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

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Abstract

The existence of intra-population variations in cooperation level has often been reported by some empirical studies. Evolutionary conditions of polymorphism in cooperation have been investigated by using a framework of the continuous snowdrift game. However, our insights from this framework have been limited because of an assumption that the cooperative reward is a function of total amount of investments within an interacting group. In many cases, payoffs may actually depend on the interactions between the *effects* of such investments, such as members share the sum of beneficial effects that are individually produced from their own investments. Alternatively, payoffs may depend multiplicatively on investment, such as when investments are complementary. In the present paper, we investigated the influence of such difference on the evolution of cooperation with respect to three aspects of the aggregating process of individuals' contributions for reward, *i.e.* (i) additive or multiplicative, (ii) aggregation of either investments or effects, and (iii) promotion of advantage or suppression of disadvantage. We analytically show that the possibilities of the emergence of polymorphism are different depending on the type of aggregation process classified from these three aspects. Polymorphism of cooperation level never emerges unless the aggregation process is the aggregation of investment or the multiplicative aggregation of effect with suppression of disadvantage. Our results show the necessary condition for the emergence of polymorphic cooperation levels that are observed in various taxonomic groups. [230 words]

Keywords

Adaptive dynamics, variance in cooperation, common good

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 about 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”), but polymorphism of defence level is also observed in some cases (Agrawal *et al.* 2002, Hare and Elle 2002).

In general, selfish individuals will obtain a higher payoff than cooperative ones because they receive the benefits of cooperation without paying cooperative costs. Therefore, explaining the reason why cooperative individuals can persist in the presence of selfish ones is a challenging and important subject in evolutionary ecology. In order to solve this problem, some mechanisms have been proposed, which include kin selection (Hamilton 1964, 1972), future benefits (Clutton-Brock 2002) and frequency dependent selection for the cooperative traits in the context of game theory (Maynard Smith 1982). In particular, because game theory is a useful tool for describing the selection for the traits related to social interactions, game theory has been used for investigating the evolution of cooperation.

One important framework in game theory is the continuous snowdrift game, which is defined by Doebeli *et al.* (2004) as a game in which investment is a continuous variable and "*investment incur costs to the donor and accrue benefits to both the donor and the recipient.*" This differs from the more well-known continuous prisoner's dilemma game in which the investment does not yield a reward directly to the investor (Killingback *et al*. 1999, Doebeli and Hauert 2005). It should be noted that some studies of public goods game (Janssen and Goldstone 2006, Deng and Chu 2011, Chen *et al.* 2012) also satisfied the condition that was proposed by Doebeli *et al.* (2004), which can be categorized into continuous snowdrift game.

Previous studies have indicated that under some conditions the continuous snowdrift game can predict evolutionary branching, and therefore dimorphism of cooperation levels (Doebeli *et al.*, 2004). 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 that is produced by such investment. These will only be equivalent if the aggregation is additive and the relationship between investment and effects are linear. However, this is likely to be unrealistic 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, we summarize those processes into two simple equations, which are ineffective for quantitative predictions but effective for 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. We 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. Moreover, we can also consider the difference of 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 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 assumed the aggregation process, which we call "additive aggregation of investments with promotion of advantage." But 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, we 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. We also compare the influence of the functional shapes of effect and cost among aggregation processes. We analytically show that these possibilities are different depending on the type of aggregation process of rewards. Our results show us the condition for the emergence of polymorphisms that are observed in various organisms.

2. Model

2.1. Payoff function

We 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, we 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 $\Sigma n_i = N-1$), respectively. When the total number of morphs in the population is m, an assemblage of group mates is represented by $\{(x_i, n_i)\}_{\{i=1...m\}}$, 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

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

where the first and second terms of the right-hand side are the reward and the cost of cooperation for the focal individual, respectively. We 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 (Σp_i=1). The probability of obtaining the composition of group mates $\{(x_i, n_i)\}_{i=1\ldots m}$ follows a multinomial distribution, which we represent in this article as

$$\binom{N-1}{\mathbf{n}}\mathbf{p}^{\mathbf{n}} = \frac{(N-1)!}{n_1!n_2!\cdots n_m!}\, p_1^{\,n_1} p_2^{\,n_2} \cdots p_m^{\,n_m} \quad . \qquad (2)$$

Averaging Eq.(1) with this probability, the expected payoff of the focal individual with phenotypic value y is

$$W\left(y\,|\{(x_i, p_i)\}_{i=1\cdots m}\right) = \sum_{\mathbf{n}}\left[\binom{N-1}{\mathbf{n}}\mathbf{p}^{\mathbf{n}} F\left(y\,|\{(x_i, n_i)\}_{i=1\cdots m}\right)\right] - g(y) \quad . \qquad (3)$$

2.2. Five possible aggregation processes

In this study, we consider the difference of the aggregation process of individual contributions on the reward. For simplicity of explanation, we represent the trait values of all group members by (z_1, z_2,..., 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. We 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. We represent the effect functions in former and latter case as $f_+(\bullet)$ and $f_-(\bullet)$, respectively.

We 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, expect 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 1). The first four functions, $f(\bullet)$ and $f_+(\bullet)$, are monotonically increasing. The bottom function, $f_-(\bullet)$, is monotonically decreasing. We also assume that z is always positive in multiplicative aggregation of investments, and that f_+ and f_- are positive in multiplicative aggregation of effects.

2.3. Evolutionary properties

We analysed the evolution of cooperation level using adaptive dynamics theory (Dieckmann and Low 1996, Metz *et al.* 1996, Geritz *et al.* 1998). We 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 monomorphic case. Consider a population with $\{(x_i, p_i^*)\}_{i=1...m}$. The former condition can be written as

$$W(x_j \,|\{(x_i, p_i^*)\}_{i=1...m}) = W(x_k \,|\{(x_i, p_i^*)\}_{i=1...m}) \quad \forall \quad j,k = 1...m. \qquad (4)$$

If these simultaneous equations have no real solutions, one morph becomes extinct. Otherwise, coexistence is achieved. For coexistence, solving Eq.(4) provides a set of equilibrium frequencies $\{p_i^*\}_{i=1...m}$ that can be expressed in terms of $\{x_i\}_{i=1...m}$, with which we can rewrite the payoff at the coexisting state as $W(y \mid x_1,x_2,\ldots x_m)$, excluding $\{p_i^*\}_{i=1...m}$. Dieckmann and Law (1996) showed that the selection gradient of x_i can be written as

$$\frac{dx_i}{dt} = \beta_i(x_1, x_2, \cdots x_m)\frac{\partial W(y \mid x_1, x_2, \cdots x_m)}{\partial y}\bigg|_{y=x_i} , \qquad (5)$$

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

$$\frac{\partial}{\partial y}W\left(y \mid x_1^*, x_2^*, \cdots x_m^*\right)\bigg|_{y=x_j^*} = 0 \quad \forall j = 1\cdots m \quad . \qquad (6)$$

On a solution that satisfies both Eqs. (4) and (6), we investigated two kinds of stabilities of the solution concerning their evolutionary property, *i.e.* convergence stability (CS) and evolutionary stability (ES). 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

$$\left.\frac{\partial^2}{\partial y^2} W\left(y \mid x_1^*, x_2^*, \cdots x_m^*\right)\right|_{y=x_j^*} < 0 \quad \forall j = 1 \cdots m \tag{7}$$

is satisfied. The condition of CS can be investigated by examining a matrix **M** whose (*i*, *j*)-element is

$$\mathbf{M}_{ij} = \frac{\partial}{\partial x_j}\left(\beta_i(x_1^*, x_2^*, \cdots x_m^*) \left.\frac{\partial W\left(y \mid x_1^*, x_2^*, \cdots x_m^*\right)}{\partial y}\right|_{y=x_i^*} \right). \tag{8}$$

The solution is CS when real parts of all the eigenvalues of **M** are negative (Leimar 2009).

2.4. Evolutionary polymorphism and sustained polymorphism

By examining these evolutionary properties, we investigate two types of possibilities of the existence of polymorphism. First, we 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, we investigate how many morphs can potentially appear through evolutionary branching. In the present study, we 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, we 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, we investigated the possibility of evolutionary polymorphism for five types of aggregation process. Although the detail of the analyses are shown in Appendix A, here we 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

$$W(y \mid x) = (N - 1)\, f(x) + f(y) - g(y) \,. \qquad (9)$$

According to Eqs. (7) and (8), the singular points x^* become CS but non-ES when

$$f''(x^*) < g''(x^*) < f''(x^*) \,. \qquad (10)$$

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

$$W(y \mid x) = f\big(a(N-1)x + y\big) - g(y) \,. \qquad (11)$$

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

$$Nf''\big(Nx^*\big) < g''(x^*) < f''\big(Nx^*\big) \,. \qquad (12)$$

This condition can be satisfied if $g(x^*) < f(Nx^*) < 0$, therefore we cannon reject the possibility that the condition (i) with l = 2 can be satisfied. Moreover, we 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 A). Consequently, in AI type, the evolutionary polymorphism with two or more morphs is potentially possible. We investigated the possibility of evolutionary polymorphism for the other types of aggregation process (MI, pME and sME) by using similar analysis (see Appendix A for the detail of the analysis).

Second, we 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 A). In the present study, we 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, we 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 we show the examples of the analysis for the possibility of the sustained polymorphism for AE type and AI type. Please see Appendix 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

$$f(x_i^*) - g(x_i^*) = f(x_j^*) - g(x_j^*) \quad \forall \quad i, j = 1...m\,, \tag{13a}$$

$$f'(x_i^*) = g'(x_i^*) \quad \forall \quad i = 1...m\,, \tag{13b}$$

have a solution. Because Eqs. (13a) and (13b) yield m-1 and m constraints respectively, there are 2m-1 constraints in total. The number of unknown variables in Eqs. (13) is, m (*i.e.*, trait value $x^*_{i=1...m}$). 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. (12) and Appendix 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, we investigated the sustained polymorphism for the other types of aggregation process (*i.e.* MI, pME and sME, see Appendix A).

It should be noticed that we 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. Our study is thus useful in elucidating evolutionary conditions for polymorphism, and it has direct implication to empirical studies.

3. Results

3.1. Influence of the aggregation process

We analytically investigate the possibilities of evolutionary and sustained polymorphism by applying the general approach described above for five types of aggregation process (see Appendix A for details of our analyses) under the condition without any restriction for the functional shapes of the effect $f(\bullet)$ and the cost $g(\bullet)$. Table 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, the detail of the simulation is written in Appendix 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. (A9) and (A10) in Appendix 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 property 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. We 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 our analysis (see Appendix A).

3.2. Influence of the functional shapes of effect and cost

The functional shapes also influence the possibility of the evolutionary branching. Next, we examine the influence of their functional shapes on the evolutionary process. To do so, we categorize the functional shapes simply into four types, *i.e.* linear, convex, concave, and the other functional shapes (*e.g.* sigmoid), we call the last type as complex type. We examine the condition for evolutionary branching by focusing on AI, MI and sME (see Appendix 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, we 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.

4. Discussion

In the present study, we show that the aggregation process of rewards significantly influences the possibility 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. The present analysis significantly generalised these works to show the potential possibility of evolution of polymorphism for a wider class of payoff functions with various aggregation processes of reward effects. We indicated that polymorphism of cooperation levels never emerges from the evolutionary process unless the aggregation process is AI, MI or sME type. Consequently, we 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 our findings to the empirical examples of cooperation, we 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 our results, cooperation level becomes always monomorphic under AE, but can be polymorphic under AI (see Table 1). In reality, yeasts may share both enzyme and decomposed products probably through the chemical reaction-diffusion process, and our classification of the type of aggregation in yeast is generally difficult to apply to realistic situations directly. However, it is possible to predict from our 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 Table 2). This prediction is supported by an experimental study (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, we 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 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 our "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 our results to such case, the result of which is consistent with the original 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 our framework by using the log translation of payoff (*e.g.* $\log[f(\Sigma z)]$ - $\log[g(z)^{-1}]$).

Although we successfully revealed the importance of the aggregation processes on the evolution of polymorphic cooperation level, there are some open questions. In the present study, we categorized the aggregation processes according to the stage of aggregation, *i.e.* the aggregation of investments or effects. However, the simultaneous aggregation of both investments and effects is also possible. 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 present analysis is based on asexual reproduction, ignoring exchanges of genetic information between individuals. In order to understand observed polymorphism in nature, we have to extend our approach to sexual reproduction. Moreover, the studies about the aggregation process with focusing on more specific cooperative processes are also important for detecting the biological factors or parameters which determine the emergence of polymorphism.

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Figure Legend

Figure 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

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 B.

Figure 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.

Table Legend

Table 1

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

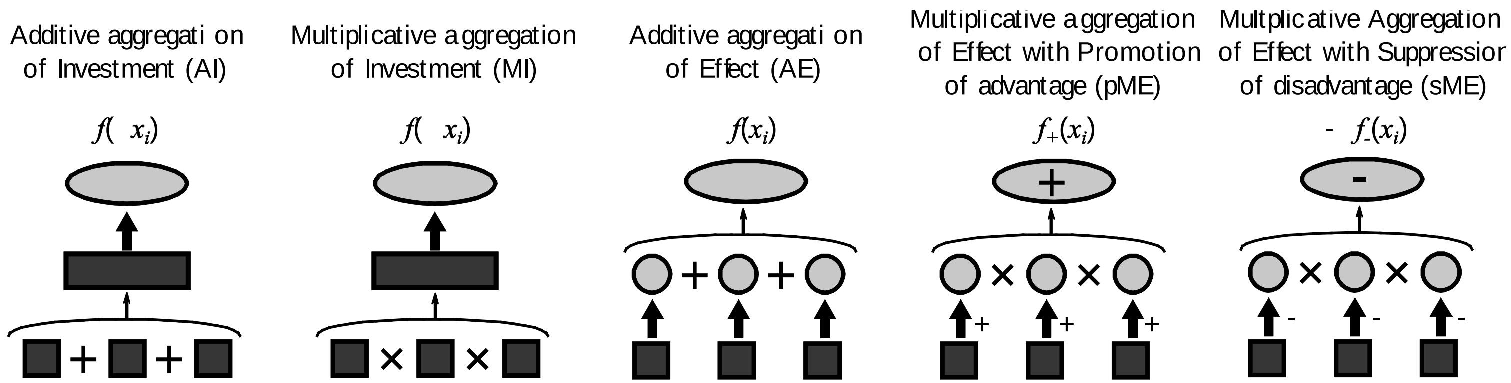

Additive aggregati on of Investment (AI)
Multiplicative aggregation of Investment (MI)
Additive aggregati on of Effect (AE)
Multiplicative aggregation of Effect with Promotion of advantage (pME)
Multplicative Aggregation of Effect with Suppressior of disadvantage (sME)
$f(\ x_i)$
$f(\ x_i)$
$f(x_i)$
$f_+(x_i)$
$-\ f_-(x_i)$

Figure 1

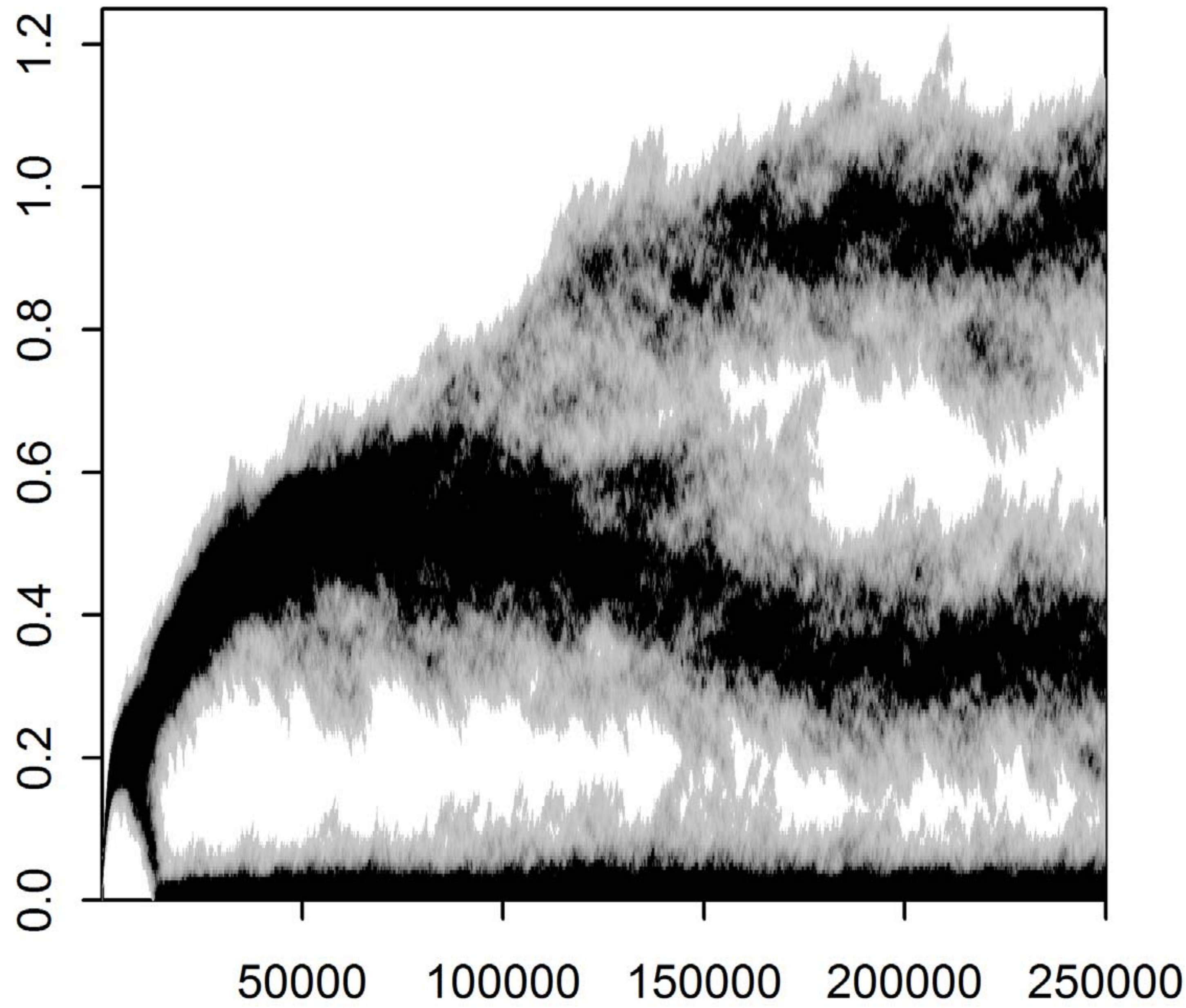
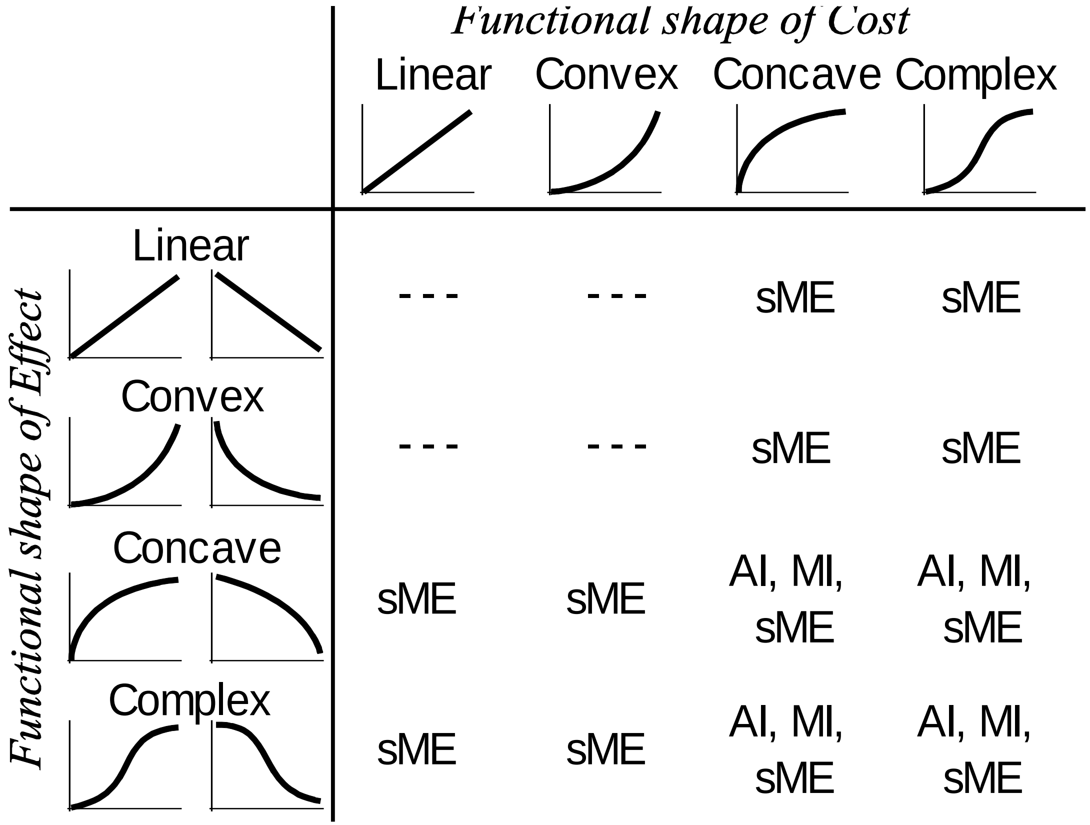


Figure 2



Functional shape of Cost
Linear
Convex
Concave
Complex
Functional shape of Effect
Linear
Convex
Concave
Complex
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sME
sME
- - -
- - -
sME
sME
sME
sME
AI, MI, sME
AI, MI, sME
sME
sME
AI, MI, sME
AI, MI, sME

Figure 3