

Evolutionary Dynamics of GAs in a Simple Model with Dynamical Environment and Neutrality

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Abstract

Biological organisms have various mechanisms of coping with the dynamical environments in which they live. Recent papers in computational biology show that individuals reside in deferent regions of neutral networks according to environmental variation. This work investigated evolutionary dynamics of GAs in dynamical environments with neutrality using a simple model. The evolutionary dynamics observed were consistent with those observed in the experiments of biological evolution, confirming that the genotype distributions change depending on the rates of environmental variation as well as mutation.

Introduction

The Neutral theory (Kimura, 1983) was developed by Motoo Kimura in the 1960s. Neutrality is caused by highly redundant mappings from genotype to phenotype or from phenotype to fitness. Based on this, it was reported that biological organisms make good use of genetic mechanisms which do not appear in phenotype to adapt to environmental variations on the evolutionary time scale.

The effects of neutrality has been discussed so much in the EC community especially since Harvey introduced the concept of neutral networks (Harvey and Thompson, 1996). These researches can be classified into two types as follows. The former researches are based on redundant mappings from phenotype to fitness, where neutral networks are included in a problem itself. Examples would be the evolution of neural network controllers in robotics (Harvey, 1997; Smith et al., 2001) and on-chip electronic circuit evolution (Thompson, 1996; Vassilev et al., 2000). In these researches, evolutionary dynamics are investigated (Barnett, 1997; Newman and Engelhardt, 1998; van Nimwegen et al., 1999; Katada et al., 2004) or the degree of neutrality in fitness landscapes is estimated (Smith et al., 2002; Katada and Ohkura, 2006). The latter based on redundant mappings from genotype to phenotype, where redundancy, that is, neutrality has been intentionally incorporated by EC researchers for problems where redundancy is largely absent to improve the performance of artificial evolution (Ohkura and Ueda,

1999; Ebner et al., 2001; Knowles and Watson, 2002; Rothlauf and Goldberg, 2003).

To the best of my knowledge, in the former type of research, neither evolutionary dynamics nor useful genetic operators in *dynamical environment* has been investigated. Independently of neutrality, representations of polyploid model in dynamical environment have been investigated where useful genes in previous environments are preserved in some kind of memories (Branke, 2001). Apparently, the feature of polyploidy is a redundant genetic material, that is, redundant mappings from genotype to phenotype. However, it seems likely that there is no research that investigate this from the view point of neutrality.

GP, whose evolved programs include many introns and functionally redundant parts, would be classified into the former research. That is why some GP researchers have claimed the importance of neutrality in recent years (Yu and Miller, 2006; Miller, 2009; Vanneschi, 2009).

Recent papers in computational biology show that individuals reside in deferent regions of neutral networks according to environmental variation. Meyers et al. (2005) analyzed evolution in a periodically changing environment using a simple model and a codon model where a locus has several alleles and some of them are functionally equal, and reported as follows: When environmental variations are rare, most individuals are located in the center of the neutral network with the highest fitness value in each environment preparing for detrimental mutation (Fig. 1(a)). This phenomenon is called *genetic robustness*. When the rates of environmental variation are intermediate, most individuals are located in the edge of the neutral network in order to obtain a new phenotype which can adapt to an alternating environment with a few mutations (Fig. 1(b)). This is called *genetic potential*. When the rates of environmental variation are high, they are settled in a phenotype with an intermediate fitness value in both environments (Fig. 1(c)). This would mean that they have tolerances and adaptivity for both environments but would never go to extremes. This is called *organismal flexibility*.

Based on these knowledges, Yu (2007) investigated evolu-

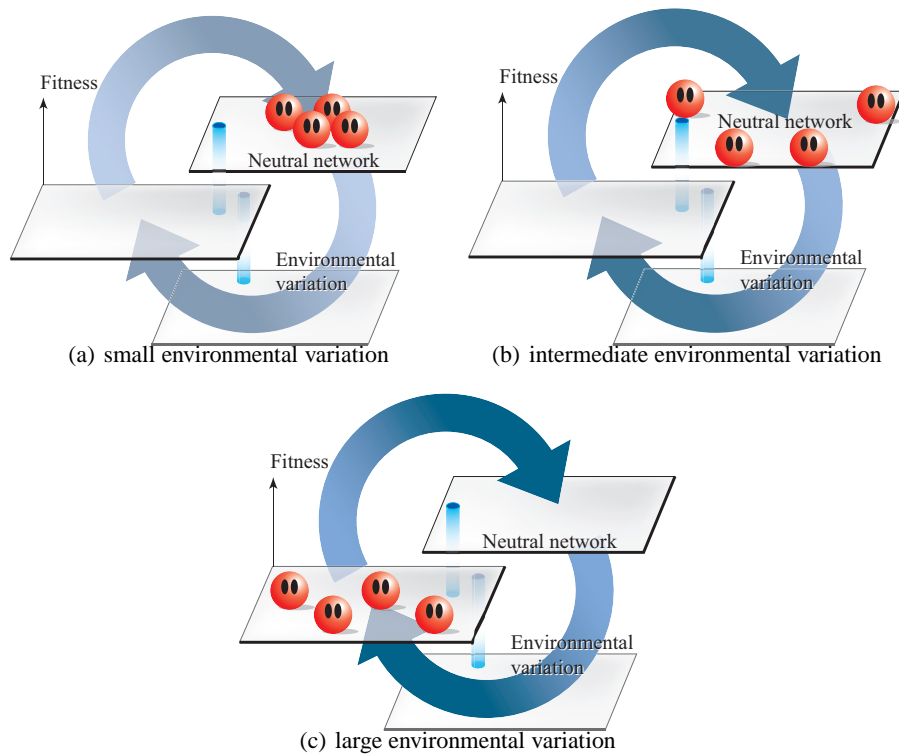


Figure 1: Distribution of individuals due to environmental variation

tionary dynamics of the GP in a boolean parity problem under environmental variations. It was reported that when the variation rate is high, the length of a program tree became long, that is, the effective mutation rate per individual became high, and when the variation rate is low, the length became short, that is, the effective mutation rate per individual became low. Yu (2007) claimed that when the variation rate becomes high, individuals of the GP tend to be located in the edge of the neutral network because the effective mutation rate per individual becomes high and individuals easily change their phenotype. However, we have trouble defining a neutral network on GPs due to its representation. Therefore, it is difficult to discuss directly the consistency of the obtained results in the GP to the computational biology because we need the concept of location on a neutral network for them.

Based on these results, the question arises as to whether we can get the same kind of dynamics of GAs in dynamical environments with neutrality because neutral networks have been found in GAs with highly redundant mappings from phenotype to fitness. In the case of GAs with redundant mappings from genotype to phenotype (including ploidy), we would get the same kind of results on the “GPs” mentioned above because it would be difficult for the GAs to devise a neutral network¹ and effective mutation rates of

¹It is possible to define a neutral network in GAs with redundant

them are variable.

This paper focuses on the former case, where GAs with redundant mappings from phenotype to fitness (more precisely, genotype to fitness) that can form neutral networks and investigates evolutionary dynamics of them in a simple model by varying the rates of environmental variation and the mutation rate. The paper is organized as follows. The next section describes a neutral network in a mathematical form. Section III describes a simple model of dynamical environments with neutrality where evolutionary dynamics of GAs is investigated. Section IV gives the results of our computer simulations. Section V discusses the consistencies with the results obtained in computational biology. Conclusions are given in the last section.

A Formal Definition of a Neutral Network

Katada and Ohkura (2009) defined a neutral network in a mathematical formula. The details are as follows;

In this study, it is assumed that genotypes are represented as binary strings and the length of them is fixed. Thus, the genetic distance between two different genotypes ($x^g, y^g \in \Phi_g, x^g \neq y^g, \Phi_g$: the set of genotypes determined by the length of the genotype, l) is described by the Hamming dis-

mappings from genotype to phenotype (See the next section) but difficult to make neutral networks emerge from genotype space in which neutrality is intentionally incorporated as mentioned earlier.

tance between them, $H(x^g, y^g)$. Thus, $\min H(x^g, y^g)$ is the smallest unit of mutation. For binary representations, $\min H(x^g, y^g) = 1$.

Based on the above consideration, I describe a neutral network caused by redundant mappings from genotype to phenotype in a mathematical form. At first, two individuals, x^g and z^g , are connected, $x^g \sim z^g$, if there exists $\{x_i^g\}_{i=0}^n \subset \Phi_g$, *s.t.*

1. $x^g = x_0^g, z^g = x_n^g$,
2. $f_g(x_i^g) = f_g(x_{i+1}^g)$,
3. $H(x_i^g, x_{i+1}^g) = 1$,

where f_g is the mapping from genotype to phenotype, $f_g : \Phi_g \rightarrow \Phi_p$, and assumed to be surjective and not injective. Φ_p is defined as the set of phenotypes.

Thus, a neutral network of a genotype z^g is

$$\Phi_g'(z^g) = \{x^g \in \Phi_g | x^g \sim z^g\}. \quad (1)$$

We can extend this definition to redundant mappings from phenotype to fitness.

Two individuals, x^g and z^g , are connected, $x^g \sim z^g$, if there exists $\{x_i^g\}_{i=0}^n \subset \Phi_g$, *s.t.*

1. $x^g = x_0^g, z^g = x_n^g$,
2. $(f_p \circ f_g)(x_i^g) = (f_p \circ f_g)(x_{i+1}^g)$,
3. $H(x_i^g, x_{i+1}^g) = 1$,

where f_p is the mapping from phenotype to fitness, $f_p : \Phi_p \rightarrow \Phi_f$, and assumed to be surjective and not injective. Φ_f is defined as the set of fitness values. Addition to this assumption, there would be two cases on f_g , which is either bijective, or surjective and not injective. In both cases, however, $f_p \circ f_g$ is surjective and not injective only if f_p is surjective and not injective. Thus, a neutral network of a genotype z^g is described in the both cases as follows:

$$\Phi_g^*(z^g) = \{x^g \in \Phi_g | x^g \sim z^g\}. \quad (2)$$

These may seem to be cumbersome at first. But this elegant definition allows us to understand clearly a setting for computational experiments in the following sections.

Simple Model with Dynamical Environment and Neutrality

In this study, computer simulations were conducted in order to compare evolutionary dynamics of GAs with those observed in the experiments of biological evolution (Meyers et al., 2005). For performing simple analysis, the length of a string is set at 4. According to the setting given in the reference (Meyers et al., 2005), a set of genotypes is defined

Table 1: Set of genotype

Genotype (g_i)	ID (i)	Nickname
1011	0	NN1-c
1111	1	NN1-e1
1101	2	NN1-e2
1001	3	NN1-e3
1010	4	NN1-e4
0011	5	NN1-e5
1110	6	INV-1
1000	7	INV-2
0111	8	INV-3
0001	9	INV-4
0100	10	NN2-c
0110	11	NN2-e1
0010	12	NN2-e2
0000	13	NN2-e3
0101	14	NN2-e4
1100	15	NN2-e5

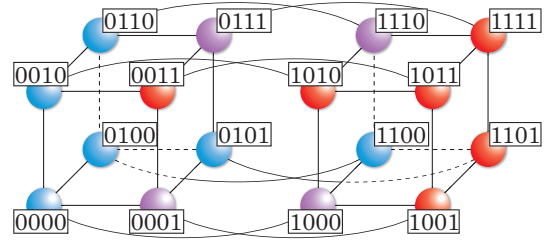


Figure 2: Space of genotype

as Table 1 and Fig.2. The fitness function is also defined as follows:

$$w_A(g_i) = \begin{cases} 1 + s & (0 \leq i \leq 5) \\ 1 + ks & (6 \leq i \leq 9) \\ 1 & (10 \leq i \leq 15) \end{cases} \quad (3)$$

$$w_B(g_i) = \begin{cases} 1 & (0 \leq i \leq 5) \\ 1 + ks & (6 \leq i \leq 9) \\ 1 + s & (10 \leq i \leq 15), \end{cases} \quad (4)$$

where w_A and w_B are fitness functions for environments E_A and E_B , respectively. s and k ($s > 0, 0 \leq k \leq 1$) are the parameters to adjust the highest and intermediate fitness values given to certain genotypes in each environment, respectively. These parameters were set as follows: $s = 1, k = 0.5$ following the recommendations given in (Meyers et al., 2005).

In this function, a fitness value is assigned to a genotype directly so no phenotype is defined. Thus, it is considered that f_g is bijective as mentioned in the previous section. Then $f_p \circ f_g$ is investigated. According to the definition of a neutral network (Eq.(2)), the genotypes with $i = 0, \dots, 5$

and those with $i = 10, \dots, 15$ form a neutral network in both environments, E_A and E_B , respectively. These neutral networks show the highest fitness value and lowest fitness value in Eqs. (3) and (4), respectively. In each neutral network, a genotype which does not mutate out of its neutral network with 1 bit is considered to be located at the center of its neutral network (NN1-c and NN2-c in Table 1) while a genotype which does mutate out of its neutral network with 1 bit is considered to be located on the edge of its neutral network (NN1-e and NN2-e in Table 1). For this setting, each neutral network has only one genotype which is located at the center of it. The other genotypes ($i = 6, \dots, 9$) show the intermediate fitness value but do not form any neutral networks.

Computer Simulation

In this computer simulations, the GA (Goldberg, 1989) were adopted to evolve individuals in both the environments, E_A and E_B , mentioned in the previous section. The length of the genotype is 4 as also mentioned in the previous section. The population size was set at 10 according to the setting in (Yu, 2007). In this study, computer simulations were conducted in order to investigate evolutionary dynamics of GAs in a simple model by varying the rates of environmental variation and the mutation rate. Thus, the genetic operations for the GA were standard bit mutation and fitness proportionate reproduction. The per-bit mutation rate, q , was set as follows: $q \in \{0.025, 0.05, 0.1, 0.2, 0.25, 0.3, 0.4, 0.5\}$. Each run lasted 2,000 generations. The initial environment was set at E_A . The environment was alternately switched every λ generations as follows: $E_A \rightarrow E_B \rightarrow E_A \rightarrow \dots$. For each run, λ was set between 1 and 1000 as follows: $\lambda \in \{1, 2, \dots, 20, 30, \dots, 100, 200, \dots, 1000\}$. 50 independent runs were conducted for each parameter. All results were averaged over 50 runs.

Fig. 3 shows the ratio of the individuals with the highest fitness value, $f = 1 + s$, the intermediate value, $f = 1 + ks$, and the lowest value, $f = 1$ with $q = 0.025$ and $\lambda = \{2, 10, 100\}$ ². For each λ , a population adapted to a new environment to produce the individuals with the highest fitness value. However, not all individuals converged to the highest fitness value.

The distribution of the individuals were dependent on λ . For short variable periods (e.g. $\lambda = 2$ in Fig. 3(a)), more than the half of individuals never had the highest fitness value and the individuals with the intermediate fitness value were dominant (approximately 45-50 %). This is because environmental variation was so rapid that there was not enough time for the individuals to adapt to each environment. This might be considered that evolution supported the individuals which can adapt faster to rapid environmental

²I plot only the first 100 generations for $\lambda = 2, 10$ and the first 400 generations for $\lambda = 100$ because the similar patterns were repeatedly observed after the generations.

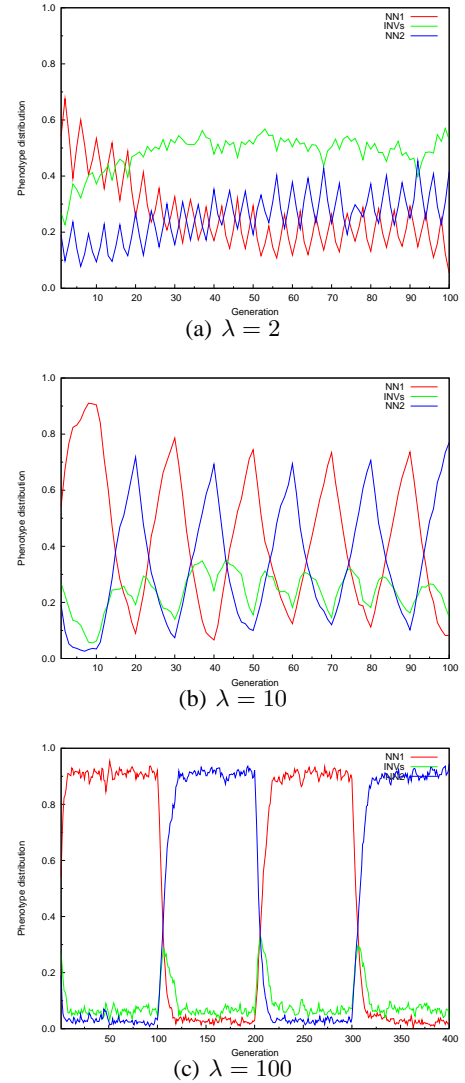


Figure 3: Individual distributions at each generation ($q = 0.025$)

variations, that is, the individuals which can mutate easily to the one with the highest fitness value. Such individuals with the intermediate fitness value would be considered to be *organismal flexibility* as mentioned earlier.

For longer variable periods (e.g. $\lambda = 10$ in Fig. 3(b)), the number of the individuals with the highest fitness value increased while the number of the ones with the intermediate fitness value decreased. For even longer variable periods (e.g. $\lambda = 100$ in Fig. 3(c)), there was enough time for the individuals to adapt to each environment and the individuals with the highest fitness value became dominant. In Fig. 3, we can not find “where” the individuals are located in the neutral network with the highest fitness. The more details can be found in Figs. 4 and 5.

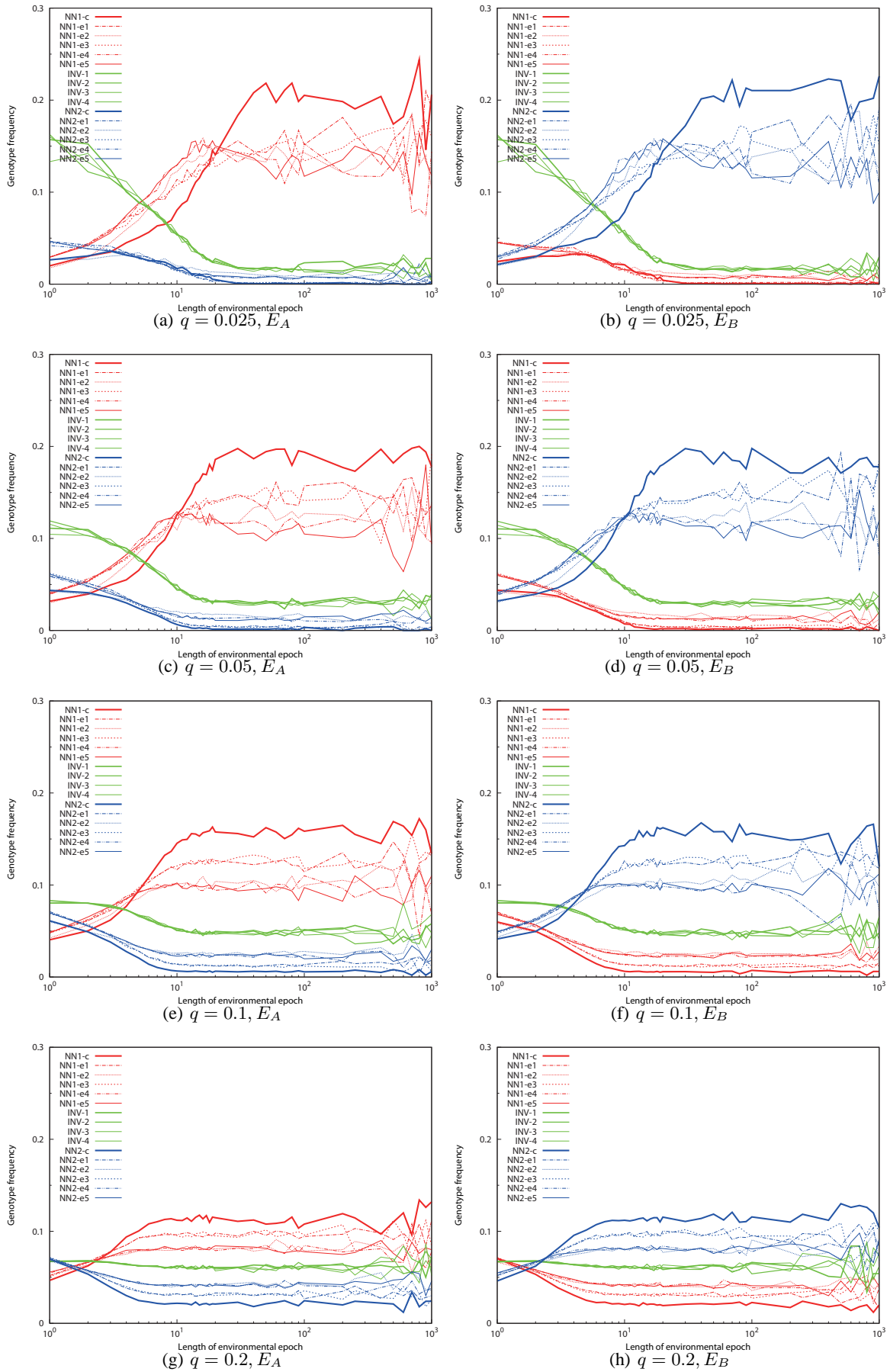


Figure 4: Individual distributions over variable periods for E_A and E_B ($0.025 \leq q \leq 0.2$)

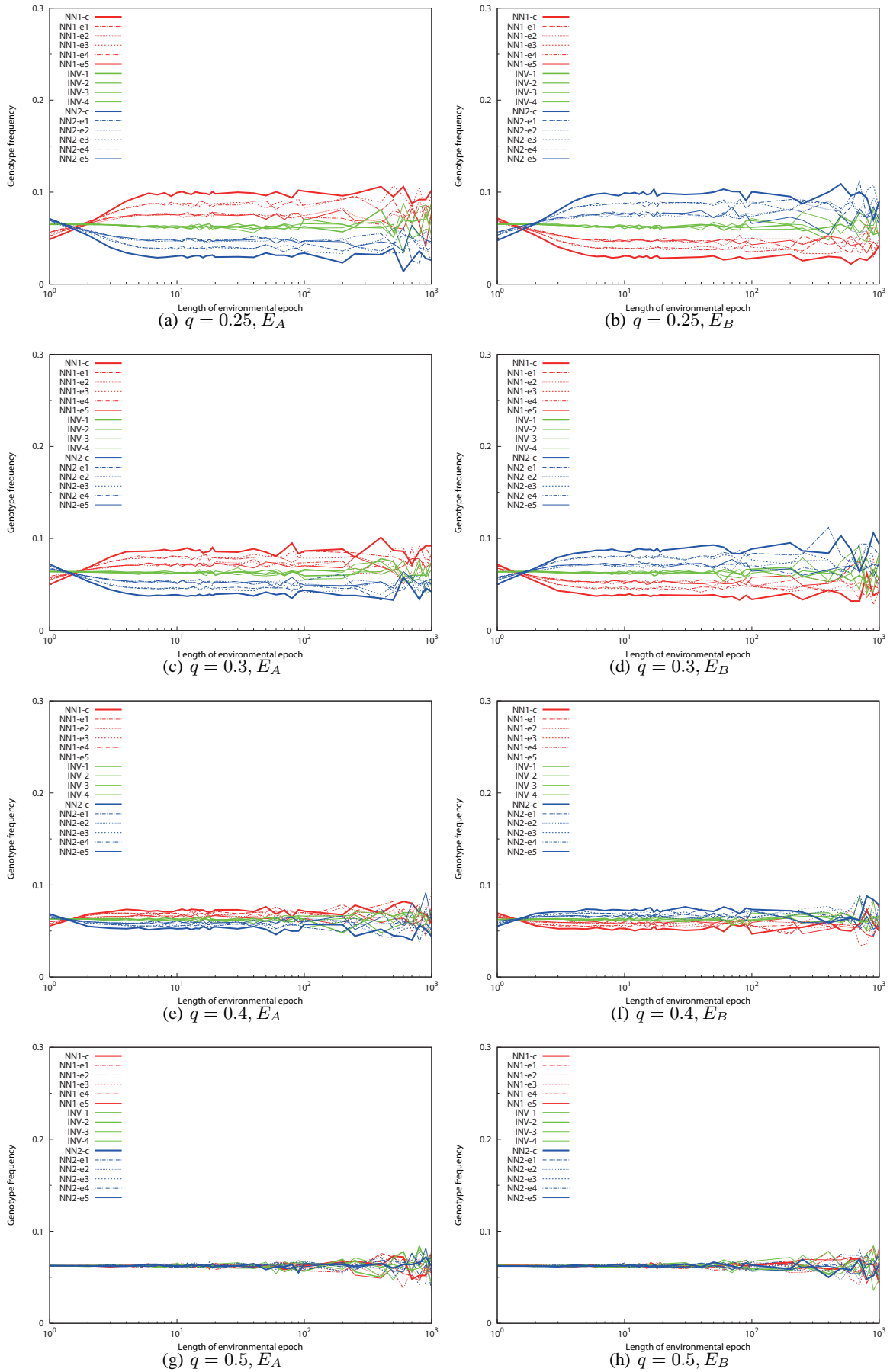


Figure 5: Individual distributions over variable periods for E_A and E_B ($0.25 \leq q \leq 0.5$)

Figs. 4 and 5 show the ratios of the genotypes over λs for each q . Here, the ratio of a genotype was calculated by dividing the sum of the values just before generations when the environment was switched with the number of switching environments and the number of runs. The bold line shows the ratio of the genotype which is located at the center of its neutral network and the thin line shows the one of the genotype which is located on the edge of its neutral network. The horizontal axis is based on a logarithmic scale.

Over the mutation rate range $0.025 \leq q \leq 0.1$ (Fig. 4(a)-4(f)), for long variable periods, the ratio of the genotype which was located at the center of the neutral network with the highest fitness value was larger than the ones of the other genotypes in both environments. The genotypes which were located on the edge of the neutral network attained the second-largest rate. For shorter variable periods, the ratios of the genotypes which were located on the edge of the neutral network were larger than the ones of the other genotypes. Among them, the ratios were different due to their own locations on the edge. Thus, the ratios of them which are adjacent to not only the genotypes with the intermediate fitness value but also the ones with the lowest fitness value were larger. The variable period range in which this phenomenon appears decreased with the increase of q . For even shorter variable periods (approximately $1 \leq \lambda \leq 3$), the ratio of the genotype with the intermediate fitness value was largest. For these shortest variable periods, the same result was obtained in Fig. 3(a).

Over the mutation rate range $0.2 \leq q \leq 0.4$ (Fig. 4(g)-4(h), Fig. 5(a)-5(f)), for long variable periods, the ratios of the genotypes which were located at the center of the neutral network and on the edge of it were large in this order. However, these values were not beyond 0.1. For even shorter variable periods, the ratios of the genotypes with the lowest fitness value were a few larger than or equal to the ones with the highest and intermediate fitness value.

For $q = 0.5$ (Fig. 5(g)-5(h)), there was no significant difference between the genotypes, which were distributed randomly.

Discussion

In the earlier section, the loosely defined phenomena, *genetic robustness*, *genetic potential* and *organismal flexibility*, were cited. In order to discuss the results obtained in the previous section, those are more accurately defined as follows: *genetic robustness*: the state where the ratio of the genotype which is located at the center of the neutral network with the highest fitness value is largest in the environment, E_A or E_B . *genetic potential*: the state where the ratio of the genotype which is located on the edge of the neutral network is largest in each environment. *organismal flexibility*: the state where the ratio of the genotype with the intermediate fitness value is largest.

According to these definitions, we can find such phase

transitions as organismal flexibility \rightarrow genetic potential \rightarrow genetic robustness for $q \leq 0.1$, and organismal flexibility \rightarrow genetic robustness for $0.2 \leq q \leq 0.4$ in Figs. 4 and 5 with the increase of the variable period. Meyers et al. (2005) described that we can find *genetic potential* in a much wider variable period range when the mutation rate decreases because it takes more time to reach the state, *genetic robustness*. This is consistent with the results in Figs. 4(a)-4(f) in which we can find *genetic potential* in the ranges, $6 \leq \lambda \leq 20$ for $q = 0.025$, $5 \leq \lambda \leq 10$ for $q = 0.05$ and, $3 \leq \lambda \leq 5$ for $q = 0.1$. Meyers et al. did not mention *organismal flexibility* for the high mutation rates. For the results obtained in this study, we can not find any *organismal flexibility* when the mutation rate was high. This would be considered to be affected by the *error threshold* on the mutation rate (Kauffman, 1995); As the mutation rate increases, the population gradually loses the current individuals. At a certain critical mutation rate, the individuals become distributed randomly.

Meyers et al. (2005) also claimed that the mutation rate per locus does not need to be variable if the phenotypical mutation rate or the effective mutation rate per genotype is variable as opposed to the argument that the variable mutation rate per locus is important for adaptation to environmental variations. This argument would be explained as follows. When the mutation rate per locus is low, individuals must change their phenotypes (or obtain the higher fitness value) as soon as possible in order to adapt to environmental variation. Thus, the individuals which are located on the edge of the neutral network are supported. When the mutation rate per locus is high, individuals can change quickly their phenotypes even though they are located at the center of the neutral network. Therefore, the dominance of the individuals which are located on the edge of the neutral network becomes invisible at such a mutation rate.

Conclusions

This study investigated evolutionary dynamics of GAs in a simple model by varying the rates of environmental variation and the mutation rate. The results can be summarized as follows:

- Two or three phase transitions were observed over the variable period range. Especially when the mutation rate is low, the results were consistent with the results obtained in computational biology.
- For long variable periods, the frequency of the genotype which was located at the center of the neutral network with the highest fitness value was largest in the population.
- For shorter variable periods, the frequency of the genotype which was located on the edge of the neutral network was largest.

- For even shorter variable periods, the frequency of the genotype with the intermediate fitness value was largest.

In this study, four-bit binary strings were used to provide simple explanatory examples. Additionally, a small population size and an alternating environment were set. Further computer simulations will be conducted in order to investigate whether these observations are consistent with more complex settings (Yang et al., 2007). Another future direction would be an analytical approach due to the simplicity of the model.

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