod 1984, Posch *et al.* 1999, well reviewed by Doebeli and Hauert 2005). In contrast, the present analysis indicates that reaction does not always promote evolution of cooperation in the continuous cooperation game, *i.e.*, promotional effect is possible only when the functional shape of benefit is convex. Because the discrete and continuous games consider different situations of the cooperation, it seems difficult to simply compare the results of them. One remarkable difference between them is the considering evolutionary process of the reaction strategies. The discrete games consider a winning strategy of the competition among multiple reaction strategies, in which completely different strategies are directly matched each other. On the other hand, the continuous games including the present study consider the reachable stable strategy in the result of the evolution with gradual change of the strategy, in which the strategy of invading mutants is only slightly different from the residents' ones. Such difference of the considering evolutionary situation might cause the inconsistent results about the influence of the reaction on the cooperation.

In continuous negotiation game, Andre and Day (2007) focused on effect of population size on evolution of reaction function, and showed that the perfect mirroring (*i.e.* positive reaction) is generally an evolutionary stable strategy in a small population, regardless of the functional form of the benefit. This is inconsistent to the result in the present study that the reaction can be either positive or negative function of the opponent's attitude depending on the curvature of the benefit function. This

inconsistency is caused from the difference of the property of selective force caused by each factor. In a small population, a frequency of interaction between mutants is not negligible, where the fitness of an individual is influenced by the payoff of interaction with same reaction strategy to its own one. In such case, more cooperative reaction against itself is always selected, which results in the evolution of positive reaction. On the other hand, the behavioural error cause the variation of the total investment in cooperation at the agreed point, which can either increase or decrease the payoff depending on the curvature of the benefit function. Because the positive and negative reaction can increase and decrease the variation of the total investment, respectively, the either positive or negative reaction function can be potentially realized depending on the curvature of benefit function in the present study.

In the result of the numerical approach, the cyclic evolutionary oscillation of the reaction strategy can occur (Figure 3.3), but its occurrence is suppressed under the large behavioural error (Figure 3.6). This pattern is related to a fact that the behavioural error makes the number of singular solutions finite. Under the absence of the behavioural error, the infinite number of reaction strategies is evolutionary stable in the negotiation game, while only some points of them becomes evolutionary stable under the presence of error. Therefore, when the magnitude of error is large, the selective force caused by behavioural error drive the reaction strategy of a population to such stable states. However, when the magnitude of error is small, the situation becomes intermediate between that under the absence of behavioural error and large behavioural error, *i.e.*, only some finite number of strategies are evolutionary stable but the selective force is too small to reach such stable state, which results in the cyclic oscillation of the reaction strategy.

The evolutionary fluctuation of the cooperation level is also reported by Wahl and Nowak (1999ab), but the mechanism of the evolutionary fluctuation is different from the present study. Wahl and Nowak (1999ab) assumed invasions of a mutant whose reaction strategy is randomly selected rather than the slightly different one from the resident population. Hence, a cooperative population can be also exposed by the invasion of fully cheating mutant, which causes the fluctuation of the cooperation level.

According to the present study, the reaction function can be either increasing or decreasing function depending on a curvature of benefit function. The reaction can be an increasing function when the benefit function has convex shape, under which evolutionarily realized cooperative investment tends to be zero or diverge to infinity (see Figure 3.5). Importantly, in such a case, we cannot detect an individual reaction substantially because the investment is constantly zero or infinity. On the other hand, the reaction can be a decreasing function when the benefit function is concave, under which an intermediate level of cooperative investment (see Figure 3.5). In this case, the individual reaction is detectable. Accordingly, it can be predicted that if a negotiation is observed in an organism, the reaction function would be decreasing function. Indeed, a lot of empirical examples of negotiation reported the negative reaction with decreasing function (Wright and Cuthill 1990, Markman *et al.* 1995, Beuchamp 2009).

Although the convex benefit function is unlikely to result in a meaningful reaction, there is an exception. When the benefit function is convex weakly ($p_f < 1$ in Fig.3.5), the benefit function can be an increasing function, which accompanied by an increasing reaction function. This trend might correspond with cooperation of microbes. In this system, the enzyme production can accelerate efficiency of activity of enzyme through biofilm formation (Hense *et al.* 2007), by which the benefit function could be convex,

resulting in an increasing reaction function. Indeed, in interactions of microbes, an individual enzyme production tends to increase with an increasing amount total enzyme (Rueness *et al.* 2003, Hense *et al.* 2007, Czechowska *et al.* 2014), indicating positive interaction.

It is notable that a negotiation process can represent a specific pattern depending on the reaction function. In the positive response with an increasing function, both players initially represent a low level of investment, and then they repeatedly increase their investment toward the agreement point. On the other hand, in the negative response with a decreasing function, one player initially represents a high level of investment, and other player subsequently represents a low level of investment. In the negotiation, the former gradually reduces its own investment, whereas the latter increases it. Since the mode of response depends on curvature of benefit function, we may be able to predict the property of benefit function if the negotiation process can be observed in cooperation of organism.

The present analysis shows that the reaction strategy is generally difficult to diverge, following evolutionary branching in the continuous negotiation game. This implies that genetic polymorphism is unlikely to occur in cooperative traits with reaction. In other words, it can be predicted that organisms with polymorphism in the cooperation level tends to lack an ability of reactively determining its cooperative interaction. This prediction might be supported by a fact that the genetic polymorphism in the cooperation level is mainly observed in plants and microbes (Agrawal *et al.* 2002, Hare and Elle 2002, Greig and Travisano 2004).

It should be remarked that cooperation with negotiation might be possible in plants. It has been known that anti-herbivore defences in plants can involve a structure of

cooperative interaction as an associational defence. It has been recently revealed that plant individual can detect chemical signals from neighbouring individual (Karban *et al.* 2014, Semchenko *et al.* 2014, Babikova *et al.* 2013). Accordingly, the chemical communication may result in negotiation game within the plant population for investments to production of defensive traits. We should investigate communication among plant individuals, considering a possibility of existence of negotiation in cooperation.

Figures

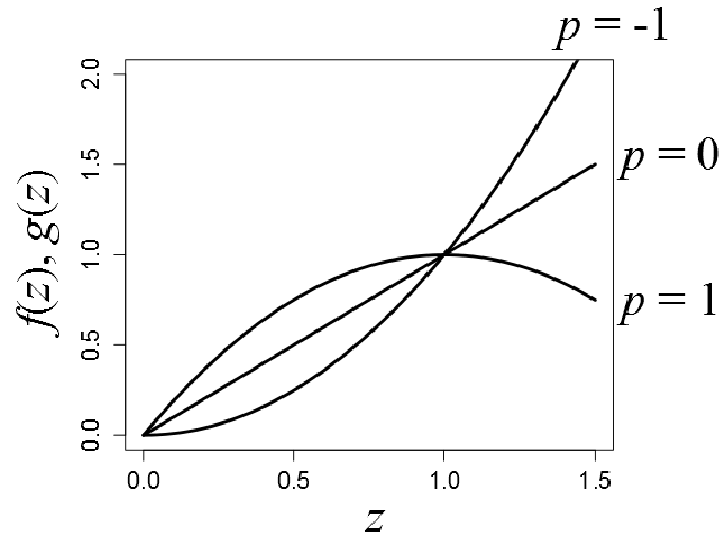


Figure 3.1

Influence of the parameter p_f and p_g on the curvature of the benefit and cost function, respectively. When p_f and p_g is positive (negative), benefit and cost function becomes convex (concave) shape, respectively

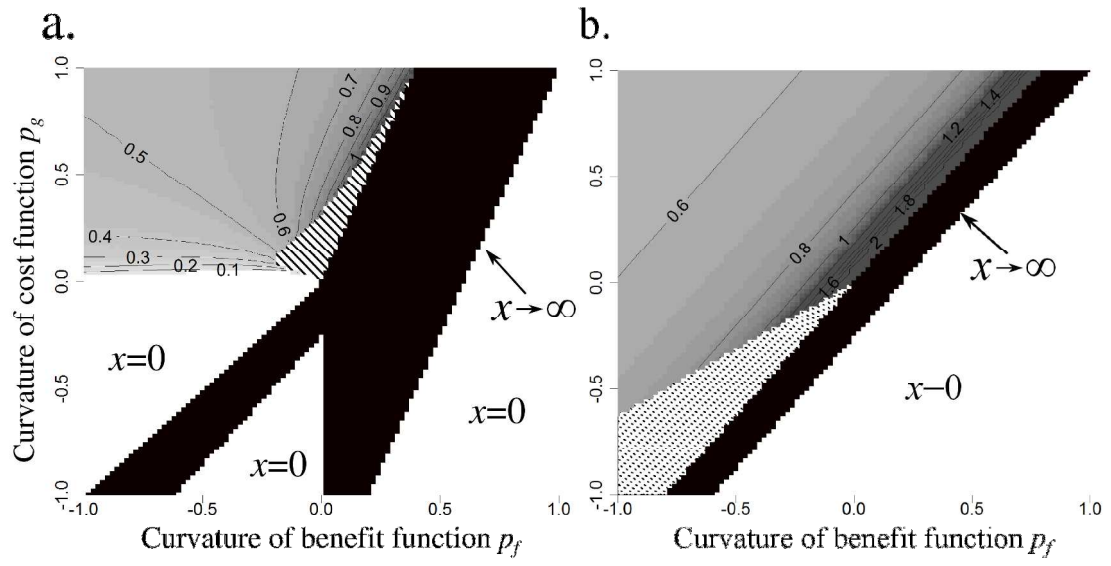


Figure 3.2

The density plot of the mean cooperation level in the cooperation with negotiation (panel a) and without negotiation (panel b). The horizontal and vertical axes show the curvature of the benefit and cost functions (*i.e.*, p_f and p_g). The colour depth shows the evolutionary realized cooperation level. In the black, cooperation level diverges to infinity in the result of the negotiation. In the dotted region, evolutionary branching occurs and the cooperation level in the population becomes dimorphic. In the hatched region, the cooperation levels evolutionary fluctuate. The parameter values are $s = 10^{-0.4}$, $\sigma = 0.1$.

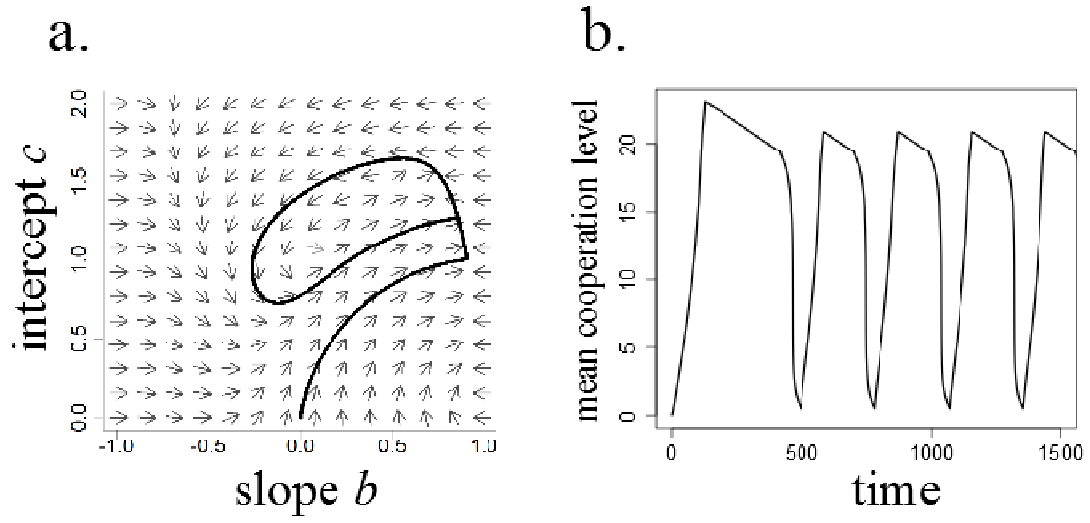


Figure 3.3

An example of the oscillation of the cooperation level. On the evolution, trait pair (b, c) show limit-cycle trajectory (panel a), in the result of which the mean cooperation level in the population fluctuated in the evolutionary time scale (panel b). The parameter values are $p_f = 0.4$, $p_g = 0.52$, $s = 10^{-0.4}$, $\sigma = 0.5$.

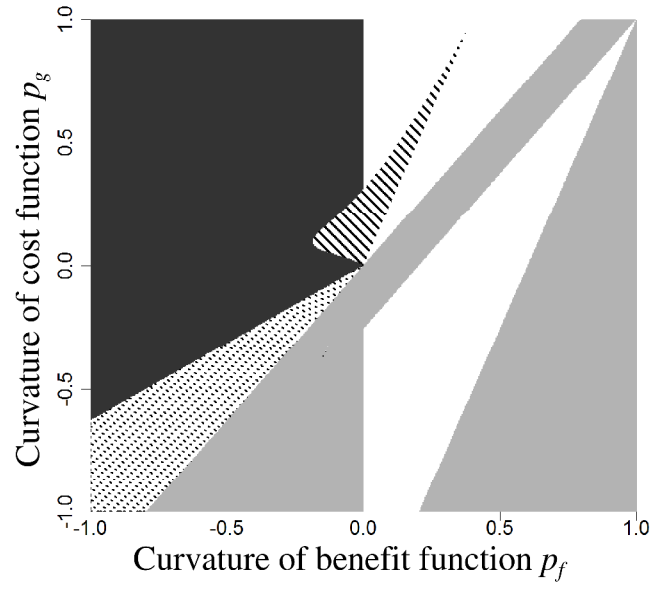


Figure 3.4

The magnitude correlation of the mean cooperation level in the cooperation with and without negotiation. The black and white regions show the mean cooperation level in the cooperation with negotiation is higher and lower than that without negotiation, respectively. In the grey region, the mean cooperation level becomes equal between them. The meaning of the dotted and hatched region and the parameter values are same with Figure 3.2.

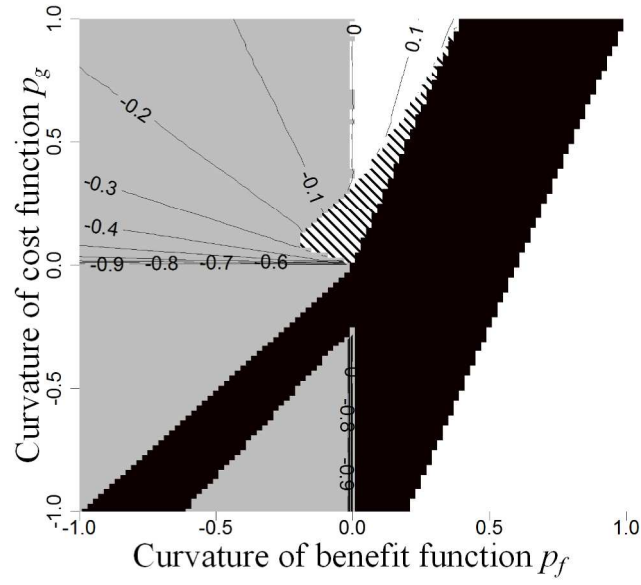


Figure 3.5

The magnitude of the slope of the reaction line. The horizontal and vertical axes show the curvature of the benefit and cost functions (*i.e.*, p_f and p_g). The slope of the reaction becomes negative in the grey region, while that becomes positive in the white region. The meaning of the black and hatched region and the parameter values are same with Figure 3.2.

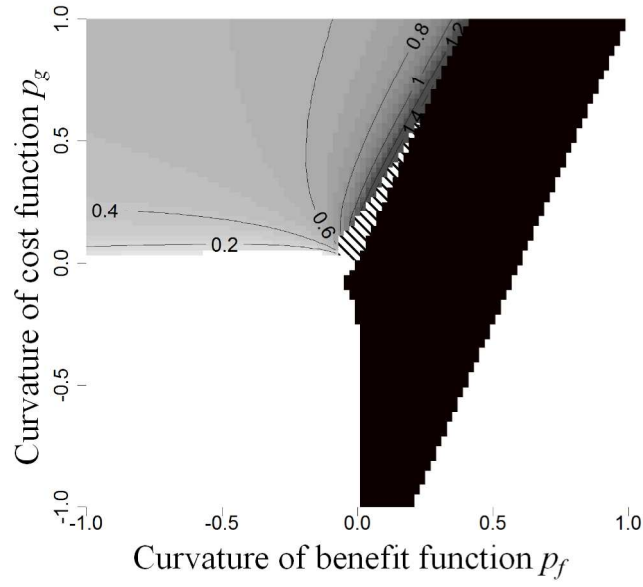


Figure 3.6

The mean cooperation level in the cooperation with negotiation under large behavioural error. The meaning of axes and colours are same with Figure 3.2. The parameter values are $s = 10^{-0.4}$, $\sigma = 1.0$.

4 General Discussion

In the present thesis, I investigated two topics in two classes of evolution of intraspecific cooperation. The first class is evolution of cooperation level itself, a study topic of which is a condition of emergence of polymorphism in cooperation level. In this topic, I showed that an aggregation process of contribution of interacting individuals in a production of reward is an important factor in emergence of polymorphism in the cooperation level. The second class is evolution of reaction to interacting partner, a study topic of which is how behavioural error affects the outcome of negotiation game. In this topic, I analytically showed that the existence of the behavioural error make the number of the singular solution finite, which enable us to investigate the evolutionary dynamics of the reaction easily. In the result, I showed that the curvature of the functional shape of benefit determine the slope of the reaction. These studies provide information that are lacked in previous studies, and develop understanding about the cooperative interactions.

The focused factors in the present thesis can be effective in various organisms. For example, it is important that associational defence in plant species can be regarded as one form of cooperative interaction. In such systems, polymorphism of defensive trait has been reported in some species (Agrawal *et al.* 2002, Løe *et al.* 2007, Wise *et al.* 2009, Archetti and Scheuring 2012), and negotiation in investment for defence might be possible between individuals via exchanges of chemical signals (Babikova *et al.* 2013, Karban *et al.* 2014, Semchenko *et al.* 2014). This suggests that interaction among plant individuals can be understood deeply from a viewpoint of cooperation games. Similarly, in microorganisms, diffusion of chemical materials often results in the share of beneficial effects, which can be also regard as cooperation. Therefore, it will be an useful way to consider empirical systems reporting polymorphism of producing ability

of chemicals (Greig and Travisano 2004) or the reactional behaviour to the density of chemicals in microorganisms based on the results of present thesis.

In this thesis, I focused on a framework of continuous snowdrift game, in which individual effort cooperation positively influences its own success. Its analysis successfully extended understanding of evolution of cooperation on the framework. On the other hand, there is also another type of framework of continuous game, *i.e.*, continuous prisoner dilemma game, in which an individual effort is assumed not to affect its own success. A difference between two frameworks may seem trivial, although cooperation is very difficult to evolve in the prisoner dilemma. On such a framework, evolutionary processes have been understood only restrictedly, where many issues remain to be solved for future studies.

In theoretical studies of the interaction, it is known that various factors can influence of its evolution. One such a factor is a kin selection that is effective in interactions among relatives, the process of which also relates to a spatial structure of population. For example, plants are immobile and its genetic diffusion relies on pollen and seed dispersals only, their genetic distribution is likely to be a cluster structure in some case (Loveless and Hamrick 1984, Kudoh and Whigham 1997, Chung and Epperson 1999). In this case, individuals tend to interact with their genetic relative, by which kin selection can work effectively to promote evolution of cooperative interaction. This could be an important mechanism for evolution of associational defence in plant species. In this thesis, the presented analysis ignored such factors, although it should be combined with them in the future to achieve further understanding of interaction in plants.

Because a cooperation reward is often influenced by the ecological properties of

other species, interspecific interaction is also an important factor for considering the evolution of cooperation. For example, since defensive traits of plants are generally their anti-herbivore strategies, we should take the herbivore responses into account to understand whole interactions, *e.g.* change of population density or acquisition of resistance to the defence. Similarly, some vertebrates often form a group for cooperative group vigilance to detect predators, in which evolution of group vigilance is influenced by behavioural response or population dynamics of predators. Those responses of interacting species could dynamically alter a cooperative reward, which may modify the evolutionary process of cooperation. This is also an important point of view to understand species interaction in ecological community, which can be a subject of the future study.

In the present thesis, I revealed the importance of the aggregation process of contributions for providing rewards and the negotiation process in the cooperation. However, these aspects have been paid less attentions in most previous empirical researches and few studies reported empirical information about them. In order to test and apply my prediction to specific systems, more empirical works focusing on these aspects are needed. Considering extended models focusing on specific systems is effective approach for connecting information from present study to empirical researches (West *et al.* 2007). Such integration between the theoretical and empirical works will enable us to understand more deeply about the evolution of cooperation.

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Appendix

Appendix 2.A: Analysis of evolutionary dynamics for five types of aggregation processes

2.A1. Inequality on the group members' contributions

In the present study, I consider five types of aggregation processes from three aspects, *i.e.* (i) additive or multiplicative aggregation, (ii) aggregation of investments or effects, and (iii) promotion of advantage or suppression of disadvantage (Figure 2.1). Moreover, I also examine the influence of the inequality on the group members' contributions. In the expressions above, I assume that all group members equally contribute to the reward of a focal individual. However, this assumption may be violated in reality. Typically, it is possible that an individual investment either more or less influences its own reward than those from other members. We can include such a bias by weighting the contribution from the other individuals by a parameter a . Accordingly, the payoff of i -th individual can be represented by $f(z_i + \sum_{j \neq i} az_j)$ in additive aggregation of investments, $f(z_i) + \sum_{j \neq i} af(z_j)$ in additive aggregation of effects, $f(z_i \prod_{j \neq i} z_j^a)$ in multiplicative investments and $f(z_i) \prod_{j \neq i} f(z_j)^a$ in multiplicative effects.

In the following analysis, I use the model considering such unequal contribution. I will show that those modifications do not alter the general results of my analysis presented in the main text.

2.A2. Additive aggregation of investments

In additive aggregation of investments (AI) type, the mean payoff of a mutant with trait value y in the resident monomorphic population with trait value x can be

represented by

$$W(y|x) = f(a(N-1)x + y) - g(y), \quad (2.A1)$$

where a is the weight of the contribution by other members. When we set $\alpha = 1$, Eq. (2.A1) becomes the same expression with Eq. (2.11). A singular solution is obtained by solving

$$f'([a(N-1)+1]x^*) = g'(x^*). \quad (2.A2)$$

and the condition for branching is

$$[a(N-1)+1]f''([a(N-1)+1]x^*) < g''(x^*) < f''([a(N-1)+1]x^*). \quad (2.A3)$$

When we set $\alpha = 1$, Eq. (2.A3) becomes the same expression with Eq. (2.12). Since $a(N-1)+1 > 1$, this condition can be satisfied only if $f''([a(N-1)+1]x^*) < 0$ and $g''(x^*) < 0$, which is a necessary condition for branching in a monomorphic population. Therefore, evolutionary branching can occur only when *both* effect *and* cost functions have a decelerating shape at the singular solution.

We can examine feasibilities and stabilities of singular coalitions of dimorphism and polymorphism with more than two morphs as shown in the main text. Although these conditions are hardly solved explicitly, we cannot reject the possibility of the existence of solutions that satisfying the condition for branching or the condition of ES and CS. Therefore, depending on functions and parameters, polymorphism with more than two morphs can potentially appear from monomorphic population as a result of the multiple branching. In fact, I found that polymorphism with more than two morphs can occur in AI by using a computer simulation (Figure 2.2). Consequently, in AI, evolutionary branching is possible in monomorphic population. Moreover, we cannot reject the possibility of both evolutionary and sustained polymorphism.

2.A3. Multiplicative aggregation of investments

In multiplicative aggregation of investments (MI), the expected payoff of a mutant with trait value y in the resident population with trait value x is

$$W(y|x) = f(x^{a(N-1)}y) - g(y), \quad (2.A4)$$

where x and y are always positive.

A singular solution of which is derived by solving

$$x^{*a(N-1)} f'(x^{*a(N-1)+1}) = g'(x^*). \quad (2.A5)$$

The condition for branching is

$$\begin{aligned} & a(N-1)x^{*a(N-1)-1} f''(x^{*a(N-1)+1}) + [a(N-1)+1]x^{*2a(N-1)} f''(x^{*a(N-1)+1}) \\ & < g''(x^*) \\ & < x^{*a(N-1)-1} f''(x^{*a(N-1)+1}) \end{aligned} \quad (2.A6)$$

Since $[a(N-1)+1] > 1$, a solution satisfying this condition potentially exists, only if

$$f''(x^{*a(N-1)+1}) < 0 \quad \text{and} \quad g''(x^*) < 0, \quad (2.A7)$$

which is a necessary condition for the occurrence of branching in monomorphic population. This shows that evolutionary branching can occur only when *both* effect *and* cost functions have a decelerating shape at the singular solution.

Similarly to AI, we can examine feasibilities and stabilities of singular coalitions of dimorphism and polymorphism with more than two morphs. As a result, we cannot reject the possibility of the existence of solutions that satisfying the condition for branching or the condition of ES and CS. Therefore, we conclude that we cannot reject the possibilities of both evolutionary and sustained polymorphism in MI.

2.A4. Additive aggregation of effects

When the formulation of reward is additive aggregation of effects (AE), the mutant payoff is

$$W(y | x) = a (N - 1) f(x) + f(y) - g(y) , \quad (2.A8)$$

When we set $\alpha = 1$, Eq. (2.A8) becomes the same expression with Eq. (2.9). A singular solution of which is the solution of

$$f(x^*) = g'(x^*) . \quad (2.A9)$$

The condition of branching for the solution is

$$f'(x^*) < g''(x^*) < f''(x^*) . \quad (2.A10)$$

When we set $\alpha = 1$, Eq. (2.A10) becomes the same expression with Eq. (2.10). Since left and right inequalities are never satisfied simultaneously, an evolutionary branching never occurs.

Although the analysis rejects the possibility of evolutionary polymorphism, I check the possibility of sustained polymorphism. The mutant payoff in the population with m morphs is

$$W(y | \{(x_i, p_i)\}_{i=1...m}) = a \sum_{\mathbf{n}} \left[\binom{N-1}{\mathbf{n}} \mathbf{p}^{\mathbf{n}} \sum_i n_i f(x_i) \right] + f(y) - g(y) . \quad (2.A11)$$

According to Eqs. (2.4) and (2.A11), coexistence of m morphs is possible if the simultaneous equations

$$f(x_i^*) - g(x_i^*) = f(x_j^*) - g(x_j^*) \quad \forall \quad i, j = 1...m , \quad (2.A12a)$$

$$f'(x_i^*) = g'(x_i^*) \quad \forall \quad i = 1...m , \quad (2.A12b)$$

have a solution. The solution can be both CS and ES when

$$f'(x_i^*) < g''(x_i^*) \quad \forall \quad i = 1...m , \quad (2.A13)$$

is satisfied. Because Eqs. (2.Aa) and (2.Ab) yield $m-1$ and m constraints respectively,

there are $2m-1$ constraints in total. The number of unknown variables is, m (i.e., trait value $x_{i=1\dots m}$). It should be noticed that Eqs. (2.A) is independent of the values of singular fraction, $p_{i=1\dots m}^*$. Accordingly, with $m = 1$, the number of variables is equal to that of sub-equations (i.e. $2m-1 = m$). However, with $m > 1$, the number of variables is fewer than that of sub-equations ($m < 2m-1$), so all equations are unlikely to be satisfied simultaneously. Therefore, two or more morphs cannot coexist; the population is generally monomorphic.

Consequently, the possibilities of both evolutionary and sustained polymorphisms are rejected in the case of AE.

2.A5. Multiplicative aggregation of effects with promotion of advantage

In the multiplicative aggregation of effects with promotion of advantage (pME), the mean payoff of a mutant is

$$W(y | x) = f_+(x)^{a(N-1)}f(y) - g(y) . \quad (2.A14)$$

A singular solution is the solution of

$$f_+(x^*)^{a(N-1)}f_+'(x^*) = g'(x^*) , \quad (2.A15)$$

and the condition for branching is

$$f_+(x^*)^{a(N-1)}f_+''(x^*) + a(N-1)f_+(x^*)^{a(N-1)-1}f_+'(x^*)^2 < g''(x^*) < f_+(x^*)^{a(N-1)}f_+''(x^*) . \quad (2.A16)$$

Since the second term of the left-hand side of Eq. (2.A16) is positive, there is no solution satisfying this condition. Therefore, evolutionary branching never occurs.

Although the analysis rejects the possibility of evolutionary polymorphism, I check the possibility of sustained polymorphism. The mean payoff of a mutant in a polymorphic population with m morphs is

$$W(y | \{(x_i, p_i)\}_{i=1 \dots m}) = \tilde{f}f_+(y) - g(y) \quad (2.A17a)$$

where $\tilde{f}$ represents an average amount of effects given by the other group mates as

$$\tilde{f} = \sum_{\mathbf{n}} \left\{ \binom{N-1}{\mathbf{n}} \mathbf{p}^{\mathbf{n}} \prod_{i=1}^m f_+(x_i)^{a_i} \right\}, \quad (2.A17b)$$

From Eqs. (2.4) and (2.A17), the singular fraction $\mathbf{p}^*$ is given by solving

$$\frac{g(x_i) - g(x_j)}{f_+(x_i) - f_+(x_j)} = \tilde{f} \quad \forall i, j = 1 \dots m, i \neq j. \quad (2.A18)$$

The condition for coexistence with m morphs can be written as

$$\frac{g(x_i^*) - g(x_j^*)}{f_+(x_i^*) - f_+(x_j^*)} = \frac{g'(x_i^*)}{f'_+(x_i^*)} \quad \forall i, j = 1 \dots m, i \neq j, \quad (2.A19a)$$

and

$$\tilde{f}f'_+(x_i^*) < g''(x_i^*) \quad \forall i = 1 \dots m. \quad (A19b)$$

If we temporarily set aside the relationship Eq. (2.A17b), but simply regards $\tilde{f}$ as an unknown constant C . Then we can rewrite the condition Eqs. (2.A18) and (2.A19a) as

$$\frac{g(x_i^*) - g(x_j^*)}{f_+(x_i^*) - f_+(x_j^*)} = C \quad \forall i, j = 1 \dots m, i \neq j, \quad (2.A20a)$$

$$\frac{g'(x_i^*)}{f'_+(x_i^*)} = C \quad \forall i, j = 1 \dots m, i \neq j \quad (2.A20b)$$

Eq. (2.A20a) yields $m(m-1)/2$ equations from the combination of i and j . However, if Eq. (2.A20a) with $(i, j) = (k_1, k_2)$ and (k_1, k_3) are satisfied, Eq. (2.A20a) with $(i, j) = (k_2, k_3)$ automatically follows. Consequently, Eq.(2.A20a) yields only $m-1$ constraints. Eq. (2.A20b) yields m constraints, so in total there are $2m-1$ constraints. Because Eq. (2.A20b) includes an unknown constant C rather than the singular fraction $p_{i=1 \dots m}^*$, the number of unknown variables is, m (i.e., trait value $x_{i=1 \dots m}$) plus one (i.e., unknown

constant, C), that is $m+1$. Therefore, with $m=2$, the number of variables is equal to that of sub-equations (*i.e.*, $m+1 = 2m-1$), and a solution for two-morphs coexistence can potentially exist. However, with $m>2$, the number of variables is fewer than that of sub-equations ($m+1 < 2m-1$), so all equations are unlikely to be satisfied simultaneously. Therefore, three or more morphs do not coexist in general. Consequently, in pME, the possibility of evolutionary polymorphism is monomorphism, while that of sustained polymorphism is dimorphism at maximum.

2.A6. Multiplicative aggregation of effects with suppression of disadvantage

In the multiplicative aggregation of effects with suppression of disadvantage (sME), the payoff of mutant is

$$W(y | x) = -f(x)^{a(N-1)}f(y) - g(y). \quad (2.A21)$$

A singular solution is a solution of

$$-f(x^*)^{a(N-1)}f'(x^*) = g'(x^*), \quad (2.A22)$$

and the condition for branching is

$$-f(x^*)^{a(N-1)}f''(x^*) - a(N-1)f(x^*)^{a(N-1)-1}f'(x^*)^2 < g''(x^*) < -f(x^*)^{a(N-1)}f''(x^*). \quad (2.A23)$$

The second term of the left-hand side of the inequality is always positive, therefore this condition can be satisfied when $f''(x^*) \geq 0$ and $g''(x^*) < 0$, or when $f''(x^*) < 0$, which can be satisfied when *either* effect *or* cost function has a decelerating shape at the singular solution.

In a dimorphic population,

$$W(y | x_1, x_2, p) = -\tilde{f}_-(y) - g(y) \quad (2.A24a)$$

where $\tilde{f}$ represents the average amount of effects given by the other group mates as

$$\tilde{f} = \sum_n \left\{ \binom{N-1}{n} p^n (1-p)^{N-1-n} f_-(x_1)^{an} f_-(x_2)^{a(N-1-n)} \right\}, \quad (2.A24b)$$

The singular fraction $\mathbf{p}^*$ is given by solving

$$\frac{g(x_1) - g(x_2)}{f_-(x_1) - f_-(x_2)} = -\tilde{f}. \quad (2.A25)$$

and the condition for a dimorphic singular coalition is

$$\frac{g'(x_1^*)}{f'_-(x_1^*)} = \frac{g'(x_2^*)}{f'_-(x_2^*)} = -\tilde{f}, \quad (2.A26)$$

Following Eq. (2.8), the condition for CS is that real parts of all eigenvalues of

$$\begin{pmatrix} \beta_1(x_1^*, x_2^*) \left[\frac{\partial \tilde{f}}{\partial x_1^*} f'_-(x_1^*) + \tilde{f} f''_-(x_1^*) - g''(x_1^*) \right] & \beta_1(x_1^*, x_2^*) \frac{\partial \tilde{f}}{\partial x_2^*} f'_-(x_1^*) \\ \beta_2(x_1^*, x_2^*) \frac{\partial \tilde{f}}{\partial x_1^*} f'_-(x_2^*) & \beta_2(x_1^*, x_2^*) \left[\frac{\partial \tilde{f}}{\partial x_2^*} f'_-(x_2^*) + \tilde{f} f''_-(x_2^*) - g''(x_2^*) \right] \end{pmatrix} \quad (2.A27)$$

are negative. Differentiating $\tilde{f}$ with respect to x_1^* and x_2^* , we obtain

$$\left. \frac{\partial \tilde{f}}{\partial x_1} \right|_{\substack{x_1=x_1^* \\ x_2=x_2^*}} = \frac{\partial}{\partial x_1} \frac{g(x_1^*) - g(x_2^*)}{f_-(x_1^*) - f_-(x_2^*)} = \frac{f'_-(x_1^*)}{f_-(x_1^*) - f_-(x_2^*)} \left(\frac{g'(x_1^*)}{f'_-(x_1^*)} - \frac{g(x_1^*) - g(x_2^*)}{f_-(x_1^*) - f_-(x_2^*)} \right) = 0 \quad (2.A28a)$$

$$\left. \frac{\partial \tilde{f}}{\partial x_2} \right|_{\substack{x_1=x_1^* \\ x_2=x_2^*}} = \frac{\partial}{\partial x_2} \frac{g(x_1^*) - g(x_2^*)}{f_-(x_1^*) - f_-(x_2^*)} = \frac{f'_-(x_2^*)}{f_-(x_1^*) - f_-(x_2^*)} \left(\frac{g'(x_2^*)}{f'_-(x_2^*)} - \frac{g(x_1^*) - g(x_2^*)}{f_-(x_1^*) - f_-(x_2^*)} \right) = 0 \quad (2.A28b)$$

respectively. Accordingly, non-diagonal elements of Eq. (2.A27) become 0, by which the eigenvalues of the Jacobian matrix coincide with the values of diagonal elements.

Therefore, the condition of CS can be rewritten as

$$\frac{g(x_1^*) - g(x_2^*)}{f_-(x_1^*) - f_-(x_2^*)} f''_-(x_1^*) < g''(x_1^*), \quad (2.A29a)$$

$$\frac{g(x_1^*) - g(x_2^*)}{f_-(x_1^*) - f_-(x_2^*)} f''_-(x_2^*) < g''(x_2^*), \quad (2.A29b)$$

On the other hand, following Eq. (2.7), I find that exactly the same expression as Eq. (2.A29) is the condition of ES. Since both stability conditions are identical, dimorphism is never followed by a further branching, implying that polymorphism with more than two morphs never evolves. Consequently, the cooperation level must be either monomorphic or dimorphic with respect to evolutionary branching.

Although the analysis rejects the possibility of evolution of polymorphism with more than two morphs, the possibility of sustained polymorphism should be examined. By similar calculations to pME case, the singular fraction $\mathbf{p}^*$ is given by solving

$$\frac{g(x_i) - g(x_j)}{f_-(x_i) - f_-(x_j)} = -\tilde{f} \quad \forall i, j = 1 \cdots m, i \neq j, \quad (2.A30a)$$

where $\tilde{f}$ represents an average amount of effects given by the other group mates as

$$\tilde{f} = \sum_{\mathbf{n}} \left\{ \binom{N-1}{\mathbf{n}} \mathbf{p}^{\mathbf{n}} \prod_{i=1}^m f_-(x_i)^{a_{n_i}} \right\}, \quad (2.A30b)$$

The condition for coexistence with m morphs can be written as

$$\frac{g(x_i^*) - g(x_j^*)}{f_-(x_i^*) - f_-(x_j^*)} = \frac{g'(x_i^*)}{f'_-(x_i^*)} \quad \forall i, j = 1 \cdots m, i \neq j, \quad (2.A31a)$$

and

$$-\tilde{f} f''_-(x_i^*) < g''(x_i^*) \quad \forall i = 1 \cdots m. \quad (2.A31b)$$

Similarly to the case of pME, a solution of these equations can exist for $m = 2$, but generally not for $m > 2$. Therefore, three or more morphs never coexist at the stable state.

Hence, the possibilities of both evolutionary and sustained polymorphism are dimorphic at maximum, in sME.

Appendix 2.B: Individual-based Simulations

In order to confirm the predictions of analytical investigation, I conducted an individual-based simulation with a continuous snowdrift game in a finite size-fixed population comprising 40,000 individuals. Each individual has a positive real value as the cooperation level. The population is randomly divided into 20,000 two-individual groups, within which two players carry out continuous snowdrift game once, gaining payoffs based on Eq. (1) with $f(x) = 2\exp(-0.1(x + 0.85)^{-6.4})$ and $g(x) = \exp(-0.1(x + 0.95)^{-6.4})$, and then the groups are dissolved. After repeating this process 32 times, all individuals reproduce offspring asexually with fecundities proportional to their own total gain, and finally die. From the offspring pool, 40,000 individuals are randomly chosen to form a next generation. In the reproduction, cooperation levels of the offspring can vary from their parent by mutation, where the trait distribution of offspring is assumed to follow a Gaussian distribution around the parent level with a standard deviation of $\sigma = 0.0004$.

Appendix 2.C: Possibility of the Emergence of Behavioural Polymorphism

In the cooperation based on the behavioural decision, individuals can behave differently for each game, which corresponds to a mixed strategy that uses a set of behavioural tactics with a certain frequency distribution. Represent the mixed strategy of each individual as $\{(x_i, p_i)\}_{i=1\dots m}$, where x_i and p_i are phenotypic value and frequency of tactics i ($p_i > 0$, $\sum p_i = 1$), respectively. The fitness of an individual with mixed strategy $\{(x'_i, p'_i)\}_{i=1\dots m'}$ in the population with a resident mixed strategy $\{(x_i, p_i)\}_{i=1\dots m}$ can be formulated as

$$\hat{W}(\{(x'_i, p'_i)\}_{i=1\dots m'} | \{(x_j, p_j)\}_{j=1\dots m}) = \sum_{i=1}^{m'} p'_i W(x'_i | \{(x_j, p_j)\}_{j=1\dots m}) , \quad (2.C1)$$

where W in the right hand side is the same expression as Eq. (2.3). The mixed strategy becomes stable and maintained when the strategy satisfies the Nash equilibrium condition,

$$\hat{W}(\{(x_i, p_i)\}_{i=1\dots m} \mid \{(x_j, p_j)\}_{j=1\dots m}) \geq \hat{W}(\{(x'_i, p'_i)\}_{i=1\dots m'} \mid \{(x_j, p_j)\}_{j=1\dots m}) \quad (2.C2)$$

for any feasible strategy $\{(x'_i, p'_i)\}_{i=1\dots m'}$. Although we cannot solve this condition explicitly, we can derive some necessary conditions for the Nash equilibrium by considering some special cases. First, we consider a mixed strategy that is different in frequencies of tactics $p'_i \neq p_i$, but the same in the other properties (*i.e.* $m = m'$ and $x'_i = x_i$) for $\forall i = 1\dots m$. By using the Bishop-Cannings theorem (Bishop and Cannings 1978, Maynard Smith 1982), $\{(x_i, p_i)\}_{i=1\dots m}$ is a Nash equilibrium only when

$$W(x_j \mid \{(x_i, p_i)\}_{i=1\dots m}) = W(x_k \mid \{(x_i, p_i)\}_{i=1\dots m}) \quad \forall j, k = 1\dots m. \quad (2.C3)$$

This is the same expression as the condition Eq. (2.4). Next, I consider a mixed strategy with a slight shift in phenotypic value of its i -th tactics $x'_i = x_i + \epsilon$ while all the others are the same; $m = m'$ and $p'_i = p_i$ for $\forall i = 1\dots m$. If $\{(x_i, p_i)\}_{i=1\dots m}$ is a Nash equilibrium,

$$W(x_j \mid \{(x_i, p_i)\}_{i=1\dots m}) \geq W(x'_j \mid \{(x_i, p_i)\}_{i=1\dots m}) \quad \forall j = 1\dots m. \quad (2.C4)$$

must be satisfied for any i , which corresponds with Eq. (2.6). This is a necessary condition for the Nash equilibrium. As a result, necessary conditions for the existence of the Nash equilibrium with m cooperation levels are equivalent to Eqs. (2.4) and (2.6). Consequently, for the benefit and cost functions considered in the present study, my results on the sustained polymorphism can be applied to the mixed strategy of behavioural decision.

Accordingly, I proved that the sustained polymorphism is a necessary condition for the behavioural polymorphism by examining the evolutionary stability of the mixed strategies with finite number of tactics. However, it is also possible to consider a mixed

strategy with infinite number of tactics, in which a strategy can be represented by a continuous distribution of the probability with cooperation level. In such cases, the analysis based on the measure dynamics (Cressman and Hofbauer 2005) is needed for investigating the evolutionary stability.

Appendix 3.A: Analysis by using adaptive dynamics

3.A1. Fitness Functions

Let's denote the cooperation level of mutant with reaction line (b', c') as x , which have a certain range of the distribution caused by behavioural error, Similarly, I denote the cooperation level of residents with reaction line (b, c) by y . According to Eqs. (3.3), the mean value of x and y are

$$E[x] = \frac{b'c + c'}{1 - bb'} \quad \text{and} \quad (3.A1a)$$

$$E[y] = \frac{bc' + c}{1 - bb'}. \quad (3.A1b)$$

The variance of x and y and the covariance of them are

$$\text{Var}[x] = \frac{b'^2 + 1}{(1 - bb')^2} \sigma^2, \quad (3.A2a)$$

$$\text{Var}[y] = \frac{b^2 + 1}{(1 - bb')^2} \sigma^2 \quad \text{and} \quad (3.A2b)$$

$$\text{Cov}(x, y) = \frac{b + b'}{(1 - bb')^2} \sigma^2. \quad (3.A2c)$$

By using Taylor expansion, the mean value of the payoff can be written as

$$\begin{aligned} H(b', c' | b, c) &= W(E[x], E[y]) \\ &+ E[E[x] - x] \frac{\partial W}{\partial x} + E[E[y] - y] \frac{\partial W}{\partial y} \\ &+ \frac{1}{2} \text{Var}[x] \frac{\partial^2 W}{\partial x^2} + \text{Cov}[x, y] \frac{\partial^2 W}{\partial x \partial y} + \frac{1}{2} \text{Var}[y] \frac{\partial^2 W}{\partial y^2} + \dots \end{aligned} \quad (3.A3)$$

Because W is a quadratic function, we can ignore the terms of more than second order differential of W . Consequently, the fitness can be rewritten as

$$H(b', c' | b, c) = W \left(\frac{b'c + c'}{1 - bb'}, \frac{bc' + c}{1 - bb'} \right) + \frac{\sigma^2}{4(1 - bb')^2} (p_f [(1 + b')^2 + (1 + b)^2] - 4sp_g (b'^2 + 1)) \quad (3.A4)$$

3.A2. Singular Solutions

A reaction line (b^*, c^*) is an evolutionary singular coalition when the selection gradient for both b and c become zero, the condition of which can be obtained by solving the following simultaneous equations.

$$\begin{cases} \left. \frac{\partial H(b', c' | b, c)}{\partial b'} \right|_{\substack{b'=b \\ c'=c}} = 0 \\ \left. \frac{\partial H(b', c' | b, c)}{\partial c'} \right|_{\substack{b'=b \\ c'=c}} = 0 \end{cases} \quad (3.A5)$$

According to Eq. (3.6),

$$\begin{aligned} \left. \frac{\partial H}{\partial b'} \right|_{\substack{b=b'=b^* \\ c=c'=c^*}} &= \beta_b(b^*, c^*) \frac{(1 + b^*)c^*}{(1 - b^{*2})^2} \left[(1 + b^*) \left(p_f \frac{c^*}{1 - b^*} + \frac{1 - p_f}{2} \right) - 2sp_g \frac{c^*}{1 - b^*} - s(1 - p_g) \right] \\ &\quad + \beta_b(b^*, c^*) \frac{\sigma^2}{(1 - b^{*2})^3} \left[\frac{p_f}{2} (1 + b^*)^3 - 4b^* sp_g \right] \end{aligned} \quad (3.A6a)$$

$$\left. \frac{\partial H}{\partial c'} \right|_{\substack{b=b'=b^* \\ c=c'=c^*}} = \beta_c(b^*, c^*) \frac{1}{1 - b^{*2}} \left[(1 + b^*) \left(p_f \frac{c^*}{1 - b^*} + \frac{1 - p_f}{2} \right) - 2sp_g \frac{c^*}{1 - b^*} - s(1 - p_g) \right] \quad (3.A6b)$$

Therefore, the condition of singular solutions can be rewritten as

$$\frac{p_f}{2} (1 + b^*)^3 - 4b^* sp_g = 0 \quad \text{and} \quad (3.A7a)$$

$$c^* = \frac{-(1-b^{*2})(1-p_f) + 2(1-b^*)s(1-p_g)}{2(1+b^*)p_f - 4sp_g} . \quad (3.A7b)$$

The mean cooperation level at the singular solution is

$$E[x^*] = \frac{-(1+b^*)(1-p_f) + 2s(1-p_g)}{2(1+b^*)p_f - 4sp_g} . \quad (3.A8)$$

3.A3. Convergence Stability

Next, I investigated the condition of convergence stability of interior singular solutions.

$$M_{CS} = \begin{pmatrix} \beta_b(b^*, c^*) \frac{\partial}{\partial b} \left[\frac{\partial H}{\partial b'} \Big|_{\substack{b'=b \\ c'=c}} \right]_{b=b^*} & \beta_b(b^*, c^*) \frac{\partial}{\partial b} \left[\frac{\partial H}{\partial c'} \Big|_{\substack{b'=b \\ c'=c}} \right]_{b=b^*} \\ \beta_c(b^*, c^*) \frac{\partial}{\partial c} \left[\frac{\partial H}{\partial b'} \Big|_{\substack{b'=b \\ c'=c}} \right]_{c=c^*} & \beta_c(b^*, c^*) \frac{\partial}{\partial c} \left[\frac{\partial H}{\partial c'} \Big|_{\substack{b'=b \\ c'=c}} \right]_{c=c^*} \end{pmatrix} , \quad (3.A9)$$

where v is the relative ratio of evolutionary speed of c against b . When all eigenvalues of M_{CS} are negative, the solution (b^*, c^*) is convergence stable. By using Routh–Hurwitz stability criterion, this condition can be rewritten as

$$tr[M_{CS}] < 0 \wedge \det[M_{CS}] > 0 , \quad (3.A10)$$

where tr and $\det$ are trace and determinant of M_{CS} , respectively. The trace and determinant of M_{CS} can be written as

$$\begin{aligned} tr(M_{CS}) = & \frac{1}{(1-b^*)^2(1+b^*)} \left\{ c^* \frac{\partial W}{\partial y} \Big|_{x=y=\hat{x}} + \frac{(1-b^*)^2}{1+b^{*2}} \left[\left(\frac{c^*}{1-b^*} \right)^2 + \frac{\beta_c(b^*, c^*)}{\beta_b(b^*, c^*)} \right] [W_{xx} + b^* W_{xy}] \right\} \\ & + \frac{\sigma^2}{(1-b^{*2})^3} [2W_{xx} + 6b^* W_{xy} + (3b^{*2} + 1)W_{yy}] \end{aligned} \quad (3.A11)$$

$$\det(M_{CS}) = \frac{\beta_c(b^*, c^*)}{\beta_b(b^*, c^*)} \frac{\sigma^2}{(1-b^*)^5 (1+b^*)^4} \frac{1-b^{*2}}{1+b^{*2}} [W_{xx} + b^* W_{xy} \{2W_{xx} + 6b^* W_{xy} + (3b^{*2} + 1)W_{yy}\}]. \quad (3.A12)$$

Therefore, the conditions for CS are

$$\frac{1}{4} [p_f (1+b^*) - 4sp_g] [3p_f (1+b^*)^2 - 8sp_g] > 0 \quad \text{and} \quad (3.A13a)$$

$$\begin{aligned} & \frac{1-b^*}{1+b^{*2}} \left[\left(\frac{c^*}{1-b^*} \right)^2 + \frac{\beta_c(b^*, c^*)}{\beta_b(b^*, c^*)} \right] [p_f (1+b^*) - 4sp_g] + \frac{\sigma^2}{(1-b^{*2})^2} [3p_f (1+b^*)^2 - 8sp_g] \\ & < - \left(\frac{c^*}{1-b^*} \right) \left(2p_f \frac{c^*}{1-b^*} + (1-p_f) \right) \end{aligned} \quad (3.A13b)$$

3.A4. Evolutionary Stability

The condition of evolutionary stability of interior singular solutions can be examined by using a following matrix

$$M_{ES} = \begin{pmatrix} \beta_b(b^*, c^*) \frac{\partial^2 H}{\partial b'^2} \Big|_{\substack{b'=b^* \\ c'=c^*}} & \beta_b(b^*, c^*) \frac{\partial^2 H}{\partial b' \partial c'} \Big|_{\substack{b'=b^* \\ c'=c^*}} \\ \beta_c(b^*, c^*) \frac{\partial^2 H}{\partial b' \partial c'} \Big|_{\substack{b'=b^* \\ c'=c^*}} & \beta_c(b^*, c^*) \frac{\partial^2 H}{\partial c'^2} \Big|_{\substack{b'=b^* \\ c'=c^*}} \end{pmatrix}, \quad (3.A14)$$

where v is the relative ratio of evolutionary speed of c . When all eigenvalues of M_{ES} are negative, the solution (b^*, c^*) is evolutionary stable.

By using Routh-Hurwitz stability criterion, this condition can be written as

$$tr[M_{ES}] < 0 \wedge \det[M_{ES}] > 0, \quad (3.A15)$$

where tr and $\det$ are trace and determinant of M_{ES} respectively. The trace and determinant of M_{ES} are

$$tr(M_{ES}) = \frac{1}{(1-b^{*2})^2} \left\{ \frac{1-b^{*2}}{1+b^{*2}} \left[\left(\frac{c^*}{1-b^*} \right)^2 + \frac{\beta_c(b^*, c^*)}{\beta_b(b^*, c^*)} \right] + \frac{\sigma^2}{1-b^{*2}} \right\} (W_{xx} + b^* W_{xy}) \quad (3.A16)$$

and

$$\det(M_{ES}) = \frac{\beta_c(b^*, c^*)}{\beta_b(b^*, c^*)} \frac{c^{*2} \sigma^2}{(1-b^*)^5 (1+b^*)^5} \frac{1-b^{*2}}{1+b^{*2}} (W_{xx} + b^* W_{xy})^2, \quad (3.A17)$$

respectively.

Consequently, the condition for the evolutionary stable is

$$p_f(1+b^*) - 4sp_g < 0. \quad (3.A18)$$

3.A5. Singular Coalition on the border

In this analysis, I assumed $-1 < b < 1$ and $0 \leq c$. Although we have investigated about the singular solution in interior region, we can also consider that on the border (*i.e.* $b \cong \pm 1$ or $c = 0$). When $c > 0$, the necessary condition for the singular coalition on the border of b (*i.e.* $b \cong \pm 1$) is

$$\lim_{\substack{b^* \rightarrow \pm 1 \\ c=c'=c^*}} \left(\frac{\partial H}{\partial c'} \bigg|_{b=b'=b^*} \right) = 0. \quad (3.A19)$$

Because Eq. (3.A6b) diverges to infinity when $b \cong \pm 1$, this condition never satisfied.

Hence, there is no singular coalition on the border of b .

Next, let us focus on the singular coalition on the border of c (*i.e.* $c = 0$). A reaction strategy on $c=0$ can be a singular coalition when the selection gradient of b becomes zero, therefore

$$\frac{p_f}{2} (1+b^*)^3 - 4b^* sp_g = 0. \quad (3.A20)$$

The condition of CS and ES on the border of c is

$$\left. \frac{\partial^2 H}{\partial b'^2} \right|_{\substack{b'=b=b^* \\ c'=c=0}} < 0 \quad \text{and} \quad \left. \frac{\partial H}{\partial c'} \right|_{\substack{b=b'=b^* \\ c=c'=0}} < 0 \quad \text{and} \quad (3.A21)$$

$$\frac{\partial}{\partial b} \left[\left. \frac{\partial H}{\partial b'} \right|_{\substack{b'=b \\ c'=c}} \right]_{\substack{b=b^* \\ c=0}} < 0, \quad (3.A22)$$

respectively.

3.A6. Influence of the magnitude of the behavioural error and the evolutionary rate

According to Eqs. (3.A7) and (3.10), the condition of singular coalition and ES is independent from the behavioural error σ and evolutionary rate β_b, β_c . On the other hand, Eq. (3.9) shows that the condition of CS is influenced by these parameters. However, the influence of these parameters depends on the evolutionary stability of the singular coalition. When the singular coalition is ES (*i.e.* Eq. (3.10) is satisfied), Eq. (3.9a) can be satisfied only when $3p_f(1+b^*)^2 - 8sp_g < 0$. In this case, large σ or large β_c / β_b always reduce the value of LHS in Eq. (3.9b), therefore, they always relax the condition of CS. On the other hand, when the singular coalition is not ES, Eq. (3.9a) can be satisfied only when $3p_f(1+b^*)^2 - 8sp_g > 0$. In this case, the value of LHS in Eq. (3.9b) is always positive and so the value of RHS in Eq. (3.9b) also should be positive in order to satisfy the condition of CS. However, it seems be generally difficult because the value of RHS becomes positive when and only when $\partial H / \partial y|_{x=y=x^*} < 0$, *i.e.*, more investment by the opponent player decrease the own payoff around the singular solution. Consequently, we can predict that the occurrence of evolutionary branching is not impossible but generally difficult under the existence of the negotiation process.

Appendix 3.B: Evolution of the reaction line from $(b, c) = (0, 0)$

3.B1. Zero-intercept evolution

When the reaction strategy of a population (b, c) is $(0, 0)$ at the initial state, we can analytically investigate the evolutionary realized cooperation level at the final state by considering some special situations.

First, I considered a situation that the reaction strategy reach to a CS solution with keeping $c = 0$. When such situation emerges on the evolutionary process, we can detect that the cooperation level becomes zero at the final state of the evolution. I call this situation as “zero-intercept evolution.” For the occurrence of the zero-intercept evolution, the selection gradient for c should be negative as long as the strategy of the population reach to a CS coalition on $c = 0$. The selection gradient for c becomes negative on $c = 0$ when

$$b < 2s \frac{1-p_g}{1-p_f} - 1 . \quad (3.B1)$$

According to Eqs. (3.A20) and (3.A21), the reachable CS coalition on $c = 0$ from the initial state (*i.e.*, $(b, c) = (0, 0)$) can be written as

$$(-1, 0) \quad \text{when } p_f \leq 0 \text{ and } p_g \leq 0, \quad (3.B2a)$$

$$(b_1^*, 0) \quad \text{when } 0 < p_f < \frac{32}{27} sp_g, \quad (3.B2b)$$

$$(1, 0) \quad \text{when } 0 < p_f \text{ and } \frac{32}{27} sp_g \leq p_f, \quad (3.B2c)$$

$$(b^*, 0) \quad \text{when } p_f \leq 0 < p_g, \quad (3.B2d)$$

where b_1^* and b^* are the solutions of Eq. (3.A20) in $0 < b_1^* < 1/2$ and $-1 < b^* < 0$, respectively. Therefore, the selection gradient of c becomes negative until the reaching

to the CS coalition on $c = 0$ when

$$1 < 2s \frac{1-p_g}{1-p_f} \quad \text{when } p_f \leq 0 \quad (3.B3a)$$

$$b_1^* < 2s \frac{1-p_g}{1-p_f} - 1 \quad \text{when } 0 < p_f < \frac{32}{27} sp_g, \quad (3.B3b)$$

$$1 < s \frac{1-p_g}{1-p_f} \quad \text{when } 0 < p_f \text{ and } \frac{32}{27} sp_g \leq p_f. \quad (3.B3c)$$

This is the condition of the zero-intercept evolution. This condition is a sufficient condition for that the intercept of the reaction line becomes zero at the final state of the evolution, but not a necessary condition for that.

3.B2. Infinity-intercept evolution

According to Eq. (3.A20), the selection gradient for c becomes positive when $b = \hat{b}$, where

$$\hat{b} = 0 \quad \text{when } 2s \frac{1-p_g}{1-p_f} \leq 1 \quad \text{or} \quad (3.B4a)$$

$$\hat{b} = 2s \frac{1-p_g}{1-p_f} - 1 \quad \text{when } 2s \frac{1-p_g}{1-p_f} > 1. \quad (3.B4b)$$

When the selection gradients of both b and c are positive in $\forall b \in \hat{b}, 1) \quad \forall c \in [0, \infty)$, c diverge to infinity. Hereafter, I call this situation as “infinity-intercept evolution.” According to Eq. (3.A6), the selection gradients for both b and c are positive when the following three inequalities are satisfied in $\forall b \in \hat{b}, 1)$.

$$(1+b)p_f - 2sp_g > 0, \quad (3.B5a)$$

$$(1+b)(1-p_f) - s(1-p_g) > 0, \quad (3.B5b)$$

$$p_f(1+b)^3 - 8bsp_g > 0. \quad (3.B5c)$$

When $p_f \leq 0$ or $0 < p_f < \frac{32}{27}sp_g$, Eq. (3.C5c) is never satisfied. When $0 < p_f$ and

$\frac{32}{27}sp_g \leq p_f$, Eqs. (3.C5) can be written as

$$0 < p_f \wedge 2sp_g < p_f \wedge s \frac{1-p_g}{1-p_f} \leq \frac{1}{2} \quad \text{or} \quad (3.B6a)$$

$$0 < p_f \wedge p_g < p_f \wedge \frac{1}{2} < s \frac{1-p_g}{1-p_f} < 1. \quad (3.B6b)$$

This is the necessary and sufficient condition of the infinity-intercept evolution. Similar to the condition of the zero-intercept evolution, this condition is a sufficient condition for that the intercept diverge to infinity in the result of the evolution, but not a necessary condition for that.

3.B3. Potential infinity-intercept evolution

Even when the condition of infinity-intercept evolution is not satisfied, the intercept c can potentially diverge to infinity in the result of the evolution. However, when the selection gradient of c is negative for $(b, \hat{c})$ in $\forall b \in (-1, 1)$, we can detect that c never becomes larger than $\hat{c}$. In other words, the intercept potentially becomes infinitely large value in the result of the evolution when the selection gradient of c becomes positive in $\forall b \in (-1, 1)$ and $\exists c \in [0, \infty)$. Hereafter, I call this condition as “potential infinity-intercept evolution,” which is a necessary condition for the evolution of infinitely large intercept. By using Eq. (3.A6b), this condition can be written as

$$D(b, c) < 0 \quad \text{in} \quad \forall b \in (-1, 1), \quad \exists c \in [0, \infty), \quad (3.B7)$$

where

$$D(b, c) = (1+b) \left(p_f \frac{c}{1-b} + \frac{1-p_f}{2} \right) - 2sp_g \frac{c}{1-b} - s(1-p_g). \quad (3.B8)$$

First, I fix c to a certain value and investigate the maximum value of $D(b, c)$ (i.e., $D_{\max}(c)$) with changing the value of b . The partial differential coefficient of Eq. (3.C8b) for b is

$$\begin{aligned} \frac{\partial D}{\partial b} &= \frac{\partial}{\partial b} \left[(1+b) \left(p_f \frac{c}{1-b} + \frac{1-p_f}{2} \right) - 2sp_g \frac{c}{1-b} - s(1-p_g) \right] \\ &= p_f \frac{2}{(1-b)^2} c + \frac{1-p_f}{2} - 2sp_g \frac{1}{(1-b)^2} c \\ &= (p_f - sp_g) \frac{2c}{(1-b)^2} + \frac{1-p_f}{2} \end{aligned} \quad (3.B9)$$

By solving this, we can obtain $D_{\max}(c)$ as

$$D \left(1 - 2 \sqrt{\frac{-p_f + sp_g}{1-p_f}} c, c \right) \quad \text{when } 0 \leq c \leq \frac{1-p_f}{-p_f + sp_g} \quad (3.B10a)$$

$$\lim_{b \rightarrow -1} [D(b, c)] \quad \text{when } \frac{1-p_f}{-p_f + sp_g} < c \quad (3.B10b)$$

By examining $D_{\max}$ in $\forall c \in [0, \infty)$, we can investigate the condition that $D_{\max}$ becomes negative, which can be written as

$$0 < p_f < sp_g < p_f + s - 1 \quad \text{or} \quad (3.B11a)$$

$$p_f < p_g < 0 \wedge p_f < sp_g \quad \text{or} \quad (3.B11b)$$

$$0 \leq p_g \wedge p_f < sp_g. \quad (3.B11c)$$

By considering the contraposition of Eqs. (3.B11), we obtain the condition of potential infinity-intercept evolution, which is

$$p_g < p_f < 0 \quad \text{or} \quad (3.B12a)$$

$$p_f + s - 1 < p_g < 0 \wedge p_g < p_f \quad \text{or} \quad (3.B12b)$$

$$sp_g < p_f \quad (3.B12c)$$

3.B4. Comparison between analytical and numerical investigations

By using Eqs. (3.8), (3.9) and (3.10), I investigated the evolutionary singular coalitions and their stabilities. Moreover, I also investigated the evolutionary trajectory by using the conditions of zero-intercept evolution, infinity-intercept evolution and potential infinity -intercept evolution. The results of them are well supported the results of the numerical investigation (Figure 3.B1).

Appendix 3.C: Analysis of the evolutionary dynamics of cooperation without negotiation

When the slope of reaction line is fixed to zero, we can investigate the evolution of cooperation by considering the evolutionary dynamics of the intercept c . According to Eq. (3.6), the fitness of a mutant with reaction line $(0, c')$ in a resident population with reaction line $(0, c)$ is

$$H(0, c' | 0, c) = W(c', c) + \sigma^2 \left(\frac{1}{2} p_f - sp_g \right) \quad (3.C1)$$

The selection gradient of c can be represented by

$$\begin{aligned} \frac{dc}{dt} &= \beta(c) \frac{\partial H(c' | c)}{\partial c'} \Big|_{c'=c} \\ &= 2(p_f - 2sp_g)c + (1 - p_f) - 2s(1 - p_g) \end{aligned} \quad (3.C2)$$

The singular solutions is

$$c^* = \frac{-(1 - p_f) + 2s(1 - p_g)}{2p_f - 4sp_g} \quad (3.C3)$$

and the condition of CS and ES are

$$p_f < 2sp_g \quad \text{and} \quad (3.C4)$$

$$p_f < 4sp_g , \quad (3.C5)$$

respectively.

When $c = 0$ at the initial state, the condition for that the cooperation level becomes zero in the result of the evolution is

$$1 < 2s \frac{1-p_g}{1-p_f} \quad (3.C6)$$

Similarly, the condition for that c diverge to infinity is

$$2sp_g < p_f \wedge s \frac{1-p_g}{1-p_f} \leq \frac{1}{2} . \quad (3.C7)$$

When both these two conditions are not satisfied, the cooperation level reach to a singular solution and sustained.

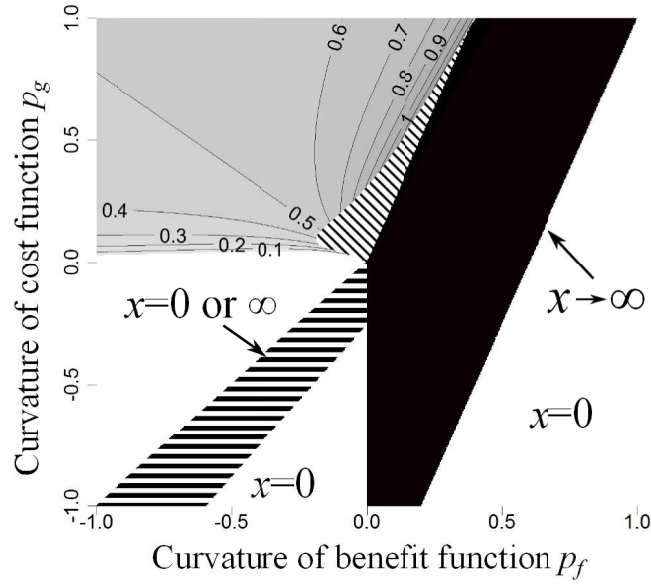


Figure 3.B1

The density plot of the mean cooperation level calculated by using analytical investigation with same parameter values in Figure 3.2a. In the white region, the condition of Zero-intercept evolution is satisfied or the singular solution exists only in intercept $c = 0$. In black region, the condition of infinity-intercept evolution is satisfied. In the horizontal hatched region, the condition of potential infinity-intercept evolution is satisfied and some singular solutions exist in intercept $c = 0$. In the hatched and grey regions, singular solutions exist in $c > 0$, but they are not convergence stable in the hatched region. The evolutionary pattern predicted by analytical investigations in Appendix 3.B well supports the results of the numerical investigation (Figure 3.2a).