

# EFFECTIVE FITNESS AS AN ALTERNATIVE PARADIGM FOR EVOLUTIONARY COMPUTATION II: EXAMPLES AND APPLICATIONS

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## **Abstract**

In paper I of this series we reviewed the recent development of an alternative paradigm for evolution on a fitness landscape – effective fitness – which offers an intuitive way to understand population dynamics as flows on an effective fitness landscape when genetic operators other than reproductive selection play an important role. In this article we demonstrate the utility of the concept using several simple analytical models and some more complex models that we simulate numerically. In particular, we show that effective fitness offers a qualitative and quantitative framework within which the phenomenon of induced symmetry breaking of the genotype-phenotype map may be understood. As explicit examples we consider: the violation of the building block hypothesis in non-epistatic landscapes; self-adaptation of genetic algorithms in time-dependent fitness landscapes and the appearance of evolutionary robustness as an emergent property in the evolution of language. In all cases we demonstrate that effective fitness offers a framework within which these diverse phenomena can be understood and in principle quantitatively studied.

# 1 Introduction

Fitness is possibly the most crucial concept in the theory of evolving systems. Interestingly, it is also one of the more controversial and less understood ones. Associated with the notion of fitness is that of a fitness landscape, which has offered a powerful paradigm and visual aid in the understanding of the population dynamics of evolving systems, visualizing the population flow, and hence evolution itself, as a hill-climbing process on a rugged landscape. In paper I [1] of this two paper series we critiqued the standard notion of fitness which in evolutionary computation (EC), as in population genetics, is associated with the probability that an individual reaches reproductive age. Such fitness we term reproductive fitness to distinguish it from that fitness which is a complete measure of reproductive success and takes into account the effect of all genetic operators, such as mutation and recombination.

The chief aim of paper I was to introduce, conceptually and mathematically, the idea of effective fitness and to develop a solid framework in which it could be understood, applied and further developed. The aim of this paper is to help the reader develop an idea for when effective fitness is a more relevant concept than reproductive fitness and under what circumstances and in what classes of systems it offers a more intuitive understanding of population dynamics.

One such class is the class of systems whose genotype-phenotype map is degenerate, i.e. certain genotypes are equivalent in terms of reproductive selection. We call such equivalence a “symmetry”. Such genotypes are by definition selectively neutral with respect to each other. However, inevitably some genotypes experience more reproductive success than others. It might be that this is a purely stochastic or finite population effect. In such circumstances one may argue that the symmetry is spontaneously broken. However, in the presence of other genetic operators, such as mutation and crossover, one observes consistent preferences for some genotypes over others. In this case the other operators themselves are affecting the reproductive success in a highly non-trivial fashion. One may speak of an induced symmetry breaking, induced by the action of operators other than reproductive selection.

Such induced symmetry breaking one can interpret as leading to a self-organization of the genotype-phenotype map wherein the distribution of synonyms in the population is non-random, becoming organized without being imposed externally. This phenomenon is not a rarity but something quite generic being at the heart of phenomena such as bloat in Genetic Programming (GP), self-adaptation in Genetic Algorithms (GAs) and the emergence of algorithmic language in genetic systems.

In section 2, for completeness, we very briefly review some key ideas from I. In particular we emphasize the idea of induced symmetry breaking in the case when the genotype-phenotype map is degenerate. In section 3 we present some simple analytical models that illustrate the strong difference between effective and reproductive fitness. In particular, we show that the effect of operators other than reproductive selection can be such as to drive population flows along flat, or neutral, directions in the reproductive fitness landscape or even against

a reproductive fitness gradient. In section 4 we consider several analytically intractable models where the genotype-phenotype map is highly non-trivial. It is shown that an induced symmetry breaking occurs that leads to self-organization of the genotype-phenotype map and a preference for those synonymous genotypes that are more evolutionarily robust. We show that these results cannot be understood simply or intuitively in terms of population flows on a reproductive fitness landscape. In section 5 we consider the results of sections 3 and 4 in terms of effective fitness showing that the latter provides a qualitative and quantitative framework within which the results may be readily understood. Finally, in section 6, we draw some conclusions.

## 2 A Brief Review of Relevant Concepts from Paper I

In this section we will briefly review the concepts of reproductive fitness and effective fitness as discussed in paper I [1]. We define the reproductive fitness for a phenotype,  $q \in Q$ , where  $Q$  is the space of phenotypes, as  $f_Q : Q \rightarrow R^+$ . On the space of genotypes,  $G$ , a fitness function,  $f_G = f_Q \circ \phi$ , is induced by the action of  $\phi$  and  $f_Q$ , where  $\phi : G \rightarrow Q$  is a map between genotype and phenotype.  $\phi$  is generally many-to-one hence, correspondingly,  $f_G$  is degenerate. Thus, fitness defines an equivalence relation on  $G$ , many genotypes being equivalent selectively. We will refer to the equivalence of a set of genotypes under the action of reproductive selection (i.e. they're all equally fit) as a ‘‘symmetry’’ between them.

Corresponding fitness landscapes can be associated with both  $f_G$  and  $f_Q$ , being height functions above some  $D_Q$  or  $D_G$ -dimensional space, where  $D_Q$  and  $D_G$  are the dimensions of the spaces  $Q$  and  $G$  respectively. To think of a rugged terrain a natural metric function is required, a very common one being Hamming distance. The action of reproductive selection is to drive populations to fitness peaks in the landscape via a hill-climbing process. In the presence of other operators if reproductive selection is the dominant operator, i.e. in a strong selection regime, then the hill climbing intuition remains valid. However, when this is not the case, i.e. in the weak selection regime, the hill climbing analogy breaks down.

This is particularly true in the presence of a synonym symmetry. Within the subset of degenerate states, by definition, there are no reproductive fitness gradients. One would therefore expect to see a random population evolution in this subspace with no preference between one state and another. For a finite population one could have an apparent preference due to nothing more than sampling effects — spontaneous breaking of the synonym symmetry. In the presence of other genetic operators one may observe a preference for some degenerate states versus others, even in the case of an infinite population. We refer to this phenomenon as an induced symmetry breaking.

In the case of weak selection, and in particular in the case of a degenerate

genotype-phenotype map, hill climbing is an inadequate paradigm for understanding population flows on a reproductive fitness landscape. A quantitative framework within which to distinguish between strong and weak selection can, in principle, be associated with any dynamical equation that governs population evolution. For instance, in the case of proportional selection, mutation, and one-point crossover (the equations are easily generalized to more general crossover operators) evolution can be described by the equation [2, 3]

$$P(C_i, t + 1) = \mathcal{P}(C_i)P_c(C_i, t) + \sum_{C_j \neq C_i} \mathcal{P}(C_j \rightarrow C_i)P_c(C_j, t) \quad (1)$$

where the effective mutation coefficients  $\mathcal{P}(C_i)$  and  $\mathcal{P}(C_j \rightarrow C_i)$  represent the probabilities that the genotype  $C_i$  remains unmutated and the probability that the genotype  $C_j$  mutates to the genotype  $C_i$  respectively.  $P_c(C_i, t)$  is the proportion of strings  $C_i$  at time  $t$  after selection and recombination. Explicitly

$$P_c(C_i, t) = (1 - p_c) P'(C_i, t) + \frac{p_c}{N-1} \sum_{k=1}^{N-1} P'(C_i^L(k), t) P'(C_i^R(k), t) \quad (2)$$

where  $P'(C_i, t) = (f(C_i, t)/\bar{f}(t))P(C_i, t)$ ,  $\bar{f}(t)$  being the average population fitness.  $p_c$  is the crossover probability and  $k$  the crossover point which ranges over the entire string. The quantities  $P'(C_i^L(k), t)$  and  $P'(C_i^R(k), t)$  are defined analogously to  $P'(C_i, t)$  but refer to coarse grained variables, i.e. schemata,  $C_i^L$  and  $C_i^R$ . Note that we are taking the defining length to be the total number of bits between and including the outermost defining positions. Equation (1) can be generalized for any schema  $\xi$

$$P(\xi, t + 1) = \mathcal{P}(\xi)P_c(\xi, t) + \sum_{\xi_i} \mathcal{P}(\xi_i \rightarrow \xi)P_c(\xi_i, t) \quad (3)$$

where

$$P_c(\xi, t) = P'(\xi, t) - \frac{p_c}{N-1} \sum_{k=1}^{l-1} (P'(\xi(k), t) - P'(\xi_L(k), t)P'(\xi_R(k), t)) \quad (4)$$

and the sum in (3) is over all schemata  $\xi_i$  that differ by at least one bit from  $\xi$  in one of the  $N_2$  defining bits of  $\xi$ . All other quantities are the schema analogs of quantities defined in (1) and (2).

We define the effective fitness in the case of strings as [2, 3, 4, 6, 1]

$$P(C_i, t + 1) = \frac{f_{\text{eff}}(C_i, t)}{\bar{f}(t)} P(C_i, t) \quad (5)$$

and analogously in the case of schemata by

$$P(\xi, t + 1) = \frac{f_{\text{eff}}(\xi, t)}{\bar{f}(t)} P(\xi, t) \quad (6)$$

Intuitively effective fitness represents the effect of all genetic operators in a single reproductive selection factor.

The exact functional form of the effective fitness obviously depends on the set of genetic operators involved. For the fairly general case of equation (1) we have

$$f_{\text{eff}}(C_i, t) = \left( \frac{\mathcal{P}(C_i)P_c(C_i, t) + \sum_{C_j \neq C_i} \mathcal{P}(C_j \rightarrow C_i)P_c(C_j, t)}{P(C_i, t)} \right) \bar{f}(t) \quad (7)$$

Note that it is time dependent and depends on the actual composition of the population. Effective fitness also naturally extends to schemata via equation (6) and equation (3) and takes a form analogous to that above showing that it is form invariant under a coarse graining. Explicitly

$$\begin{aligned} f_{\text{eff}}(\xi, t) &= \mathcal{P}(\xi) \bar{f}(\xi, t) + \sum_{\xi_i} \mathcal{P}(\xi_i \rightarrow \xi) \frac{P(\xi_i, t)}{P(\xi, t)} \bar{f}(\xi_i, t) \\ &\quad - \frac{p_c}{N-1} \mathcal{P}(\xi) \bar{f}(t) \sum_{k=1}^{l-1} \left( \frac{P'(\xi(k), t) - P'(\xi_L(k), t)P'(\xi_R(k), t)}{P(\xi, t)} \right) \\ &\quad - \frac{p_c}{N-1} \sum_{\xi_i} \mathcal{P}(\xi_i \rightarrow \xi) \bar{f}(t) \sum_{k=1}^{l-1} \left( \frac{P'(\xi_i(k), t) - P'(\xi_{i_L}(k), t)P'(\xi_{i_R}(k), t)}{P(\xi, t)} \right) \end{aligned} \quad (8)$$

where  $\bar{f}(\xi, t)$  is the average fitness of the schema  $\xi$ . In the limit  $p \rightarrow 0$ ,  $p_c \rightarrow 0$  (or in more generic circumstances when the strengths of operators other than reproductive selection  $\rightarrow 0$ )  $f_{\text{eff}}(\xi, t) \rightarrow \bar{f}(\xi, t)$ . An effective selection coefficient is defined via  $s_{\text{eff}} = f_{\text{eff}}(\xi, t)/\bar{f}(t) - 1$ .

The above dynamical equations enable us to determine when the other genetic operators are playing an important role. In particular, they show quite clearly under what circumstances one may speak of weak versus strong reproductive selection, being governed by the ratio  $F = f_{\text{eff}}(C_i, t)/f(C_i, t)$ .  $F \sim 1$  signifies a strong selection regime. Any significant deviation is associated with a weak selection regime.

### 3 Effect of other genetic operators: analytic examples

In this section we consider the effect of genetic operators other than reproductive selection on the population flow on fitness landscapes in the context of some simple, analytically tractable models. We will see behavior that is not naturally explained in terms of hill climbing on a reproductive fitness landscape. The intuition behind the idea of fitness is to a large extent that of giving a reproductive edge to certain genotypes, i.e. that certain genotypes give rise to more offspring than others. Also, that the intuition behind population flows on a

fitness landscape is that of hill-climbing. We will now critically examine the above in the light of some interesting counter-examples.

We first consider some simple one and two locus systems. Consider a single gene with two alleles, 0 and 1, which have the same reproductive fitness value,  $f$ , i.e. the genotype-phenotype map is degenerate of degree 2. In the absence of mutations both the reproductive fitness and the effective fitness are the same. In the infinite population limit, or on average in the finite population case,  $\Delta P(t) = P(1, t) - P(0, t)$  is time independent. Therefore, any initial deviations from homogeneity in the initial population will be preserved. For non-zero mutation rate any initial inhomogeneity will be eliminated by the effect of mutations. Thus, if  $\Delta P > 0$  one will find that the effective fitness of allele 0 is greater than that of allele 1 until the deviation is eliminated. Thus, the effect of mutations is to bring the system into equilibrium, i.e. into the homogeneous population state. During this approach to equilibrium the less numerous allele, 0, is selected more than the allele 1 in that it leaves more offspring, even though 0 and 1 both have the same reproductive fitness.

If the mutation rates for changing allele 1 to allele 0 and for changing allele 0 to allele 1 are not equal but are  $p_1$  and  $p_2$  respectively then the differences between reproductive fitness and effective fitness are even more pronounced as can be seen by

$$\Delta P(t+1) = (1 - 2p_1)\Delta P(t) + 2(p_2 - p_1)P(1, t) \quad (9)$$

which is obtained by considering the infinite population model with the two equations

$$\begin{aligned} P(1, t+1) &= (1 - p_1)P(1, t) + p_2P(0, t) \\ P(0, t+1) &= (1 - p_2)P(0, t) + p_1P(1, t) \end{aligned}$$

In this case  $\text{Lim}_{t \rightarrow \infty} \Delta P(t) \rightarrow ((p_2 - p_1)/(p_1 + p_2))$ . Thus we see a population flow from 0 to 1 even though there is no reproductive fitness gradient in that direction.

Now, consider a two-locus system, once again with two alleles, 0 and 1. The fitness landscape we take to be:  $f(00) = f(01) = 1$ ,  $f(11) = 10$ ,  $f(10) = 0.1$ . The fitness landscape in this case is only partially degenerate: the states 00 and 01 having the same fitness value. However, although the reproductive fitness values are the same the effective fitness values are different. The degeneracy in this case is lifted by the effect of mutation as can be seen from the equations

$$\begin{aligned} P(00, t+1) &= \frac{f(00)}{\bar{f}(t)}(1 - p)P(00, t) + p^2 \frac{f(11)}{\bar{f}(t)}P(11, t) \\ &\quad + \frac{p(1 - p)}{\bar{f}(t)}(f(01)P(01, t) + f(10)P(10, t)) \end{aligned} \quad (10)$$

$$\begin{aligned} P(01, t+1) &= \frac{f(01)}{\bar{f}(t)}(1 - p)P(01, t) + p^2 \frac{f(10)}{\bar{f}(t)}P(10, t) \\ &\quad + \frac{p(1 - p)}{\bar{f}(t)}(f(00)P(00, t) + f(11)P(11, t)) \end{aligned} \quad (11)$$

which are equivalent to equation (1) in the limit  $p_c = 0$ .

For  $p < 1/2$ , and starting with a random initial population, in terms of number of offspring the configuration 01 will be preferred to 00. It is not hard to see why: the fittest configuration is 11 and this can more easily mutate to 01 than to 00. Thus, there is a population flow from 00 to 01 in spite of the fact that there is no gradient in the reproductive fitness landscape to induce it. On the contrary, even if there were a gradient in the direction from 01 to 00 if it were not too large the mutation induced flow from 00 to 01 could overcome it, i.e. the population can flow downhill against the reproductive fitness gradient! Thus, there is a tendency for the system to evolve along a preferred direction not because of selection constraints but because the system has preferred directions of change in the face of *random* mutations. This is the phenomenon of orthogenesis, i.e. genetic drives in the presence of random mutations.

Naturally, this phenomenon encourages one to ask just when neutral evolution [7] is actually neutral. In the above case although the flow is reproductively neutral in the direction 00, 01 the neutrality, or symmetry, is broken by the presence of non-neutral adjacent mutants. For a flat fitness landscape where all genotypes have fitness  $f$

$$P(c_i, t + 1) = \sum_{j=1}^{2^N} P(c_j, t) p^{d_{ij}} (1 - p)^{N - d_{ij}} \quad (12)$$

For a homogeneous population the number of states of Hamming distance  $d_{ij}$  from  $c_i$  is  ${}^N C_{d_{ij}}$ , where  ${}^N C_{d_{ij}}$  is a binomial coefficient, which implies that the effective fitness is the same for all genotypes. Small deviations from homogeneity will be manifest in small differences between the reproductive fitness and the effective fitness which will gradually diminish as the population homogenizes. If the initial population,  $\mathcal{M}(0)$ , is homogeneous then it is preserved to be so in the evolution — on the average.

The equations we are using here are of course mean field equations and as such do not capture finite size effects that can play an important role in neutral evolution. If the landscape only has a flat subspace then how well one can describe the population evolution as being neutral will depend on where the population is located and, if located predominantly in the flat subspace, what is the Hamming distance to states not within the subspace and what is the fitness of those states. Pictorially, if one thinks of a bowl with a flat bottom then the sides of the bowl with the largest gradient will attract the population most strongly. As we will see later the degree of attraction can be quantified in terms of effective fitness.

Another example is that of the NIAH landscape in the presence of mutation and selection. The landscape is  $f(c_i) = f_0$ ,  $i = \text{opt}$ ,  $f(c_i) = f_1$ ,  $i \neq \text{opt}$ ,  $\text{opt}$  being the optimum genotype. One can use as a measure of order in the population the relative concentration of the optimum genotype,  $P(c_{\text{opt}}, t)$ ; and in particular in the long time limit,  $P(c_{\text{opt}}, \infty)$ , where a steady state population is reached — the quasi-species. In this case as is well known [8]  $P(c_{\text{opt}}, \infty)$

monotonically decreases as a function of the mutation rate  $p$  until a critical rate,  $p_{\text{cri}}$ , is reached beyond which  $P(c_{\text{opt}}, \infty) = 1/2^N$ .

It is important to realize that the fitness landscape is constant throughout this behavior. Thus, for  $p = 0$ , i.e. in the absence of mutations, the entire population climbs the fitness peak until  $\bar{f}(t) = f_{\text{opt}}$ , while for  $p \geq p_{\text{cri}}$  the population is uniformly dispersed throughout the entire landscape. Clearly no intuition about these very different types of population flow endpoints can be gleaned from the structure of the landscape itself. In one limit selection dominates, in the other it has no effect. Whether or not the population will ascend a fitness peak due to reproductive selection depends crucially on the presence of another genetic operator — mutation.

The above also serves as a good example of induced symmetry breaking. In the NIAH landscape there are only two phenotypes,  $Q_0$  and  $Q_{\text{opt}}$  where the phenotype  $Q_0$  corresponds to all genotypes save  $c_{\text{opt}}$ . Thus there is a  $(2^N - 1)$ -dimensional degeneracy associated with the reproductive fitness landscape. Hence, in terms of reproductive fitness one would expect to find all genotypes but the optimum in equal proportions. However, the steady state population — the quasi-species — exhibits a preference for those sub-optimal genotypes that are closer in Hamming distance to the optimum. Thus the effect of the mutation operator is to lift the large landscape degeneracy. There still remains a residual symmetry associated with the fact that, at least starting with an homogeneous population, all genotypes of a given Hamming distance from the optimum will have the same probability of reproductive success.

Above, we considered only mutation to support the supposition that reproductive fitness and offspring fitness can be very different in the presence of other genetic operators. Similar considerations also apply to recombination. To take an extreme example of this consider the following simple two-locus system in the presence of selection and recombination, but not mutation, defined by a fitness landscape:  $f(01) = f(10) = 0$ ,  $f(11) = f(00) = 1$ . The steady state solution of the evolution equation (1) is  $P(11) = P(00) = \frac{1}{2} (1 - \frac{p_c}{2})$ ,  $P(01) = P(10) = \frac{p_c}{4}$ . For  $p_c = 1$  one sees that half the steady state population is composed of genotypes that have zero fitness. In this case we see that populations can even flow against infinite fitness gradients! We define the fitness gradient between 11 and 10, say, as  $(f(11) - f(01))/f(01)$ . Such a definition captures the fact that after one generation without crossover there are zero genotypes of type 01 or 10, irrespective of their number in the previous generation. In other words there is infinite resistance to their propagation. Note also that this fixed point of the dynamics is in fact a stable one. For the other two-locus system mentioned above  $P(00, 1) = (1 - (9.9p_c/12.1))P(00, 0)$ ,  $P(01, 1) = (1 + (9.9p_c/12.1))P(01, 0)$ . Hence, once again we see a degeneracy in reproductive fitness being broken by the effect of another genetic operator, in this case recombination, with a consequent differential in offspring fitness.

## 4 Effect of other genetic operators: examples from simulations

Having shown how genetic operators such as mutation and recombination can drastically alter the directions in which populations flow on fitness landscapes in some simple analytic models we will now illustrate the same phenomenon in the case of some much more complex, analytically intractable models. We will be brief in detail referring, where applicable, the reader to the original literature.

### 4.1 Size Dependence of Building Blocks

We will consider first the evolution of schemata of order two (which we will refer to as 2-schemata) of various defining lengths in strings of size 8 in the case of a simple counting ones landscape in the presence of selection and recombination, but without mutation [9]. In the absence of crossover there is clearly no preference for one schema length versus another, i.e. the effective fitness as well as the reproductive fitness of any given 2-schema is on average the same.

To analyze this situation consider the quantity  $M(l)$  where  $M(l) \equiv (n_{opt}(l) - n_{opt}(8))/n_{opt}(8)$ . Here,  $n_{opt}(l)$  is the number of optimal 2-schemata of defining length  $l$  normalized by the total number of length  $l$  2-schemata per string, i.e.  $9-l$ . By optimal 2-schemata we mean schemata containing the global optimum 11.  $n_{opt}(8)$  is the number of optimal 2-schemata of defining length 8. We may consider a fitness landscape, which is a subspace of the complete fitness landscape, that graphs fitness as a function of static schema average for the seven directions that correspond to the optimal schemata, 11\*\*\*\*\*,...,1\*\*\*\*\*1. In this case the landscape is flat, i.e. there is a degeneracy in the landscape of degree 7, in other words for every 2-schemata phenotype there correspond 7 2-schemata genotypes all with the same fitness. Thus, for every optimal 2-schemata phenotype there are seven optimal 2-schemata genotypes.

A large population of 5000 8-bit strings was considered. Figure 1 shows an average over 30 different runs of  $M(l)$  versus time with  $p_c = 1$ . As mentioned, without crossover there is essentially no preference for schemata of a given length, any experimental differences being a result of statistical noise. The inclusion of crossover leads to a remarkable change: Schemata prevalence is ordered monotonically with respect to length but with the larger schemata being favored. Thus, although there is no preference in terms of reproductive fitness for one schema length versus another, quite the contrary is true in terms of effective fitness. Thus we see that, counter to the building block hypothesis, there is a reproductive preference for long schemata. Put differently, there are population flows in the reproductive fitness landscape along flat directions, crossover breaking the genotype-phenotype degeneracy.

### 4.2 Auto-adaptation in a Simple GA

In the next example we will consider the differences between reproductive and effective fitness in the case of a simple auto-adaptive system. Specifically, one

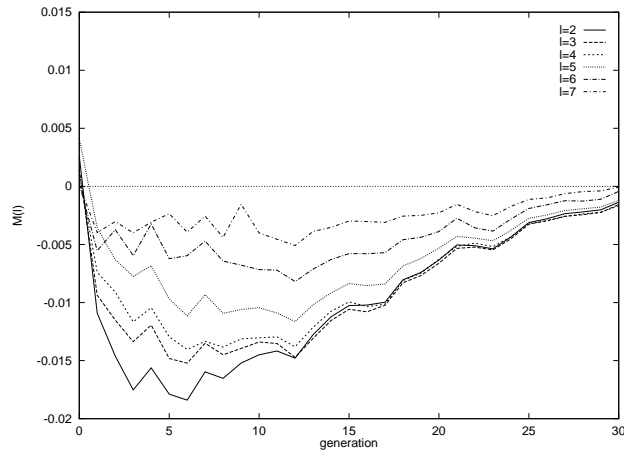


Figure 1: Graph of  $M(t)$  versus  $t$  in unitation model with  $p_c = 1$ .

codes the mutation and 1-point crossover probabilities into an  $N_c$ -bit binary extension of an  $N$ -bit genotype which is represented by a non-degenerate fitness landscape, i.e.  $f_G = f_Q$ . This leads to a new  $(N + N_c)$ -bit genotype whose landscape has a degree of degeneracy of order  $2^{N_c}$ , i.e. the phenotype-genotype map is now  $2^{N_c}$  fold degenerate. It is clear in this case that any observed systematic differences in offspring number in strings with the same reproductive fitness but different mutation and crossover rates cannot have as its origin any property of the reproductive fitness landscape.

In practice, starting off with a random population, where the average rates are 0.5, one finds that the population in a class of interesting model landscapes self-organizes until preferred mutation and recombination rates appear [10]. Such self-organization, as mentioned, cannot come about due to any bias in terms of reproductive fitness, as by construction there is no such bias. Neither can it come about by a spontaneous symmetry breaking (i.e. a spontaneous breaking of the genotype-phenotype degeneracy) due to stochastic effects, i.e. finite size effects, as in the majority of the simulations the size of the population was much bigger than  $D_G$  where  $D_G$  is the dimensionality of the space of genotypes. What is happening is that even though particular values for  $p$  and  $p_c$  are not selected for in terms of reproductive fitness they are selected for in terms of effective fitness. Thus, in  $G$  there is a flow to a certain subregion of the space wherein the mutation and recombination probabilities take on preferred values. Additionally, the probability distribution associated with the various values of  $p$  and  $p_c$  narrows as time increases indicating that there is convergence of the population.

As a specific example, consider a time-dependent landscape defined on 6-bit chromosomes that code the integers between 0 and 63. The landscape is time dependent in the following way: the initial landscape has a global optimum

situated at 10 and 11 and a local optimum at 40 and 41. However, after 60% of the population reaches the global optimum the landscape changes instantaneously, converting the original global optimum into a local one. The original local optimum at 40 and 41 remains the same but with a higher fitness value than the new local optimum at 10 and 11. Additionally, a new global optimum appears at 63. We denote this landscape the “jumper” landscape. In Figure 2 one sees the results of an experiment where the mutation and crossover probabilities were coded with eight bits. Tournament selection of size 5 was used and a lower bound of 0.005 for mutation imposed.

The success of the self-adapting system in converging to the time dependent global optimum was compared to that of an “optimal” fixed parameter system with  $p = 0.01$  and  $p_c = 0.8$ . The results of the latter are not seen in the graph as the fixed parameter GA was incapable of following the evolution of the global optimum. The upper curves show the relative frequencies of the optima using 8-

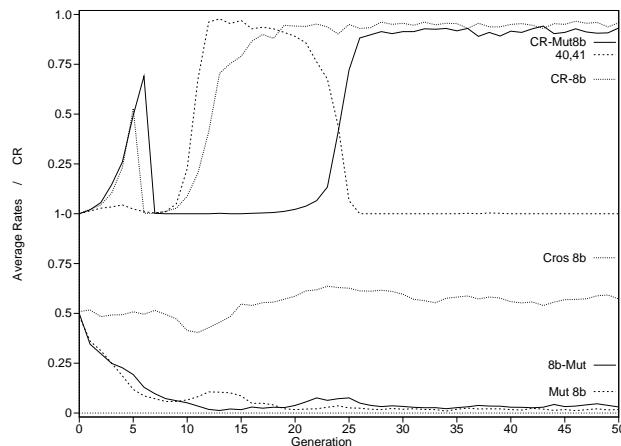


Figure 2: Graph of relative concentration of the global optimum (CR) (upper graph) and average crossover and mutation probabilities (lower graph) as a function of time for the “jumper” landscape. CR-8b is the result for the 8-bit encoded algorithm and CR-Mut8b is the result for 8-bit coded mutation with  $p_c = 0$ , with 40,41 being the relative concentration of strings associated with the local optimum at 40 and 41. Mut 8b and Cross 8b are the average mutation and crossover probabilities in the 8-bit representation. The solid line for 8b-Mut is the average mutation rate in the case  $p_c = 0$ .

bit codification and also what happens when  $p_c = 0$  and only the mutation rate is coded. It is notable that the optimal fixed parameter system was incapable of finding the new optimum whereas the coded system had no such problem. For the case  $p_c = 0$  the curve 40,41 shows the relative frequency of the strings associated with the optimum at 40 and 41. Before the landscape “jump” this optimum is local, being less fit than the global optimum at 10 and 11. After

the “jump” it is fitter but less fit than the new global optimum 63 which is an isolated point.

Notice that the global optimum was found in a two-step process after the landscape change. First, the strings started finding the optima 40, 41 before moving on to the true global optimum, 63. Immediately after the jump the proportion of the population at the new global optimum is essentially zero. The number of strings associated with 40 and 41 first starts to grow substantially at the expense of 10 and 11 strings. At its maximum the number of optimum strings is still very low. However, very soon thereafter the algorithm manages to find the optimum string which then increases very rapidly at the expense of the rest.

The striking result here can be seen by comparing the changes in the relative frequencies with the changes in the average mutation rate, especially in the case  $p_c = 0$ . Clearly they are highly correlated. First, while the population is ordering itself around the original optimum, there is negative selection in terms of effective fitness against high mutation rates as one can see by the steady decay of the average mutation rate. After the jump there is a noticeable increase in the mutation probability as the system now has to try to find fitter strings. As the global optimum is an isolated state it is much easier to find fit strings associated with 41 and 40. The population is now concentrated on this local optimum and the average mutation rate decreases again only to find that this is not the global optimum, whereupon the average rate increases to aid the removal of the population to the true global optimum. It is clear that there is a small delay between the population changes and changes in the mutation rate. This is only to be expected given that there is no direct reproductive selective advantage in a given generation for a particular mutation rate. The reproductive advantage in terms of the effective fitness of a more mutable genotype over a less mutable one arises via a feedback mechanism.

One can regard this process from another point of view: the new optimum is more likely to be reached by strings with high mutation rates which then grow strongly due to their reproductive selective advantage. Thus high  $p$  strings will naturally dominate the early evolution of the global optimum. After finding the optimum however it becomes disadvantageous in terms of offspring fitness to have a high mutation rate. Hence, low mutation strings will begin to dominate. Once again we emphasize, although there is no direct selective benefit in terms of reproductive fitness associated with different mutation and crossover probabilities their ability to produce offspring that can adapt to the changing landscape is very different and this is manifest in the different degrees of reproductive success. Once again we emphasize that the symmetry of the genotype-phenotype map is being broken by the effect of mutation and this breaking leads to a self-organization associated with the augmented reproductive success of strings with certain mutation rates.

In the case of crossover there are no correlations between the landscape changes and the crossover rate. Neither does the average rate change significantly as a function of time. In this case then there is no obvious induced symmetry breaking associated with the genotype-phenotype map as there are

no preferred values for the crossover rate.

These results have been qualitatively confirmed in other experiments. Below we show another type. This consists of a counting ones landscape that changes stochastically into a “counting zeros” landscape. In other words certain generations were chosen at random (generations 100, 200, 210, 220, 230, 240, 400, 700 and 900) wherein the landscape was changed from counting ones to counting zeros, however in each run the changes were carried out at the same generation.

The comparison is between chromosomes with codified mutation and crossover rates and chromosomes with fixed values. For the latter the fixed values chosen were once again  $p = 0.01$ ,  $p_c = 0.8$ . For the chromosomes with codification mutation and crossover rates were both codified with nine bits. Eight bits were used to represent reproductive fitness. The results represent averages over 10 different runs with a population of 500. For the codified strings a minimum mutation rate of 0.001 was used. In Figure 3 we see the average fitness of the population (online fitness) as a function of time. The dashed curve represents the codified population. Both codified and uncoded GAs were capable of following the landscape changes and reaching a population composition associated with a quasi-species centered on the global optimum of 8. Note the online performance of the codified GA is always superior to that of the uncoded given time and a not too high a frequency of landscape change due to the fact that the former can self-organize in such a way that the average mutation rate for strings with all 1s is much less than the average mutation rate for the entire population, or of that of the non-codified strings. For high frequency changes in the landscape neither GA was capable of tracking the changes well. In other words the landscape changes were such that exploration could never lead to a successful exploitation phase.

In Figure 4 we show the average mutation and crossover rates in the codified population. The lower curve is the mutation rate. Note the exact coincidence between the large changes in the mutation rate and those of the landscape, the former changing by more than an order of magnitude in response to the landscape changes. It is clear that there is a very high degree of self-organization in the genotype-phenotype map taking place here. As stressed previously, in terms of reproductive fitness there should be no preference for one rate versus another. It is clear that the degree of correlation between the landscape changes and that of the crossover rate is small. The latter has some significant variation early on, for which we have no explanation, but settles down to a fairly constant rate.

### 4.3 A Neuro-genetic Model

Our third example is associated with a Neuro-genetic model. In this case an analysis was made [11] of the population dynamics of a variant of Kitano’s neuro-genetic model [12, 13] wherein the chromosome encodes the rules for cellular division and the phenotype is a 16-cell organism interpreted as a connectivity matrix for a feed-forward neural network. Specifically, an artificial ecological environment was studied which consists of a single species composed of neural

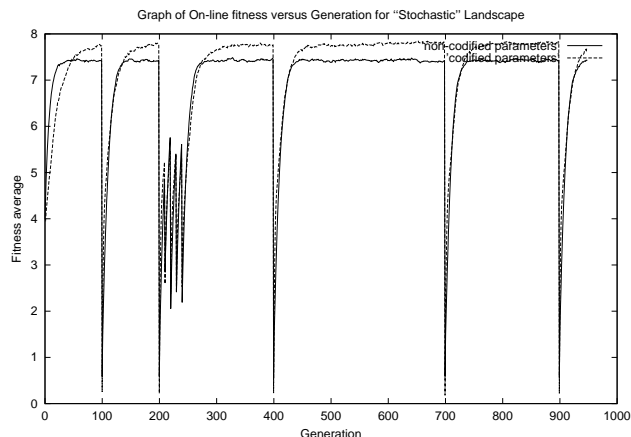


Figure 3: Graph of average population fitness (online fitness) versus time for stochastic time-dependent landscape. The solid curve corresponds to the fixed parameter GA and the dashed curve to the auto-adaptive GA

networks as individuals. Every chromosome, or genotype, is used to produce a particular architecture for a feed-forward NN that consists of 12 input neurons, 4 hidden and 1 output neuron — the phenotype. A GA is then applied to the chromosomes present in the population at each epoch which induces a search of the connectivity matrix space determined by the structure of the NN. Environmental effects are included in the fitness function that measures the learning capacity of a particular individual.

A chromosome consists of eight blocks of four genes each one of which is a three bit structure. Both the blocks and the genes themselves are labeled from  $a$  to  $h$ . The reproduction process always begins with block  $a$ . Thus the first four genes have a privileged role as they label the cells that are going to be reproduced in the second step of reproduction. As an example consider the chromosome  $baea.dcaa.defa.becd.aaea.aafh.haec.fgaa$ . The two step reproduction process specified by this chromosome can be written

$$\begin{aligned}
 a &\longrightarrow \begin{pmatrix} b & a \\ e & a \end{pmatrix} \longrightarrow \begin{pmatrix} d & c & b & a \\ a & a & e & a \\ a & a & b & a \\ e & a & e & a \end{pmatrix} \\
 &\leftrightarrow \begin{pmatrix} 0 & 1 & 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \end{pmatrix} \quad (13)
 \end{aligned}$$

Thus the first block,  $baea$ , codes for the division of the original cell  $a$  into four cells. The first of these cells,  $b$ , then divides into four more which form the

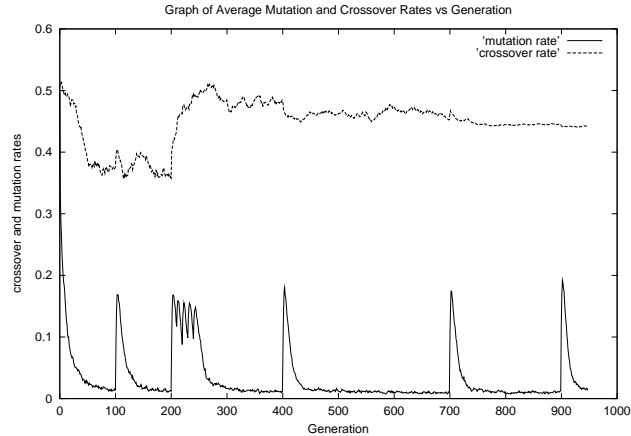


Figure 4: Graph of average mutation and crossover rate versus time for stochastic time-dependent landscape

upper left quadrant,  $dca$ , of the matrix. The second cell,  $a$ , maps block  $a$  of the chromosome into the upper right quadrant etc. Finally, the genes are rewritten in their binary representation and the resultant connectivity matrix is constructed by reading left to right, row by row. Thus a 1 specifies a connection between an input neuron and a hidden neuron and a 0 its absence.

The genotype-phenotype map in this case is highly degenerate. For example, in the above we can change blocks  $c$ ,  $e$ ,  $f$ ,  $g$  and  $h$  without changing the resulting phenotype. It is also a non-local function on the chromosomes since entries of block number one can target any one of the other blocks irrespective of their distance. To define a fitness function the learning speed of the NNs on a given test function was measured

$$y_c = \frac{\epsilon}{3}(x_1 + x_2 + x_3) + (1 - \epsilon)X \quad (14)$$

where  $x_1$ ,  $x_2$  and  $x_3$  are the first three inputs of the neural network,  $\epsilon$  is a noise control parameter and  $X$  is a randomly generated number. A GA was used to search the space of network architectures for the one capable of learning this function with the smallest number of attempts.

Given the highly degenerate nature of the genotype-phenotype map one might expect to see an optimum phenotype emerge with a random distribution of the corresponding genotypes. However, this was not the case — certain genotypes were consistently preferred thus indicating that the genotype-phenotype symmetry was broken. The reason for this is that although degenerate genotypes were equivalent in terms of reproductive selection the other genetic operators, mutation and recombination, broke the symmetry picking out the more robust or less brittle genotypes, i.e. those that were most likely to lead to other fit neural networks.

Remarkably, the induced symmetry breaking in this context can be described in terms of the emergence of an “algorithmic language” [11]. Each genotype of the model is composed of eight four-letter combinations, while each phenotype is composed of four four-letter combinations, hence the degree of degeneracy is substantial as four of the four-letter combinations do not code for anything in the phenotype. All combinations are composed of letters taken from an eight letter alphabet, hence there are 3928 different four-letter combinations. If we think of a fitness landscape for this system which is flat, in that all NNs have the same fitness, then in terms of forming possible NN connections every four-letter combination is “meaningful”. Hence, we have a language composed of 3928 possible four-letter words.

The first word of the chromosome governs the grammar of the system by determining the syntax of the four-word combinations that make up the algorithm that generates the phenotype, i.e. the NN architecture. The algorithmic language in this case is not an emergent property as every four-word algorithm formed by the switchboard block that governs the syntax is meaningful irrespective of the effects of the genetic operators. There is no brittleness problem here as every genotype is equally fit, if we regard fitness purely as being associated with if or not a viable NN architecture is formed. As there is no non-trivial fitness function at work here any preference for one architecture versus another can only come about through a symmetry breaking mechanism.

With respect to the fitness function associated with the learning rate for the function (14) a very different picture emerges. Now the requirement is that of forming a NN that learns well. In this case many four-word algorithms are “meaningless” in the sense that they lead to networks of zero or very low fitness. Which words are chosen and their associated syntax is now crucially important, and one must confront the brittleness problem as mutation and crossover can convert a very fit NN into a very unfit one. It is precisely in this sense that a preferred language and grammar emerged with respect to which algorithms are written that lead to fit NNs. For instance, it was found that the switching block,  $a$ , which can play a role as a word as well as a grammatical rule rarely appeared as a word. This helped in making the system less susceptible to destructive mutations and hence more evolutionarily robust. Hence, chromosomes where  $a$  did not play a role as a word were of higher effective fitness.

#### 4.4 Giraffe Necks

The final example concerns the size of giraffe necks [14]! This model consists of a population of one thousand genotypes subject to random mutations. A genotype is a cellular automaton with binary elements which gives rise to a giraffe neck size, i.e. a phenotype, given by the number of automata elements that are “switched on” at the fixed point (steady state) of the automata dynamics. As there are many different automata that can evolve to the same fixed point the genotype-phenotype mapping is once again highly degenerate. One master gene in particular plays a special role as it governs the way in which the Boolean rules used in the evolution mutate.

Each member of the population is selected for the next generation with probability  $P_i = f_i / \sum_j f_j$ , where  $f_i$  is the fitness of phenotype  $i$ . Initially there are ample resources available from both small and large trees, the only selective criterion being that giraffes prefer to choose a mate from among those that have similar neck size. This social pressure landscape is modeled by defining the fitness of the  $i$ th giraffe to be a function of its neck size  $n_i$  and the average neck size of the population,  $\langle n \rangle$ , with value one if  $\langle n \rangle - \delta < n_i < \langle n \rangle + \delta$  and zero otherwise. Here,  $\delta > 0$  is a tolerance window. Note that landscape fitness depends only on neck size, hence all genotypes that correspond to the same dynamical fixed point (phenotype) have the same reproductive fitness. Thus, as in the other examples, there is no direct selective advantage for one genotype versus another. To introduce time dependence into the landscape one imposes a short period of drought in which food begins to be available only in taller and taller trees. This period is mimicked by making  $f_i = 1$  if  $\langle n \rangle - \delta + \epsilon < n_i < \langle n \rangle + \delta + \epsilon$ , where  $\epsilon$  is a stress parameter, and zero otherwise. After this drought the landscape is restored to its original state.

The master gene divides the population into two genetic categories, type zero and type one, which can mutate one into the other due to the effect of purely random mutations that have a probability  $\mu$  except for the master gene which mutates at a rate  $\nu$ . Type zero chromosomes, by nature of the dynamical evolution rules they are associated with, tend to give rise to giraffe offspring with shorter necks, while type one chromosomes, when they are expressed, tend to lead to giraffes with longer necks. Before the drought there is a period in which type one is not expressed. At a certain moment in time it becomes expressed then afterwards the drought starts. The social pressure landscape implies there are two possible attractors: all type one or all type zero. The effect of the drought is to change between one and the other.

A typical experiment leads to the following results, the general behavior can be seen in Figure 5: In the initial period of evolution, before the drought, average neck size is short. After the drought arrives the average neck size grows very quickly. After it ends it continues to grow, albeit more slowly, for a substantial amount of time until a steady state is reached.

These results can be explained quite simply: in the period before the drought, and before expression, type one chromosomes increase due to the effect of neutral drift. After expression they are effectively selected against due to their tendency to produce giraffes with longer necks that pass outside the tolerance threshold and therefore cannot reproduce. Thus, before the drought the effective fitness of type one chromosomes is low. However, due to the effect of mutations type one chromosomes are not eliminated totally but constitute about 1 – 5% of the total population. After the drought starts the effective fitness of type one chromosomes increases substantially, given that they lead to giraffes with longer necks. The result is that the population becomes dominated by type one chromosomes, with a small fraction of type zero remaining due to the effects of mutation. After the end of the drought, as type one chromosomes tend to produce longer necks, the average neck size increases until a steady state is reached and it cannot grow anymore.

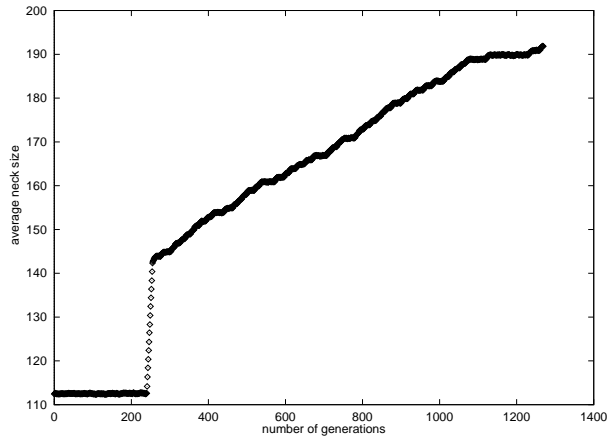


Figure 5: Graph of average giraffe neck size (in arbitrary units) as a function of time for a population of 1000 giraffes. The drought starts at generation 240 and lasts for 30 generations. Subsequent neck growth lasts for another 1000 generations. The parameter values used were:  $\mu = 0.0025$ ,  $\nu = 10^{-6}$ ,  $\delta = 2.0$  and  $\epsilon = 1.0$ .

In this model there is absolutely no direct reproductive selective difference between type one and type zero chromosomes. The only advantage of one versus the other is in how they produce well adapted offspring, as measured by the effective fitness or reproductive success.

## 5 Effective Fitness

The previous two sections showed that it is difficult to intuitively understand population flows on reproductive fitness landscapes when genetic operators other than selection play an important role. This is manifest in the fact that the most selectively fit individuals reproductively do not always give rise to the most offspring. In fact we have seen that populations can flow against the reproductive fitness gradient and that other operators generically lead to a self-organization of the genotype-phenotype map. Thus, under many circumstances the hill-climbing analogy is not a good one. We emphasize that we are not just talking about a pathology that in practice is very unlikely to occur, but rather a phenomenon that is central to both biology and EC whenever genetic operators other than pure reproductive selection are of importance.

### 5.1 Effective Fitness Interpretation of the Results of Section 3

Let us see how the concept of effective fitness and an effective fitness landscape can help us better understand the results of section 3. In the simple one-locus model there; in the absence of mutations,  $p = 0$ ,  $f_{\text{eff}}(C_i, t) = f(C_i) = f$ ,  $\forall i = 0, 1$ . For  $p \neq 0$

$$f_{\text{eff}}(C_i, t) = ((1 - 2p) + (p/P(C_i, t))) f \quad (15)$$

Thus, we can see explicitly that when the population is homogeneous effective fitness is the same as reproductive fitness. Deviations from homogeneity result in a higher effective fitness for the less numerous genotype. The effective fitness advantage then decreases as the system approaches equilibrium.

The effective fitness landscape for this model when the mutation rates from 1 to 0 and 0 to 1 are different can be seen in Figure 6. In this case,  $f =$

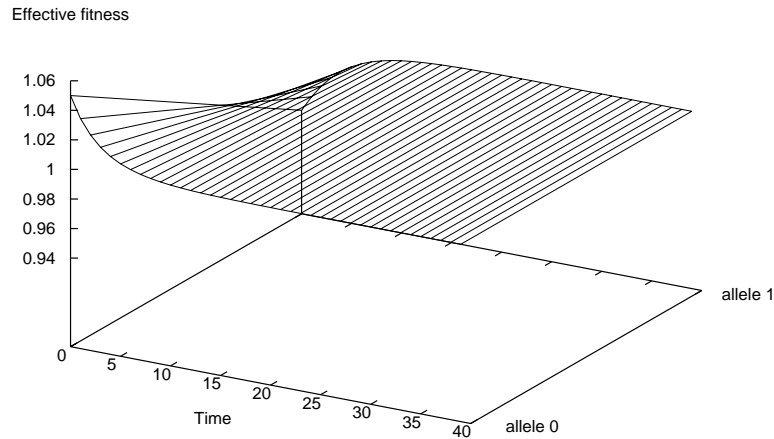


Figure 6: Graph of effective fitness as a function of time for the one-locus model of section 3 with different mutation rates.

2,  $p_1 = 0.15$ ,  $p_2 = 0.1$  and  $P(0,0) = P(1,0) = 0.5$ . Note the significant differences in  $f_{\text{eff}}(C_i, 0)$  as a result of which there is a population flow from 1 to 0 along this effective fitness gradient even though there is no reproductive fitness gradient. This gradient decreases monotonically as a function of time; thus the effective landscape becomes flat asymptotically. This will be a generic

property of any effective fitness landscape, the only steady state solutions of the evolution equations being  $f_{\text{eff}}(C_i, t) = \bar{f}(t) \forall C_i$ , or  $P(C_i, t) = 0$ . Thus, already we see the usefulness of effective fitness — it indicates by its deviation from flatness how close the population is to a steady state.

For the two-locus model the reproductive fitnesses of 00 and 01 are equal. However, their effective fitnesses are quite different being:  $f_{\text{eff}}(00, 0) = (1 - 0.9p + 9.9p^2)$  and  $f_{\text{eff}}(01, 0) = (1 + 9p - 9.9p^2)$  respectively, where initial proportions of all four states are taken to be equal. The effective fitness landscape in this problem is shown in Figure 7 for  $t = 0$  with  $p = 0.05$ ,  $P(00, 0) = 0.3$ ,  $P(01, 0) = 0.2$ ,  $P(10, 0) = 0.4$  and  $P(11, 0) = 0.1$ . Notice the initial effective fitness gradient

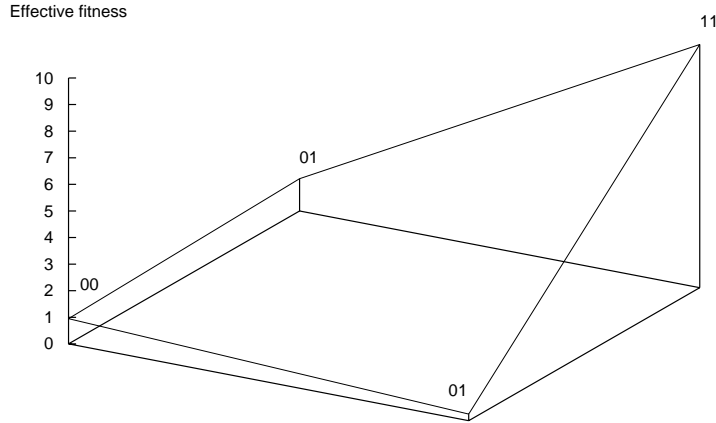


Figure 7: Graph of effective fitness at  $t = 0$  for the two-locus model of section 3.

from 00 to 01 that  $\rightarrow 0$  as  $t \rightarrow \infty$  as can be seen in Figure 8 which shows the same effective fitness landscape as in Figure 7 but at late times. Once again note the flatness of the effective landscape at late times.

In the case of a strictly flat fitness landscape characteristic of neutral evolution the effective fitness is

$$f_{\text{eff}}(C_i, t) = f \sum_{j=1}^{2^N} \frac{P(C_j, t)}{P(C_i, t)} p^{d_{ij}} (1-p)^{N-d_{ij}} \quad (16)$$

For a homogeneous population  $f_{\text{eff}}(C_i, t) = f \forall C_i, t$ . Thus, under these circum-

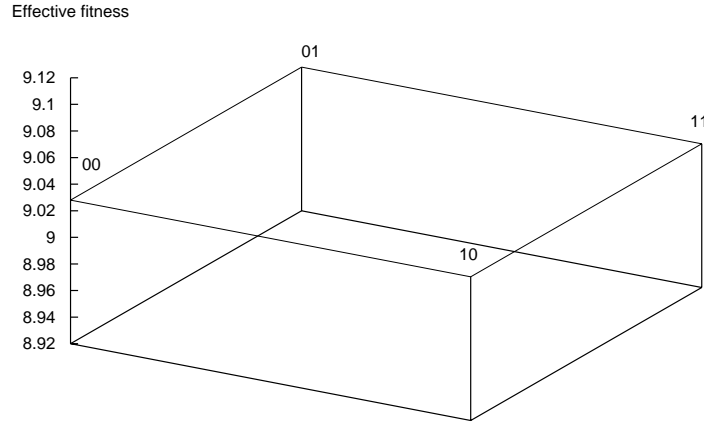


Figure 8: Graph of effective fitness at late times for the two-locus model of section 3.

stances the effective fitness landscape is as flat as the normal one. Small deviations from homogeneity will be manifest in small corrugations of the effective fitness landscape which will gradually diminish as the population homogenizes. If the landscape only has a flat subspace the system will seek to escape the flat subspace by way of the direction with the highest effective fitness gradient.

In the case of the NIAH landscape the effective fitness of the optimum string is

$$f_{\text{eff}}(C_{\text{opt}}, t) = f_0(1-p)^N + f_1 \sum_{C_j \neq C_{\text{opt}}} \frac{P(C_j, t)}{P(C_{\text{opt}}, t)} p^{d_{\text{opt}j}} (1-p)^{N-d_{\text{opt}j}} \quad (17)$$

In Figure 9 we see a plot of the effective fitness for the optimum genotype of the Eigen model in the steady state as a function of  $p$ . In this case  $f_0 = 10$  and  $f_1 = 1$ . For  $p = 0$ ,  $f_{\text{eff}}(C_{\text{opt}}, \infty) = f_0$  i.e. reproductive and effective fitness are the same. Note how the error threshold manifests itself in terms of the effective fitness — that at and above the threshold  $f_{\text{eff}}(C_{\text{opt}}, t) \rightarrow \bar{f}(t) \approx f_1$ . i.e. once again the effective fitness landscape will be flat. Thus, the effective fitness itself can serve as an order parameter to distinguish the selection dominated regime from the mutation dominated one, i.e. strong selection from weak selection.

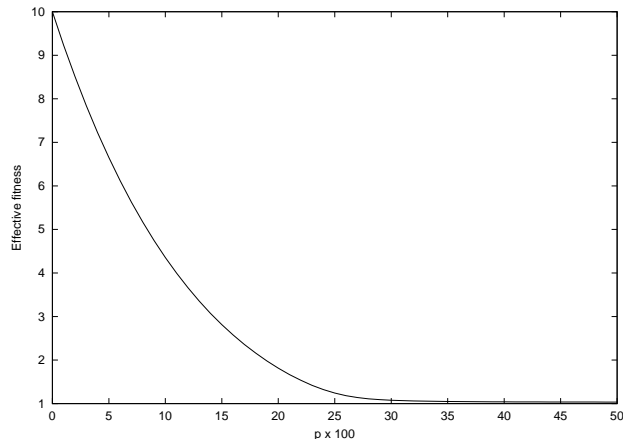


Figure 9: Graph of effective fitness versus  $p$  ( $\times 100$ ) in the steady state limit of the NIAH landscape.

## 5.2 Effective Fitness Interpretation of the Results of Section 4

Consider now the examples of section 4. In the first example, we graph  $F(l) \equiv (f_{\text{eff}}(l) - f_{\text{eff}}(8)) / f_{\text{eff}}(8)$ , where  $f_{\text{eff}}(l)$  is the effective fitness of optimal 2-schemata of size  $l$  and  $f_{\text{eff}}(8)$  is the analogous quantity for optimal 2-schemata of size 8. Note that the effective fitness of larger schemata is greater than that of shorter ones for the first 6 or so generations. A positive effective selection coefficient is associated with a schema that is growing in number relative to another. After 6 generations the curves in Figure 1 start to converge again which coincides with the effective fitness now being larger for the smaller schemata. Roughly speaking one can think of the effective fitness as being a measure of the gradient of the curves in Figure 1. It is interesting here that effective fitness is directly measuring the important effect of schema creation as without it, as is well known, there is a preference for short schemata. Note that here we see a type of induced symmetry breaking given that in terms of static schema averages there is no preference between optimal 2-schemata of one size versus another. Crossover breaks the symmetry by giving a reproductive advantage to long schemata as they can be most easily built up by crossover by using optimal 1-schema building blocks and effective fitness directly measures the strength of this induced symmetry breaking.

For the self-adaptive system, restricting to just reproductive selection and mutation, the effective fitness of a given string is

$$f_{\text{eff}}(C_i, t) = f(C_i, t)(1 - p_i)^N + \sum_{C_j \neq C_i} p_j^{d_{ij}} (1 - p_j)^{N - d_{ij}} f(C_j, t) \frac{P(C_j, t)}{P(C_i, t)} \quad (18)$$

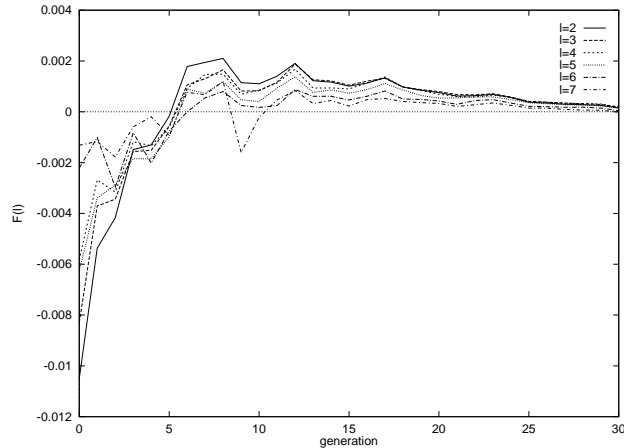


Figure 10: Graph of  $F(l)$  versus time for the unitation model of Figure 1.

where  $p_i$  is the mutation rate associated with the genotype  $c_i$ . To understand the behavior shown in Figure 2 we first realize that there are two contributions to  $f_{\text{eff}}(c_i, t)$ : one from the genotype  $c_i$  itself and another from all the other genotypes that can mutate to it. For the first contribution we can see that genotypes with low mutation rates will be preferred while for the second contribution genotypes with higher mutation rates will tend to be preferred.

Thus, we can see a quantitative way of evaluating the explanation given in section 4. Initially, before the landscape jump, selection dominated in that the first term in (18) was the most important. Consequently, the average mutation rate decreased as genotypes of low  $p_i$  were more effectively fit. After the jump there is at first a preference for the local optimum at 40, 41. This is due to the fact that both terms in the effective fitness are playing an important role whereas for the needle-like global optimum, as the original population before the jump had converged to 10, 11, there was no contribution from the first term to  $f_{\text{eff}}(63, t)$ . The fact that the average Hamming distance from 10 and 11 to 63 is 3.5, while from 10, 11 to 40, 41 it is 2.75, explains why the system first converges to 40, 41 before passing on to the global optimum. It is clear too why the average mutation rate increases at two distinct points in the search process. It is precisely when the second contribution in the effective fitness is playing a dominant role in aiding the search.

In the second case of the “counting ones” landscape that stochastically changes to a “counting zeroes” landscape we see in Figure 11 that the effective fitness of the codified strings is higher than that of the fixed rate strings. This is especially so where the landscape suddenly changes. These changes correspond exactly to the moments when the average mutation rate rapidly rises in the case of the codified strings thus allowing the codified population to adapt much more rapidly and efficiently to the landscape changes.

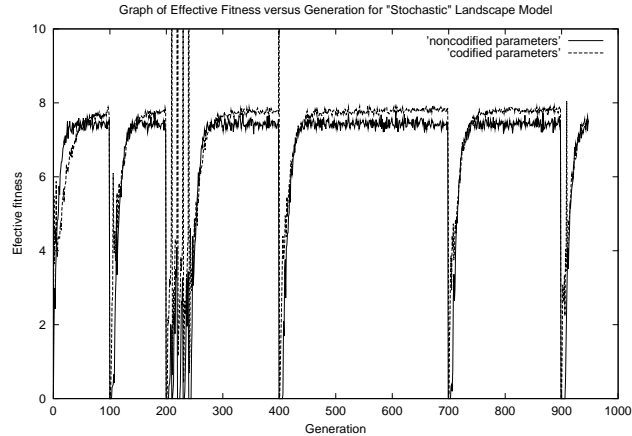


Figure 11: Graph of effective fitness versus time for the “Stochastic” landscape model of Figure 3.

In both self-adaptation problems we can see effective fitness as being a direct measure of the induced symmetry breaking of the genotype-phenotype map by the action of the mutation operator. The symmetry breaking is stronger in the counting ones  $\rightarrow$  counting zeroes problem when the landscape is changing rapidly (generations 200-250) as there is a bigger reproductive advantage for the codified strings during this period as a higher average mutation rate helps the population better keep track of the landscape changes.

In the more subtle neurogenetic problem it is more much more difficult to think of calculating the effective fitness due to the fact that the fitness function has to be experimentally measured rather than being algorithmically determined. Additionally, given that in this case the population size is far smaller than the size of the state space an experimental determination of the effective fitness would be very “noisy”. However, it is clear that the example has a ready explanation in terms of effective fitness. Basically, in this context one can think of the difference between effective fitness and reproductive fitness as being a measure of the evolutionary robustness of a genotype. Certain classes of genotypes are picked out from others of equal reproductive fitness because they are more robust in the presence of mutation and crossover and therefore enjoy, in the long term, a greater degree of reproductive success. Thus, genotypes that have block  $a$  both as a word and a grammatical rule have less reproductive success than those where  $a$  represents only a grammatical rule even though both, in a given generation, lead to the same NN, i.e. the same phenotype. Thus there is a population flow along an effective fitness gradient from genotypes where  $a$  plays a dual role to those where it is specialized.

The giraffe example is rather similar to that of the self-adapting system, the master gene being analogous to the part of the genotype that codes for the

mutation and recombination rates in the latter. It plays no role in reproductive selection but does play an important role in effective selection, type 1 chromosomes having a higher effective fitness than type 0 during and after the drought. Once again there is an induced symmetry breaking, type 1 chromosomes being preferred to type 0 even though both have the same reproductive fitness.

All these examples show clearly how different the effective fitness landscape is from the reproductive fitness landscape and how population flows can be understood much better within the framework of the former.

## 6 Conclusions

We have seen that in many situations high/low reproductive fitness does not correspond to high/low effective fitness and that it is the latter that really determines reproductive success. Effective fitness landscapes may serve as a conceptual tool, even without a quantitative method for computing them, in the same way as standard reproductive fitness landscapes have served an important purpose even though they can very rarely be computed. The further ability to compute the landscape adds an extra dimension to the theoretical framework.

The analytical and numerical examples considered in this paper were chosen to show phenomena that could not be readily understood in terms of a reproductive fitness landscape. We showed that flows could be directed in certain preferred directions of a flat fitness landscape and that flows could even go against the prevailing reproductive fitness gradient. One may argue as to whether the examples are generic or pathological. We strongly believe them to be generic, or at least that they illustrate generic phenomena. This is certainly the case in real biological systems where non-trivial genotype-phenotype maps are the rule. We also believe it to be true in EC when landscapes more closely resemble the real world, i.e. there is uncertainty, time dependence etc.

The object of this paper was not to argue that effective fitness is very useful in, for example, obtaining the optimal parameter values or representation for a GA solution to the traveling salesman problem, rather it is to argue and provide evidence that it is the appropriate conceptual framework in which to understand topics such as evolutionary robustness and other important phenomena when modeling EC systems that are more akin to real evolutionary systems. We would argue that the underlying principles associated with finding the optimum route of a 2000 city traveling salesman problem are very far away from those of a real evolutionary system. Having said that we do also think that effective fitness can play an important role, in conjunction with the exact evolution equations, for discussing the effects of deception for example, or evaluating the validity of theoretical ideas such as the Block hypothesis and Schema Theorem. In fact the results of section 4.1 and the evolution equations themselves are exactly in this spirit. Remember, that the original block hypothesis was based on an incomplete dynamics (without string/schema creation). The dynamical equations of section 2 allow one to quantify exactly how much fitter one block versus another is, and particularly in the case of two blocks of the same reproductive fitness. One can

get an intuition for the effects of deception by comparing the effective fitness landscape with the reproductive fitness landscape.

We believe that effective fitness can play a very important role in understanding evolutionary robustness and how to overcome the brittleness problem. Effective fitness can directly measure the robustness of one genotype versus another when they have the same reproductive fitness. Thus it may be used to quantify the utility of bloat. In the case of the algorithmic language example it also shows that robustness could play a fundamental role in the emergence of real languages both genetic and linguistic where in both cases a high degree of degeneracy exists.

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