

# Tracking the Red Queen Effect by Estimating Features of Competitive Co-Evolutionary Fitness Landscapes

Yoshiaki KATADA, *Member, IEEE* and Yuta HANDA

**Abstract**—Open-ended evolution is considered to be caused by several factors, one of which would be co-evolution. Competitive co-evolution can give rise to the “Red Queen effect”, where the fitness landscape of each population is continuously changed by the competing population. Therefore, if such continuous changes are captured, co-evolutionary progress would be measured. In this paper, we estimate features of competitive co-evolutionary fitness landscapes on a predator-prey problem in computer simulations and investigate the Red Queen effect on the fitness landscape. Two types of method were proposed to estimate features, *ruggedness* and *neutrality*. One was calculated based on accumulated data so far at each generation, and the other was based on accumulated data during a certain period. The results suggest to us that our method can track the progress of fitness landscapes on competitive co-evolutionary robotics.

## I. INTRODUCTION

Open-ended evolution is considered to be caused by several factors, one of which would be co-evolution [1]. In competitive co-evolution, “Red Queen hypothesis” has been discussed where a species must evolve for its existence and it becomes extinct if it stops evolving. In the simplest scenario of two competing species, an advantage of one species might lead to the disadvantage of the other species, then the other species also responds with counter-adaptive strategies to get its own advantage, which appear “a co-evolutionary arms race”.

In competitive co-evolution, the fitness landscapes of competing populations might be continuously changed by such arms races. These changes could prevent populations from being stuck on local areas of the landscape [2] as well as stimulate them to move better regions. Therefore, if such changes could be captured, co-evolutionary progress would be measured.

In the Evolutionary Computation community, the geography of a fitness landscape has been discussed with respect to problem difficulties. These are conceptualized as *isolation*, *deception*, *multimodality* and *flatness*. In recent years, those are measured as the features of a fitness landscape, *ruggedness* (*epistasis*) and *neutrality* [3][4][5][6][7][8][9][10][11][12][13]. Ebner *et al.* [14] investigated the dynamics of competitive co-evolution by a simple model where fitness landscapes are deformed by the existence of other species. Within the limit of our knowledge, however, there is no literature to investigate competitive co-evolutionary dynamics with respect to the features of a fitness landscape.

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In this paper, we propose methods to estimate features of competitive co-evolutionary fitness landscapes on a predator-prey problem in computer simulations in order to investigate the Red Queen effect on the fitness landscape. Pursuit and evasion have been studied in various fields, behavioral biology, neuroethology, game theory and embodied cognitive science. This is straightforward to study competitive co-evolution. Predator-prey problems in our computer simulations are implemented in the context of evolutionary robotics where a mobile agent has its own neural controller with sensory-motor architectures and interacts with the competing agent and the environment. It has been known that such evolutionary robotics fitness landscapes include both ruggedness and neutrality [10][11][12][13]. In [13], we proposed a method to estimate the degree of neutrality and ruggedness in fitness landscapes, then confirmed the validity of the proposed approach in an evolutionary robotics problem. However, that was a problem with single species. Therefore, we need to make some modifications of the proposed method [13] in order to capture changes of fitness landscapes for competitive co-evolutionary problems.

The paper is organized as follows. The next section describes the method to estimate the degree of ruggedness and neutrality in fitness landscapes, which we proposed in [13], and then extends it for competitive co-evolution. Section III describes an experimental setup for predator-prey in a robot control problem. Section IV gives the results of our computer simulations. Section V discusses performances of the best individuals across generations. Conclusions are given in the last section.

## II. METHODS FOR MEASUREMENTS OF FEATURES OF FITNESS LANDSCAPES

In this section, the procedure for estimating features of a fitness landscape is described. Features to be measured are ruggedness and neutrality. Ruggedness is estimated based on the Smith’s measurement [12] and neutrality is based on our measurement, the Standard Genetic Distance [15][13].

### A. Measure of Ruggedness

In real-world problems, ruggedness of a fitness landscape is predicted by fitness correlation [5][12]. In this paper, the measurement proposed by Smith *et al.* [12] was employed for the measure of ruggedness because fitness correlation can be expressed as a scalar value in their measurement. In [12], it has been reported that fitness correlation is expressed by the gradient of the expected offspring fitness versus parent

fitness graph. The expected offspring fitness for parent fitness  $k$  is given by

$$\bar{f}^k = \frac{\sum_{g \in G^k} f(g)}{|G^k|} \quad (1)$$

where,  $G^k$  is the set of offspring from parents with the fitness  $k$  over generations,  $g$  is an offspring genotype and  $f(\cdot)$  is the fitness function. It has been also reported in [12][13] that the gradient,  $r$ , increases with the decrease of ruggedness, that this gradient is independent of neutrality and that  $r \simeq 1.0$  without any epistatic linkages between genes and  $r \simeq 0.0$  with maximum epistatic linkages.

### B. Standard Genetic Distance and its characteristics

Genetic distance is a term of population genetics used for estimating gene differences per locus between populations. Although there are several definitions for this, the Nei's standard genetic distance[15] is adopted in our method[13].

The Nei's standard genetic distance is defined as follows. Consider two populations,  $X$  and  $Y$ . Let  $x_{il} = n_{il}/M$  and  $y_{il} = n_{il}/M$  be the frequencies of the  $l$ -th alleles ( $i = 1, \dots, N$ ,  $N$ , the length of the genotype,  $l \in \{1, 2\}$  in a binary coded GA,  $n_{il}$ , the number of the  $l$ -th allele,  $M$ , the population size) in  $X$  and  $Y$ , respectively. The probability of identity of two randomly chosen genes is  $j_{xi} = x_{i1}^2 + x_{i2}^2$  in the population  $X$ , while it is  $j_{yi} = y_{i1}^2 + y_{i2}^2$  in the population  $Y$ . The probability of identity of a gene from  $X$  and a gene from  $Y$  is  $j_{xyi} = x_{i1}y_{i1} + x_{i2}y_{i2}$ . The normalized identity of genes between  $X$  and  $Y$  with respect to a locus is defined as

$$I_i = \frac{j_{xyi}}{\sqrt{j_{xi}}\sqrt{j_{yi}}}, \quad (2)$$

where,  $I_i = 1.0$  if the two populations have the same alleles in identical frequencies, and  $I_i = 0.0$  if they have no common alleles. The normalized identity of genes between  $X$  and  $Y$  with respect to the average in all loci is defined as

$$I = \frac{J_{XY}}{\sqrt{J_X}\sqrt{J_Y}}, \quad (3)$$

where,  $J_X = \sum_{i=1}^L j_{xi}/L$ ,  $J_Y = \sum_{i=1}^L j_{yi}/L$ ,  $J_{XY} = \sum_{i=1}^L j_{xyi}/L$  and  $L$  is the number of loci. The genetic distance between  $X$  and  $Y$  is defined as

$$D = -\log_e I. \quad (4)$$

The above definition cannot be applied to the GAs directly, because it is assumed that a new allele always appears on a locus when a mutation occurs, while "back mutations [16]" frequently occur in the GAs, due to the binary coding scheme. Therefore, the genetic distance of GAs between populations at the initial generation and at the last generation is calculated as:

$$D_{1,t_l} = \sum_{t=1}^{t_l-1} D_{t,t+1} \quad (5)$$

where  $t_l$  is the number of the last generation and  $D_{t,t+1}$  is the genetic distance between the population in the  $t$ -th and the  $(t+1)$ -th generation.

In [17], we investigated the characteristics of the Nei's standard genetic distance (equation (5)) in the fitness landscapes with ruggedness and neutrality. These characteristics can be summarized as follows:

When the mutation rate per locus is sufficiently small,

- 1) The genetic distance increases approximately linearly over generations in fitness landscapes with neutrality.
- 2) The genetic distance increases with the increase of neutrality.
- 3) The genetic distance decreases with the increase of ruggedness in landscapes with neutrality.
- 4) The genetic distance decreases with the increase of the population size.

Due to the characteristics 1) and 2), the gradient of the genetic distance over generations,  $\alpha$ , can be an index of the increase of neutrality. Moreover, we need to consider the effect of ruggedness on the genetic distance due to 3). Considering these, we proposed a method to estimate the degree of neutrality in fitness landscapes on a real-world problem [13]. The next subsection shows the procedure in details.

### C. Procedure for Estimating the Degree of Neutrality

In this paper,  $r$  and  $\alpha$  which are described in previous subsection II-A and II-B are calculated by using the method of least squares on the result of each run (For details, readers may refer to [13][17]). Thus, the procedure for estimating the degree of neutrality in a fitness landscape on a real-world problem can be summarized as follows:

- i) Confirm the existence of neutrality in a fitness landscape on a real-world problem by investigating transitions of the genetic distance over generations.
- ii) Calculate a point,  $(r, \alpha)$ , from each run on the real-world problem.
- iii) Calculate a set of  $r$ - $\alpha$  curves in test functions with different levels of ruggedness and neutrality.
- iv) By using a set of  $r$ - $\alpha$  curves as a baseline, judge where a point,  $(r, \alpha)$ , obtained from the real-world problem locates in the graph of  $(r, \alpha)$ . Then estimate indirectly the degree of neutrality on the real-world problem.

The reason why the step iii) and iv) are conducted is that the genetic distance is affected by both neutrality and ruggedness as mentioned in Section II-B. Test functions, the NKp[18] and NKq[19] fitness landscapes (see the details in Appendix), are adopted for obtaining a set of  $r$ - $\alpha$  curves. The landscape parameters of the NKp and the NKq should be decided at the step iii) for conducting the step iv). Addition to this, the parameters of the GAs (a mutation rate, a population size, a tournament size, etc.) for test functions should be the same as those for a real-world problem due to the characteristics of the standard genetic distance.

### D. Small Modifications for Competitive Co-evolution

The previous subsection described the measurement for single species. Because they assume a fixed fitness landscape, only average features of a fitness landscape are calculated

based on the accumulated data from the initial generation to the last generation at the end of each run. In order to measure changing features of competitive co-evolutionary fitness landscapes, we did two kinds of modification for the number of generations over which calculations are made in Equation (1) and (5) as follows;

**Metric A)** The first metric is similar to the original one, where changing features are measured based on the accumulated data from the initial generation to the current generation,  $t_c$ .  $\bar{f}_{1,t_c}$  is calculated based on Equation (1) as follows:

$$\bar{f}_{1,t_c}^k = \frac{\sum_{g \in G_{1,t_c}^k} f(g)}{|G_{1,t_c}^k|} \quad (6)$$

where,  $G_{1,t_c}^k$  is the set of offspring from parents with the fitness  $k$  over  $t_c$  generations, In the same way,  $D_{1,t_c}$  is calculated based on Equation (5) using the following equation:

$$D_{1,t_c} = \sum_{t=1}^{t_c-1} D_{t,t+1} \quad (7)$$

Thus,  $r_{1,t_c}$  and  $\alpha_{1,t_c}$  are calculated by using Equation (6) and (7), respectively.

**Metric B)** In the second metric, features are measured only based on the accumulated data for certain generations.  $\bar{f}_{t_s,t_e}$  is calculated using the following equation,

$$\bar{f}_{t_s,t_e}^k = \frac{\sum_{g \in G_{t_s,t_e}^k} f(g)}{|G_{t_s,t_e}^k|} \quad (8)$$

where,  $G_{t_s,t_e}^k$  is the set of offspring from parents with the fitness  $k$  from  $t_s$  to  $t_e$  generation, and  $t_s$  is the first generation for the certain generations and  $t_e$  is the last one. In the same way,  $D_{t_s,t_e}$  is calculated using the following equation:

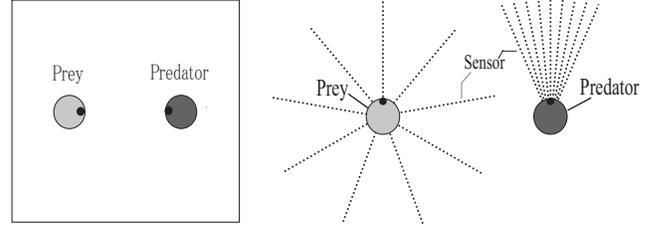
$$D_{t_s,t_e} = \sum_{t=t_s}^{t_e-1} D_{t,t+1}. \quad (9)$$

Thus,  $r_{t_s,t_e}$  and  $\alpha_{t_s,t_e}$  are calculated by using Equation (8) and (9), respectively.

In the remainder of this paper, for simplicity, we occasionally denote  $r_{1,t_c}$  or  $r_{t_s,t_e}$  by  $r$ , and  $\alpha_{1,t_c}$  or  $\alpha_{t_s,t_e}$  by  $\alpha$ .

### III. CONTROL TASK AND FITNESS FORMULA

The control task used in this paper was a predator-prey problem, and is based on a task originally implemented by Floreano [2]. Following the setting given in [2], this problem was implemented in the context of evolutionary robotics. The simulated environment is shown in Figure 1(a), where a predator seeks to hit (capture) a prey. Generally, predators and preys are set belonging to different species which have different sensors and motors. Following this setting, two kinds of sensor arrangement were employed, one (the predator) is equipped with linear while the other (the prey) is equipped with omni-direction (Figure 1(b)). Both agents were equipped with 18 infrared proximity sensors: the 9 ones for detecting the other agent and the other ones for



(a) Two species evolved in a square arena with walls

(b) Simulated models of the sensors for predator and prey robots.

Fig. 1. Experimental setup for a predator-prey problem

walls. The agent's behavior is controlled by artificial neural networks (ANN), which details are described in Section IV.

Employing a mathematical model of a mobile robot, the displacement of the agent (the position:  $x_m, y_m$ , the orientation:  $\theta_m$ ) was computed as follows:

$$\begin{aligned} x_{m+1} &= x_m + \frac{V_R + V_L}{2} \cos \theta_m \\ y_{m+1} &= y_m + \frac{V_R + V_L}{2} \sin \theta_m \\ \theta_{m+1} &= \theta_m + \frac{V_R - V_L}{2R}, \end{aligned} \quad (10)$$

where  $V_R$  and  $V_L$  are the velocities applied to the right and left wheel respectively,  $R$  is the radius of an agent,  $2R$  is the interval between the wheels. The maximum speed is equally set for both agents. The system error was not assumed due to simple analysis.

At the beginning of each trial, the predator and prey were always positioned on a horizontal line at the four random orientations in the middle of the environment at a distance corresponding to half the environment width (Figure 1(a)). One trial ended either when the predator hits the prey or when 400 steps are performed without the hit. Based on the fitness function used by [2], the performance measure to be maximized for the predator,  $pr$ , and the prey,  $py$ , were as follows:

$$Fitness_{pr} = \sum_{i=1}^{NumTrials} \frac{1 - Step_i/MaxStep}{NumTrials}, \quad (11)$$

$$Fitness_{py} = \sum_{i=1}^{NumTrials} \frac{Step_i/MaxStep}{NumTrials}. \quad (12)$$

where  $NumTrials$  is the number of trials for an individual (16 trials for each individual) and  $MaxStep$  is set at 400. The fitness function increases as the predator catches the prey more quickly while the prey escapes longer before being caught by the predator.

## IV. COMPUTER SIMULATIONS

### A. Simulation Conditions

In the general settings of competitive co-evolution, an individual  $I$  from generation  $t$  is evaluated against representatives of  $I$ 's opponent population from each previous

generation  $t - t'$ :  $t' \in T$ ,  $T \subset \{0, 1, \dots, t\}$  [20]. In Last Elite Opponent (LEO) evaluation[20], each individual's fitness is evaluated only in trials against the best individual from the previous generation of the opponent population,  $T \in \{1\}$ : we refer to this as BP1. In [2][21][22], each individual is evaluated against the best competitors of the ten previous generations,  $T \in \{1, 2, \dots, 10\}$ : BP10. For  $T \in \{0\}$ , each individual is evaluated only against an individual selected randomly from the same generation of the opponent population: SG. In this paper, we employed these three evaluations.

In this work, the agent controller was constructed by the ANN with 18 sensory neurons, 2 fully interconnected motor neurons and 3 fully interconnected hidden neurons. The connection weights among neurons were genetically encoded and evolved. The total number of parameters is equal to 115. The parameters were mapped linearly with the range,  $\omega \in [-1.0, 1.0]$ . The output of neurons is given by the sigmoid function,  $f(x) = 1/(1 + \exp(-x))$ .

In computer simulations, the simple GA (SGA) [23] were adopted to evolve ANN parameters as well as calculate the genetic distance. Each individual was encoded as binary strings with 10 bits for each parameter. Therefore, the total length of the genotype is  $L = 1150$ . The genetic operation for the SGA was standard bit mutation following the setting given in [13]. Based on the assumption of the genetic distance in Section II-B, the per-bit mutation rate was set at  $1/L$ . A set of landscape parameters of the NKp and the NKq for the step iii) in Section II-C was decided in the preliminary computer simulations. In this experiment, the following landscape parameters were adopted:  $N = 20$ ,  $K \in \{0, 1, \dots, 19\}$  for the NKp and NKq.  $P = 0.99$  for the NKp and  $F = 2$  for the NKq. With these parameters, the NKp includes a higher degree of neutrality than the NKq does. According to the procedures in Section II-C, all the parameters of the SGA must be the same among fitness landscapes to compare the features. Thus, the other parameters were set as follows. Tournament selection was adopted. Elitism was applied. The tournament size was set at 2. A generational model was used. Each run lasted 5,000 generations. The parameters in **Metric A** and **B** were as follows:  $t_c \in \{1, 2, \dots, 500\}$ ,  $t_s \in \{1, 1001, 2001, 3001, 4001\}$  and  $t_e = t_s + 999$ . We conducted 10 independent runs.

We did not notice significant differences among these runs with respect to all the measures and analyses reported here. Therefore, for clarity of explanation, we give data for a single run, which will be described below.

### B. Simulation Results

Figure 2 shows the maximum fitness at each generation for each evaluation. Although dominance of  $pr$  against  $py$  in the fitness level does not completely correspond to the one in the behavioral level due to the environmental settings, the predators always outperformed the preys over generations in all the runs.

Figure 3 shows the  $r$ - $\alpha$  curves obtained in the NKp and the NKq, where  $F$  and  $P$  are constant for each curve. These were

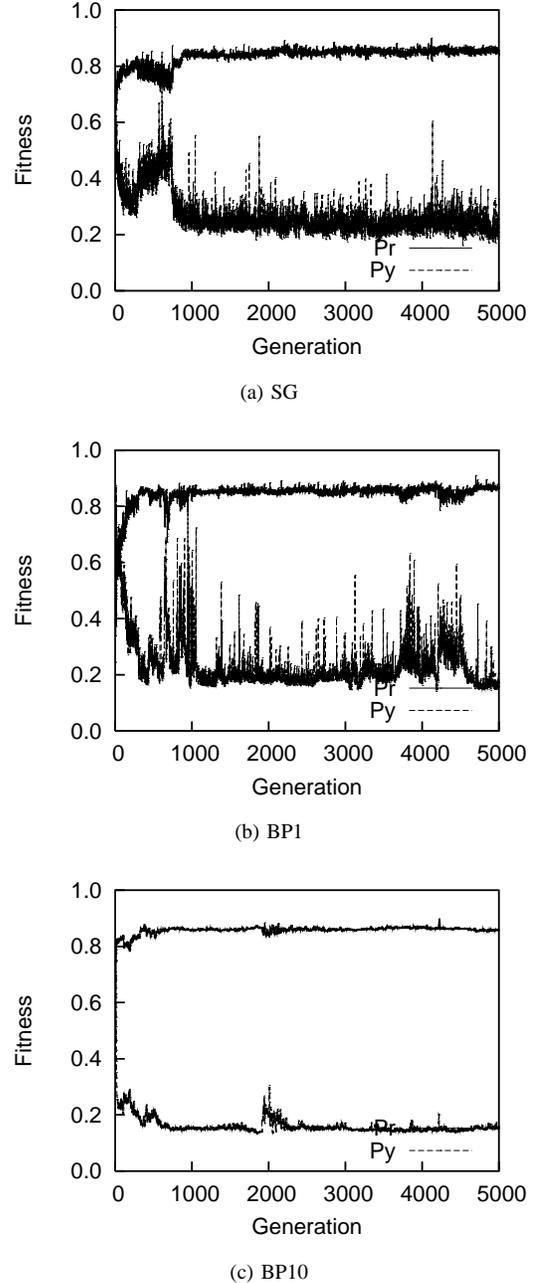


Fig. 2. Maximum fitness at each generation for each evaluation

used as a baseline when compared to the results obtained in each run on the predator-prey problem. Figure 4(a), 4(c) and 4(e) show  $r$  and  $\alpha$  at each generation for each evaluation in **Metric A**. Compared to Figure 3, the degree of neutrality in the landscapes for all evaluations were estimated indirectly. The points,  $(r, \alpha)$ , for  $pr$  and  $py$  in the early generations locate above the curve for  $P = 0.99$ . This means that their fitness landscapes in the early generations include high neutrality. During the process of evolution, the points for  $pr$  locate in the high  $r$  region, that is, high correlation while those for  $py$  locate in the low  $r$  region except for  $py$  for BP1.

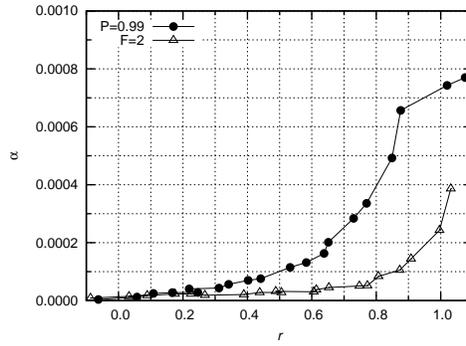


Fig. 3.  $\alpha$  as a function of the correlation,  $r$  for the NKp with  $P = 0.99$  and the NKq with  $F = 2$

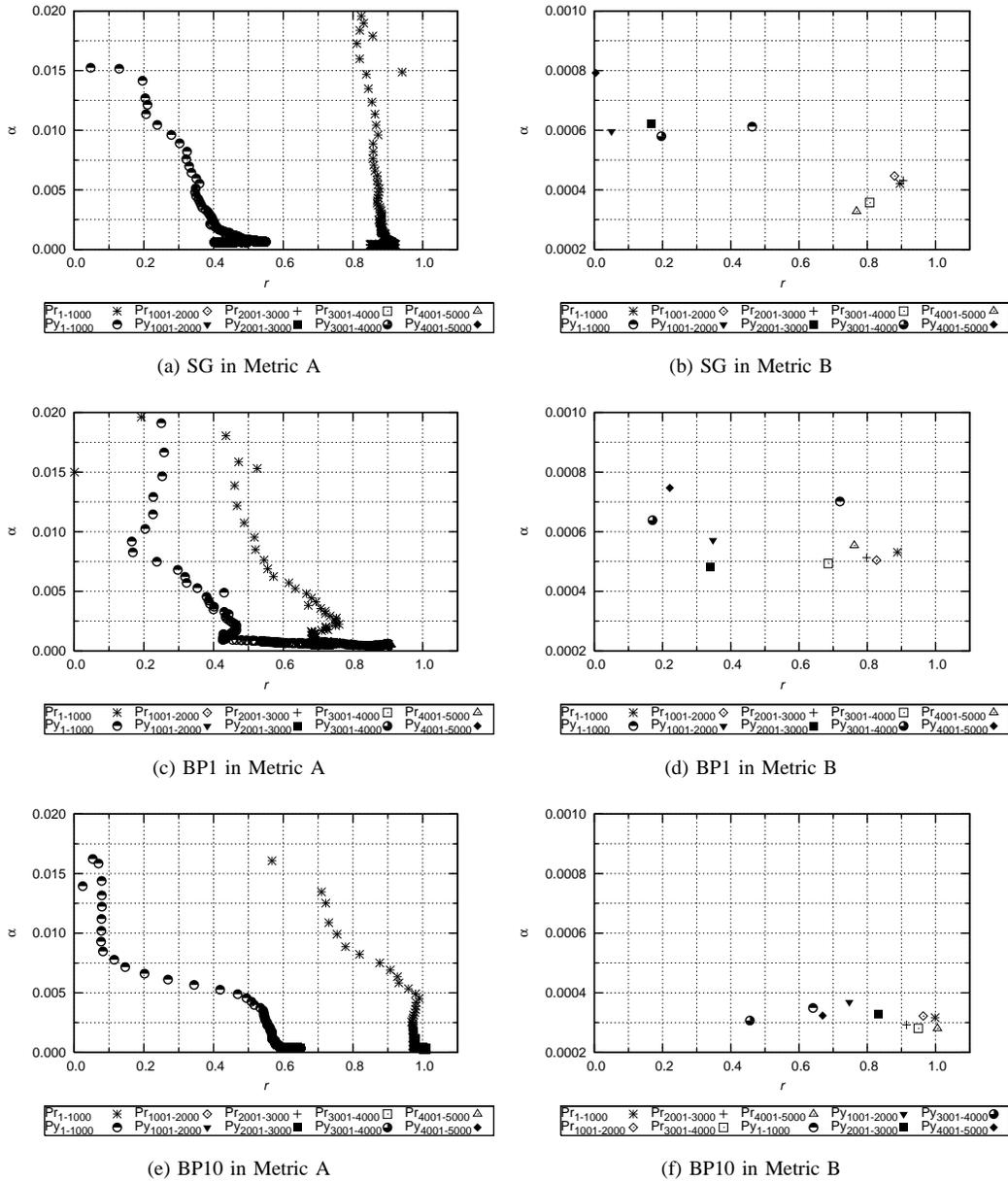


Fig. 4.  $\alpha$  as a function of the correlation,  $r$ , for each generation calculated by **Metric A** and **Metric B**

This means that it was easy for the predator to evolve while it was difficult for the prey to evolve in these settings. With respect to the change of the fitness landscape, we can confirm the transition of the points in the early 1,000 generations. After that, however, those almost converged at a certain point. In the first metric (the equation (6)(7)), the amount of accumulated data becomes larger with the increase of the generation. In the last generations, the new data obtained in one generation do not have large effect on the total amount of data obtained over the generations. Thus, it seems likely that the transition of the points becomes smaller after the 1,000 generation. These results were completely different from what we expected in Section I. This shows the difficulty to confirm ever-changing fitness landscapes by **Metric A**.

Figure 4(b), 4(d) and 4(f) show  $r$  and  $\alpha$  for each generations in **Metric B**. The points for  $pr$  locate in the high  $r$  region while those for  $py$  locate in the relatively low  $r$  region. These tendencies to locate in those regions were the same as the results obtained in Metric A. Comparing those features in the evaluations, those of SG and BP1 locate higher than those of BP10, that is, the degrees of neutrality for SG and BP1 were larger than the one for BP10. It seems likely that BP10 has the strongest selection pressure in the evaluations. This was why the fluctuations in fitness for BP10 were smaller than those for SG and BP1. Moreover, we can confirm the transition of the points among all the periods in **Metric B**.

## V. DISCUSSION

In the previous section, we can confirm ever-changing fitness landscapes over generations by one of the proposed methods. However, the evolutionary dynamics of the obtained results in Figure 2 show that one species  $py$  were overcome by the other species  $pr$  over generations. Therefore, we need to investigate whether co-evolutionary progress has generated by a complementary method. Figure 5, 6, 7 show CIAO (Current Individual vs. Ancestral Opponents [20]) plots for SG, BP1, BP10, respectively, where the brightest cells represent the highest scores and the darkest the worst, and each row represents fitness scores of the elite in one species at the generation against all of their ancestral opponents. We can confirm some patterns (e.g.  $pr$  fare slightly badly against  $py$  from the generation 1700 to 2000 in Figure 5(a),  $py$  do well against  $pr$  around the generation 1000 and 3900 in Figure 6(b) and  $py$  do well against  $pr$  around the generation 2000 in Figure 7(b)). In ideal co-evolutionary progress, where there is continuous progress in both populations, a CIAO plot would show specific patterns: the darker (low-score) cells towards the diagonal edge while the lighter (high-score) cells towards the left-hand edge [20]. In Figure 5, 6 and 7, we cannot find any such patterns. These results mean that an ever-changing fitness landscape is a necessary condition for ideal competitive co-evolutionary progress, *open-ended evolution*, but it is not a sufficient one.

## VI. CONCLUSIONS

In this paper, we proposed methods to estimate features of competitive co-evolutionary fitness landscapes on a predator-

prey problem in computer simulations in order to investigate the Red Queen effect on the fitness landscape. Our results can be summarized as follows:

- In the metric calculated based on the accumulated data from the initial generation to the current one, transition of the features in the fitness landscape almost converged after the early generations. Thus, we can not confirm ever-changing fitness landscapes in this metric.
- In the metric calculated based on the accumulated data for certain generations, we confirm the transition of the features over generations.

From these results, we can confirm ever-changing fitness landscapes over generations by the proposed method. On the other hand, there was no continuous progress in both populations for the CIAO evaluations. Future work will investigate which GA should be applied to this problem according to the features of the fitness landscapes obtained in this paper and which transition pattern of features of fitness landscapes should appear in ideal co-evolutionary progress.

## APPENDIX

The NKp and NKq fitness landscapes are the tunably neutral NK landscapes, which are extended forms of Kauffman's NK fitness landscape[4]. The former was proposed by Barnett [18] and the latter proposed by Newman and Engelhardt [19].

### A. NKp Fitness Landscape

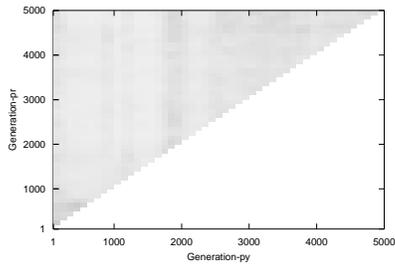
The NKp fitness landscape has three parameters:  $N$ , the length of the genotype;  $K$ , the number of epistatic linkages between genes; and  $P$ , the parameter to tune the degree of neutrality. The fitness value is calculated as follows: The fitness contribution of the  $i$ -th locus,  $v_i$ , is an real value generated randomly in the range  $0.0 \leq v_i \leq 1.0$ ,  $i = 1, \dots, N$  based on its allele and the alleles of  $K$  other loci. At the same time,  $v_i$  is set at 0.0 with the probability,  $P$  ( $0.0 \leq P \leq 1.0$ ) for involving neutrality in the landscapes. To calculate the fitness,  $V$ , of a genotype, the fitness contribution of each locus is averaged.

$$V = \frac{1}{N} \sum_{i=1}^N v_i. \quad (13)$$

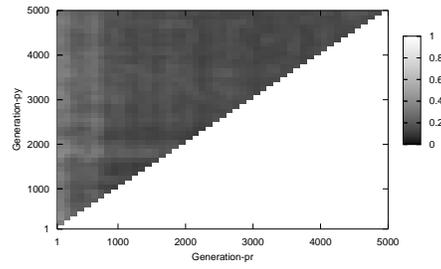
The degree of ruggedness of the landscape can be tuned by changing the value of  $K$ . The ruggedness of the landscape is maximized when  $K = N - 1$ , and is minimized when  $K = 0$ . Also, the degree of neutrality of the landscape can be tuned by changing the value of  $P$ . The neutrality of the landscape is maximized when  $P = 1.0$ , and is minimized when  $P = 0.0$ .

### B. NKq Fitness Landscape

The NKq fitness landscape also has three parameters:  $N$ ,  $K$ , which are the same as those of the NKp and  $F$ , the parameter to tune the degree of neutrality. The fitness contribution of the  $i$ -th locus,  $v_i$ , is an integer generated randomly in the range  $0 \leq v_i < F$ ,  $i = 1, \dots, N$  based

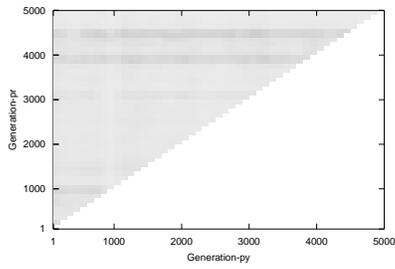


(a) *pr*: predator generations 0 to 5000 run bottom to top in steps of 10, prey generations 0 to 5000 run left to right in steps of 10.

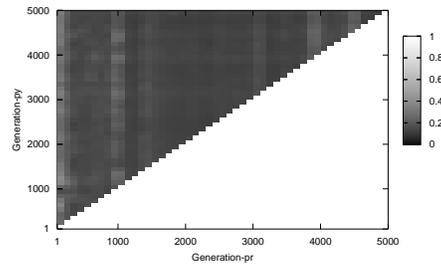


(b) *py*: prey generations 0 to 5000 run bottom to top in steps of 10, predator generations 0 to 5000 run left to right in steps of 10.

Fig. 5. Current individual vs. ancestral opponents for SG.

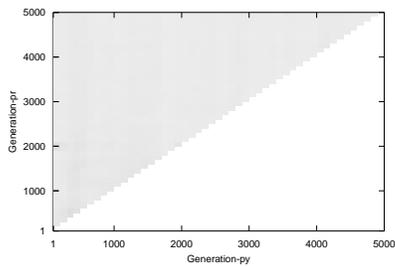


(a) *pr*: predator generations 0 to 5000 run bottom to top in steps of 10, prey generations 0 to 5000 run left to right in steps of 10.

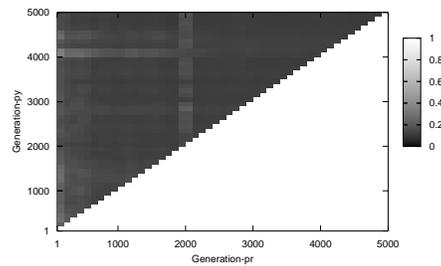


(b) *py*: prey generations 0 to 5000 run bottom to top in steps of 10, predator generations 0 to 5000 run left to right in steps of 10.

Fig. 6. Current individual vs. ancestral opponents for BP1



(a) *pr*: predator generations 0 to 5000 run bottom to top in steps of 10, prey generations 0 to 5000 run left to right in steps of 10.



(b) *py*: prey generations 0 to 5000 run bottom to top in steps of 10, predator generations 0 to 5000 run left to right in steps of 10.

Fig. 7. Current individual vs. ancestral opponents for BP10

on its allele and the alleles of  $K$  other loci. To calculate the fitness,  $V$ , of a genotype, the fitness contribution of each locus is averaged, and then divided by  $F - 1$ , normalizing  $V$  to the range 0.0 to 1.0. More formally:

$$V = \frac{1}{N(F-1)} \sum_{i=1}^N v_i. \quad (14)$$

The neutrality of the landscape can be tuned by changing the value of  $F$ . The neutrality of the landscape is maximized when  $F = 2$ , and is effectively non-existent as  $F \rightarrow \infty$ .

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