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# Cooperation Achieved by Migration and Evolution in a Multilevel Selection Context

Genki Ichinose
Graduate School of Information Science
Nagoya University
Furo-cho, Chikusa-ku, Nagoya 464-8601, JAPAN
Email: genki@alife.cs.is.nagoya-u.ac.jp

Takaya Arita
Graduate School of Information Science
Nagoya University
Furo-cho, Chikusa-ku, Nagoya 464-8601, JAPAN
Email: arita@nagoya-u.jp

*Abstract*— **The idea that natural selection can be meaningfully applied at the group level may be more important than previously thought. This perspective, a modern version of group selection, is called multilevel selection. Multilevel selection theory could incorporate previous explanations for the evolution of cooperation including kin selection. There is general agreement that natural selection favors noncooperators over cooperators in the case of an unstructured population. Therefore, the evolution of cooperation by multilevel selection often requires positive assortment between cooperators and noncooperators. The question is how this positive assortment can arise. We constructed an individual-based model of multilevel selection and introduced migration and evolution. The results showed that positive assortment was generated especially when a migration strategy was adopted in which individuals respond specifically to bad environmental conditions. It was also shown that the evolution could further facilitate positive assortment by working with migration. The fact that cooperation was achieved by such migration and by evolution highlights the importance of sensitiveness to the environment and of fluctuations in group size, respectively.**

## I. INTRODUCTION

Altruistic behaviors are common in humans and some other animals, and are essential in the formation of the society. However, the evolution of cooperation is paradoxical, since an altruistic trait confers a cost to the actor and a benefit to other individuals and thus natural selection should favor selfish individuals. Evolutionary biologists have developed theoretical frameworks to explain this paradox. One explanation is reciprocal altruism [1] and another one is kin selection [2]. In 1998, Sober and Wilson proposed a modern version of group selection called “multilevel selection” [3]. This idea has attracted considerable attention because it might incorporate previous theories for the evolution of cooperation.

Consider a population that is subdivided into groups. An individual in a group including many cooperators gets a higher payoff than the one in a group including many defectors (between-group selection). At the same time, a defector gets a higher payoff than a cooperator within the group (within-group selection). Multilevel selection theory shows cooperators evolve when the former selection predominates over the latter selection (Fig. 1). Here, one of the most important questions is how the assortment (or variation) between cooperators and defectors is continually generated. In other words, the evolution of cooperation by multilevel selection requires a structured population in which cooperators interact more frequently with cooperators and defectors interact more frequently with defectors.

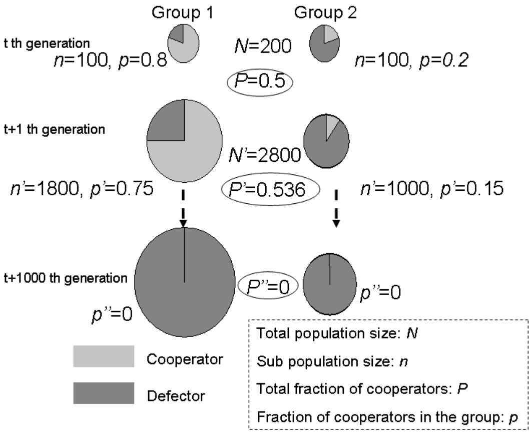

Fig. 1. Cooperation can evolve by the effect of between-group selection (center). However, cooperators eventually go extinct by the effect of within-group selection (bottom) unless the variation between groups is continually generated.

In the past, multilevel selection models that attempted to answer this question had assumed a simple genotype-phenotype relationship. However, genetic and phenotypic variations become tightly linked to each other and the variation between groups is only determined by sampling error in this case. Therefore most evolutionary biologists regard that common ancestry is the only plausible mechanism which generates variation between groups [4]. It is well known that limited dispersal of offspring can generate a population structure. This structure has been called “population viscosity.” Kin selection works well in this structure. Population viscosity has both a positive effect (by increasing the degree of variation) and a negative effect (by exposing clusters of cooperators to stiffer local competition). These opposing forces exactly cancel when population density is fixed, so that limited dispersal does not promote the evolution of cooperation [5]–[7]. Conversely, Mitteldorf and Wilson [8] showed limited dispersal promoted cooperation when population density was permitted to fluctu-

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ate.

On the other hand, human groups often vary greatly in their phenotypic properties. Wilson and Kniffin [9] have discussed the decoupling of genetic and phenotypic variations leads the nonrandom phenotypic variation, and then cooperation can evolve. This decoupling may occur by two cultural mechanisms in human groups: moralistic punishment and conformist bias [10]. Such institutions of culture and cooperation may coevolve [11]. Institutions can reduce within-group selection operating against altruistic traits. For example, resource sharing and segmentation are such institutions. Resource sharing has the effect of reducing payoff differences between cooperators and defectors, and segmentation has the effect of reducing the expected payoff disadvantage of cooperators because cooperators interact more frequently with cooperators than defectors in the group.

In this paper, we investigate the following two points: first, how migration as environmental response affects assortment between groups. Second, how evolution working with such migration affects assortment between groups. Migration is a more general mechanism than phenotypic plasticity seen in human culture. But in general, it has been regarded that migration cancels between-group selection [10], [12]–[16], because all individuals leave and enter the group with equal probability and thus frequent random migration reduces the variation between groups. However, a few studies like Pepper and Smuts's [17], [18] have suggested migration has the reverse effect. They have proposed environmental feedback as a mechanism for generating assortment. In their models [17], each individual can detect the condition of its environment, specifically the amount of food in its patch, and it tends to migrate if the food is not enough there. They showed that positive assortment required for the evolution of cooperation was generated by such migration. But there remains the question what type of environmental migration is effective for the evolution of cooperation. In order to answer this question, we consider some typical types of migration as environmental response, including the one adopted in Pepper's model [18], and focus on the effects caused by such patterns of migration. We also discuss the effect of evolution working with migration on assortment. Previous models of multilevel selection (or group selection) did not fully discuss the relationship between evolution and migration, particularly when group size varies greatly by evolution. In those models, evolution was not considered [17], [18], or when migration and evolution were considered, the groups size was always [13] or regularly [19] constant.

We begin by showing whether migration as environmental response can generate positive assortment without evolution. Then, we investigate the effect of varying group size on assortment by introducing evolution into the model.

## II. MODEL

We constructed an individual-based model of multilevel selection with migration as environmental response. We adopted the N-person Prisoner's Dilemma (NPD) game in our multilevel selection model because NPD can offer the tension between within-group and between-group selection when multiple groups are considered. In this game, $N$ persons independently choose actions from cooperate or defect without knowing the other players' choices, then each player obtains the payoffs according to the fraction of cooperators ($p$). NPD is defined to satisfy the following two conditions. First, defection is a dominant strategy because each player is better off by choosing defection than cooperation in all fraction of cooperators. Second, but if all cooperate they can get better payoffs than if all defect.

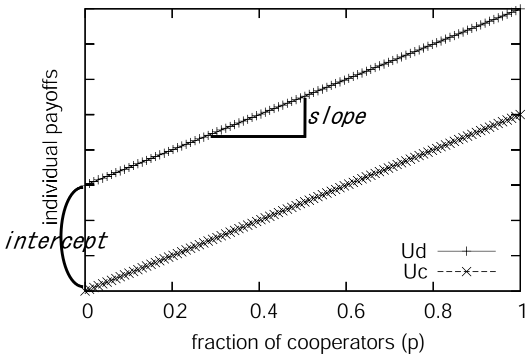

Fig. 2. N-person prisoner's dilemma (NPD).

We introduced migration into the model, in which typical patterns of environmental response are investigated.

### A. Algorithms

The population is composed of $N$ individuals and they are divided into $n$ patches in the initial state. The set of individuals occupying a patch constitutes a group. This is often regarded as a "trait group" [20] because behaviors of the individual affect the fitness of other members in the group each other. An individual is a Cooperator (C) or a Defector (D). All individuals follow the same migration rule (Sec. II-B). The simulations are conducted using the following procedures:

1) The population is composed of $N$ individuals, and C (1) is assigned to half of the individuals and D (0) is assigned to the others. In the evolutionary experiment (Sec. III-C): instead, C (1) or D (0) is randomly assigned to individuals.
2) They are randomly divided into $n$ patches.
3) They play NPD in each group independently. C (D) gets the payoff of $U_{Ci} = slope \times p_i$ ($U_{Di} = slope \times p_i + intercept$), where $p_i$ is the fraction of cooperators in group $i$, $slope$ and $intercept$ denote slope and intercept of the NPD function (Fig. 2).
4) Each individual decides whether it migrates or not by using the migration function explained in the next section. In the evolutionary experiment (Sec. III-C): in addition, a new population is generated by the roulette wheel selection according to the payoffs until the population size reaches $N$, and then mutation is performed on the

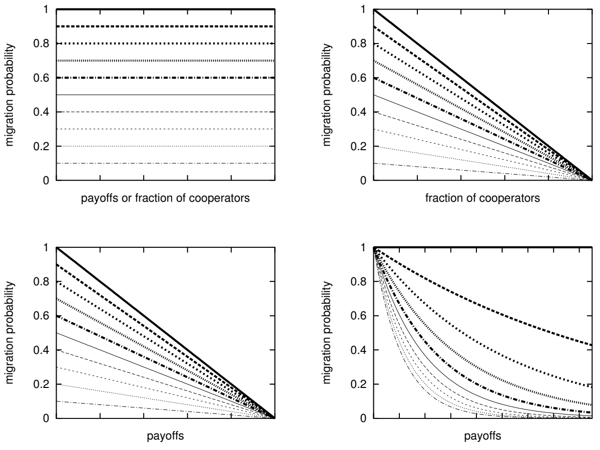

Fig. 3. Migration functions. Each line is drawn from $a, b, c, d = 0.1$ to $a, b, c, d = 1.0$ at intervals of 0.1.

dilemma strategy, with probability $m$. A current strategy is changed into an opposite strategy by mutation. Each offspring belongs to the group in which her parent was. Whether the offspring migrate or not depends on the decision in the parent stage.

5) Individuals chosen by the migration function migrate to a randomly chosen other patch.
6) A sequence of procedures of 3)-5) is taken as a step (or generation), and repeated for 3000 steps (or generations).

### *B. Migration functions*

We assume that each individual monitors its environmental quality by the fraction of the cooperators in its group or the obtained payoff. In this model, groups including many defectors are regarded as poor environment, and those who belong to them tend to migrate into other patches. Specifically, we assumed different migration functions as follows (Fig. 3). $a, b, c$ and $d$ are parameters and $p_{mig}$ is a migration probability.

- Nonenvironmental Response (upper left in Fig. 3): individuals migrate independently of the environment condition, which will be served as the control experiment. The migration probability is a constant:

$$p_{mig} = a. \tag{1}$$

- Environmental Response (i) (upper right in Fig. 3): individuals tend to migrate if the group contains a high fraction of defectors:

$$p_{mig} = b(1 - N_{Ci}/N_i), \tag{2}$$

  where $N_{Ci}$ is the number of cooperators in the group $i$, $N_i$ is the number of individuals (cooperators and defectors) in the group $i$. Migration function at $b = 1$ is equivalent to the that of Pepper's model [18].

- Environmental Response (ii) (lower left in Fig. 3): individuals who get lower payoff tend to migrate:

$$p_{mig} = c(1 - U_{ij}/U_{max}), \tag{3}$$

  where $U_{ij}$ is the payoff of the individual $j$ in the group $i$, and $U_{max}$ is the hypothetically maximum payoff in NPD, then $U_{max} = slope + intercept$.

- Environmental Response (iii) (lower right in Fig. 3): individuals tend to migrate only when payoffs are extremely low:

$$p_{mig} = e^{-(1-d)U_{ij}}, \tag{4}$$

Note that cooperators always get lower payoffs than defectors in each group. Therefore, unlike in the cases of Nonenvironmental Response and Environmental response (i), cooperators tend to migrate more often than defectors in the cases of Environmental Response (ii) and (iii).

## III. EXPERIMENTS

The parameters common to all experiments were set as follows: population size $N = 400$, number of patches $n = 100$, mutation probability $m = 0.01$, slope of the NPD function $slope = 5$, intercept of the NPD function $intercept = 3.5$. Note that empty patches sometimes exist since $n$ is relatively large in comparison with $N$. A range of parameters of each migration function is $0.00 \le a, b, c, d \le 1.00$ at intervals of 0.01 (a total of 404 cases were investigated). We conducted 100 runs of 3000 steps with each migration pattern and compared the average of 100 runs of assortment between groups from 1000th step to 3000th step.

### *A. Relatedness as an assortment index*

We use the following (extended) relatedness [21]–[23] in order to measure the assortment between cooperators and defectors:

$$r = \frac{V_B}{V_B + \overline{V_W}}, \tag{5}$$

where $V_B$ and $\overline{V_W}$ are the genetic variance between groups and the average genetic variance within groups, respectively, and thus $r$ represents the between-group variance over the total variance. To calculate the variance involving just two types of individuals, we regard that all cooperators have one genotypic value and all defectors have another (C:1, D:0).

Pepper [24] termed "whole-group" altruistic traits where the benefit is divided among all group members including the actor, and "other-only" altruistic traits where the altruist's benefits do not come back to itself. The value of $r$ differs for other-only and whole-group traits because in the latter case altruists are recipients of their actions [24]. In our models, we use $r$ as the relatedness of "whole-group" traits since the benefits of altruists come back to the actor itself.

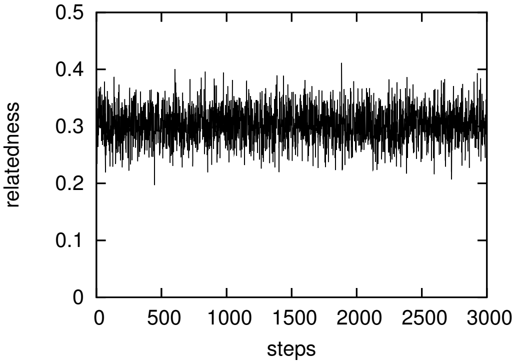

Fig. 4. The change in relatedness as a function of steps. Nonenvironmental Response, $a = 0.50$.

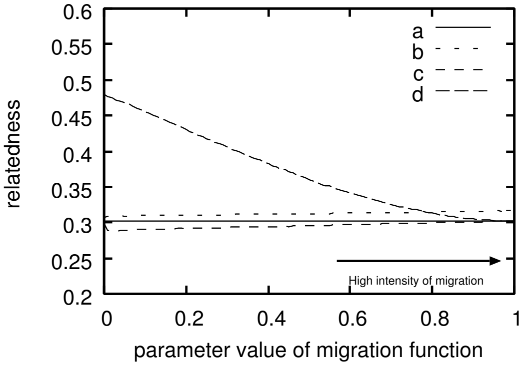

Fig. 5. The average of 100 runs of the relatedness as a function of each migration parameter ($a, b, c$ or $d$) in no evolution results.

### B. No evolution results

The fraction of cooperators was fixed at 0.5 and never changed from the initial state in no evolution results. Hence, we only investigated the relatedness as an assortment index in this experiment. Relatedness changed dynamically in each run (e.g. Fig. 4) and thus we compared the average of 100 runs of relatedness between the cases with four different migration functions in order to investigate the effect of the environmental response in detail. In Fig. 5, 7 and 8, the intensity of migration increases as the parameters take higher values although the meaning of each parameter in each migration function is different and thus quantitative comparison using the horizontal axis has little meaning.

Fig. 5 shows the value of $r$ in Environmental Response (iii) increased as the intensity of migration became low. The max value of $r$ is about 0.48 at $d = 0$. It is a remarkable fact that a little difference of migration functions generates a large difference of assortment. We illustrate this reason using a simple example. Consider the situation in which a cooperator is in the group of defectors by chance (Fig. 6). Such a cooperator tends to continue to migrate until he enters the group with a high fraction of cooperators (or the empty patch), thus cooperators and defectors are separated. This tendency is strong when the value of $d$ is low. That value in Environmental Response (ii) was the lowest on the whole. The possible cause of this is the number of migrating cooperators in cooperative groups is larger than in noncooperative groups, and the number of migrating defectors in noncooperative groups is larger than in cooperative groups as a result, hence variation between groups tend to be reduced. The value of $r$ in Nonenvironmental Response was a little higher than the one in Environmental Response (ii). The reason for this is all individuals leave the group with equal probability at a given parameter value and migrate randomly, and thus all groups tend to be the equal distribution of C and D. That value in Environmental Response (i) was a little higher than the one in Nonenvironmental Response probably because a concentration of cooperators tends to be maintained when $b$ is high. We also found that Pepper's model ($b = 1$) generated little assortment in comparison with Environmental Response (iii).

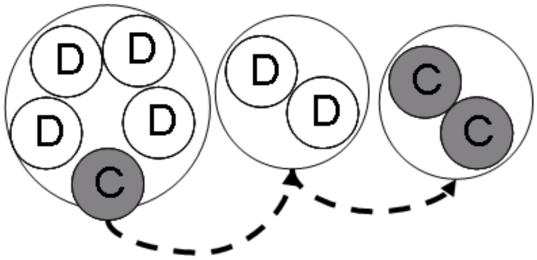

Fig. 6. A cooperator in the group of defectors by chance.

The minimum value of $r$ is not 0 but about 0.3 in all functions. The reason for this is relatedness to self is always 1 and self makes up $1/s$ (where $s$ is a size of the group) in a group [24].

### C. Evolution results

We conducted evolutionary experiments on the condition that II. 1) and II. 4) were changed as stated in the previous section, but all of the other settings and parameters are the same as previous ones. We compared the average of 100 runs of the fraction of cooperators from 1000th generation to 3000th generation (we use the term "generations" instead of "steps" in evolution results) in each migration function (Fig. 7), in addition to the average of 100 runs of the relatedness (Fig. 8).

First of all, we found the peaks of the cooperation existed in the intermediate intensity of migration in all cases (Fig. 7). The dominant reason for this is considered to be the "founder effect" [25]. The founder effect is an extreme example of genetic drift and is the alteration of gene frequencies resulting from the establishment of a new population generated by a few individuals isolated from the parental population.

We consider that the following process occurs in our simulations (Fig. 9). First, evolution leads to dynamic change in the group size and sometimes creates the empty patches. And then migration changes group size again except for the no migration case. The groups tend to be returned to a similar

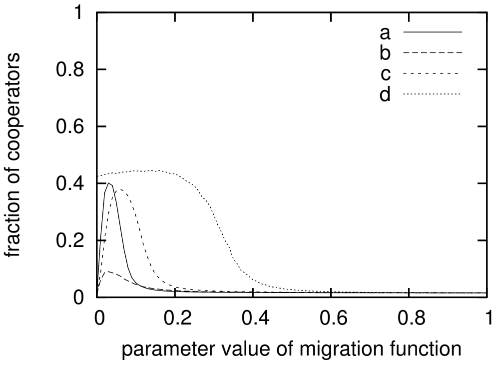

Fig. 7. The average of 100 runs of the fraction of cooperators as a function of each migration parameter ($a, b, c$ or $d$) in evolution results.

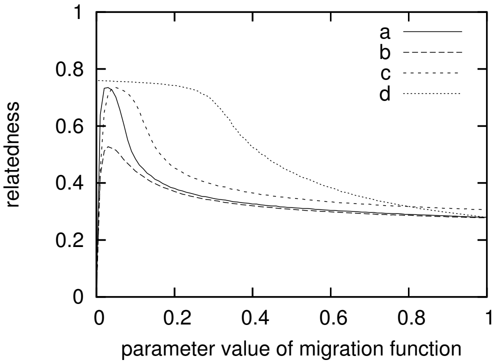

Fig. 8. The average of 100 runs of the relatedness as a function of each migration parameter ($a, b, c$ or $d$) in evolution results.

size in the high migration case. On the other hand, intermediate (or low in the case of these parameters) migration keeps the variation of group size. In the intermediate case, we considered a few individuals migrate to the empty patches, and as a result, a founder might tend to arise by evolution and migration, and thus the variation between groups became high (Fig. 10). We investigated this assumption by plotting the correlation between the average fraction of small groups and the average fraction of cooperators (or the average relatedness) in the case of Nonenvironmental Response (Fig. 11), and confirmed that cooperation tended to evolve when the average fraction of small groups is high by the effect of evolution working with migration.

Fig. 7 shows the relationship between the peak values as follows: Environmental Response (iii) (0.445 at $d = 0.16$) $>$ Nonenvironmental Response (0.401 at $a = 0.03$) $>$ Environmental Response (ii) (0.379 at $c = 0.06$) $>$ Environmental Response (i) (0.090 at $b = 0.03$). Therefore we found that Environmental Response (iii) had the highest peak of the cooperation. The possible cause of this is the effect of the decoupling C and D as stated in the previous section works in addition to the founder effect and thus a cooperator tends to become a founder. We also found that Environmental Response

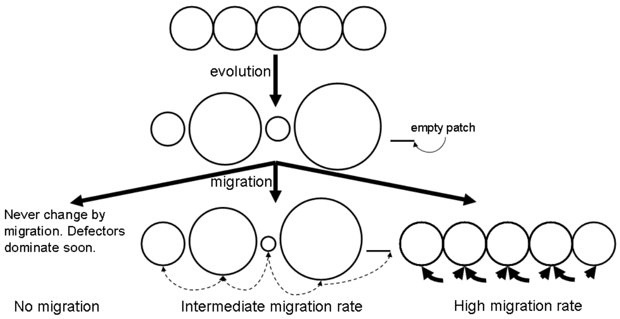

Fig. 9. Evolution coupled with migration leading to positive assortment.

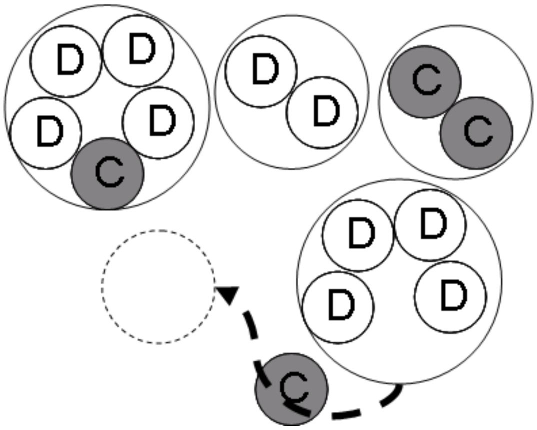

Fig. 10. The appearance of founder of cooperator in intermediate migration.

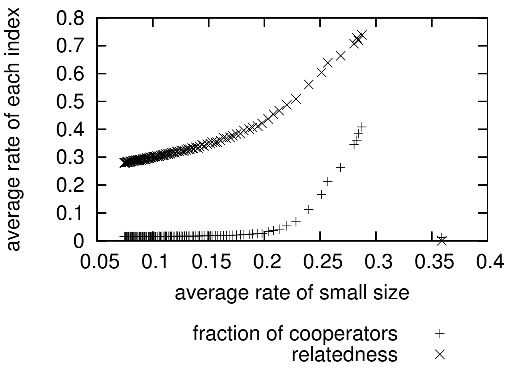

Fig. 11. The correlation between the average fraction of small groups (with the size of 1) and the average fraction of cooperators (or the average relatedness) in the case of Nonenvironmental Response. Each point corresponds to the pair of values in the case with the different setting of $a$.

(i) had the lowest peak of the cooperation. The possible cause of this is the situation that migration do not occur and the following founder of cooperator hardly arise continues for a while although the fraction of cooperators decreases gradually after once it becomes high by the founder effect, and thus the average fraction of cooperators becomes low.

Fig. 8 shows the average of 100 runs of the relatedness in each migration function. The shape of the curve roughly corresponds to the one of the fraction of cooperators (Fig. 7). We confirmed that the variation of different types led to the evolution of cooperation.

### *D. Summary of the results*

In the case of no evolution results, migration as a specific response to bad environment like Environmental Response (iii) notably led to the variation between groups. Additionally, in the case of evolution results, the variation between groups was generated in all migration functions, but nevertheless Environmental Response (iii) still had the most variation between groups. Therefore, we confirmed the importances of migration as environmental response and evolution working with such migration to the evolution of cooperation.

### *E. Parameter dependence*

We also investigated the model with different parameter settings. The model has five parameters: population size $N$, number of patches $n$, mutation probability $m$, slope and intercept of the NPD function $slope$ and $intercept$. We varied the ratio ($n/N$) instead of varying $N$ and $n$ independently as it seems sufficient for understanding basic properties.

Fig. 12 shows the peaks of fraction of cooperators in each migration function with different parameter values. First of all, it has been shown that $n/N$ and $slope$ have a positive effect and $m$ and $intercept$ have a negative effect on the evolution of cooperation. A high ratio of $n/N$ leads to a large variance between groups and a high $slope$ makes cooperative groups more advantageous than noncooperative groups. Therefore, these two parameters enhance the effect of between-group selection. On the other hand, $m$ and $intercept$ enhance the effect of within-group selection because a high $m$ leads to a breakdown of cooperative groups and a high $intercept$ makes defectors more advantageous than cooperators within the group.

Another important aspect is Environmental Response (iii) is more effective in evolving cooperation than others especially when varying the parameter $intercept$. The possible cause of this is the decoupling C and D occurs effectively since only cooperators tend to migrate in the cases with a high $intercept$.

## IV. APPLYING HAMILTON'S RULE

We also applied the Hamilton's rule to predict a short term of the evolution of cooperation. Theoretically, cooperation evolves if Hamilton's rule is satisfied. Hamilton [2] stated that the condition for an altruistic trait to increase in the next generation is:

$$rb - c > 0, \tag{6}$$

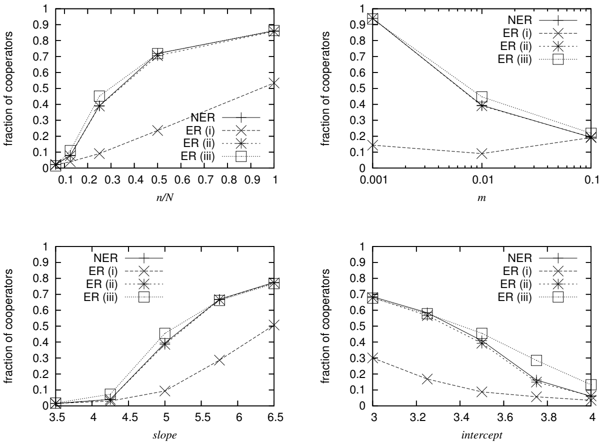

Fig. 12. Each line is Nonenvironmental Response (NER), Environmental Response (ER) (i), (ii) or (iii). Each point represents the peak value of the fraction of cooperators when varying each migration parameter (a, b, c or d), averaged over 10 runs.

where $r$ is the relatedness (we use the between-group genetic variance over the total genetic variance as relatedness (5)), $b$ is the fitness effect on the recipients of the act, $-c$ is the fitness effect on the actor.

Hamilton [2] originally conceived relatedness as a measure of a kinship. Later, it is suggested that relatedness can be treated as a measure of assortment among altruistic traits in group-structured populations [24], [26]. Multilevel selection theory is equivalent to Hamilton's inclusive fitness theory in this sense.

Fig. 13 shows the correlation between the amount of the change in the fraction of cooperators ($\Delta C$) and the relatedness between groups. In each graph, the dashed line represents the regression line of the data. The dotted line represents the theoretical threshold $c/b$ (where $c$ and $b$ are $intercept$ and $slope$ respectively in the NPD game) which determines whether cooperation will increase in the next generation. We see that the relatedness roughly reflects whether cooperation would increase in the next generation and its tendency was consistent with the theoretical threshold. Therefore, we confirmed that our results corresponded approximately to the theoretically predicted ones.

## V. CONCLUSION

The main purpose of this paper is to show that migration as environmental response and evolution working with such migration can generate the variation between groups, which is required for the evolution of cooperation. We constructed an individual-based model of multilevel selection with four typical patterns of the environmental response and with evolution. We found that migration as a specific response to bad environment and the founder effect on the process of the evolution generated the variation between groups. These results imply that sensitiveness to environments and fluctuations in group size may promote cooperation.

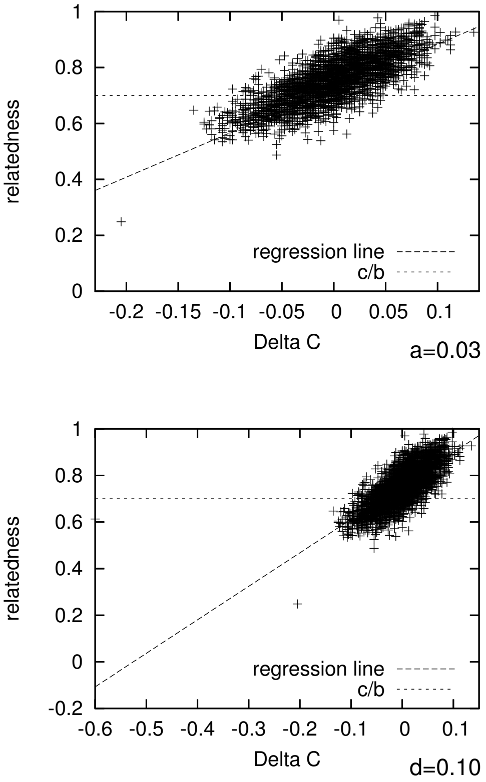

Fig. 13. Correlation between the amounts of the change in the fraction of cooperators and the relatedness between groups. The regression line describing the data exceeds the threshold value of $c/b$ in the vicinity of $\Delta C = 0$, as the Hamilton's rule predicts.

This model can be extended in several directions. It might be interesting to consider the patterns of not only the emigration but also of the immigration. This perspective is important especially when considering the evolution of cooperation in human groups. Another direction would be to attempt to evaluate our results concerning the effects of migration in the purely biological context.

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