B2.7.2 NK Fitness Landscapes*

Lee Altenberg
Hawai'i Institute of Geophysics and Planetology, University of Hawai'i at Manoa,
Honolulu, HI U.S.A. Internet: altenber@mhpcc.edu

November 27, 1996

Abstract

NK fitness landscapes are stochastically generated fitness functions on bit strings, parameterized (with N genes and K interactions between genes) so as to make them tunably 'rugged'. Under the 'natural' genetic operators of bit-flipping mutation or recombination, NK landscapes produce multiple domains of attraction for the evolutionary dynamics. NK landscapes have been used in models of epistatic gene interactions, coevolution, genome growth, and Wright's shifting balance model of adaptation. Theory for adaptive walks on NK landscapes has been derived, and generalizations that extend beyond Kauffman's original framework have been utilized in these applications.

Keywords:

adaptive landscape, adaptive walk, coevolution, computational complexity, 'edge of chaos', epistasis, 'House of Cards' model, multiple domains of attraction, pleiotropy, random field, random number generators, 'Red Queen' Hypothesis, representation problem, self-organized criticality, shifting-balance model, spin glass

B2.7.2.1 Introduction

A very short time after the first mathematical models of Darwinian evolution were developed, Sewall Wright (1932) recognized a deep property of population genetic dynamics: when fitness interactions exist between genes, the genetic composition of a population can evolve into multiple domains of attraction. The specific fitness interaction is *epistasis*, where the effect on fitness from altering one gene depends on the allelic state of other genes (Lush, 1935). Epistasis makes it possible for the population to evolve toward different combinations of alleles, depending on its initial genetic composition. (Wright's framework also included the complication of diploid genetics, which augments the fitness interactions that produce multiple attractors.)

*Section B2.7.2 in *The Handbook of Evolutionary Computation*, ed. T. Back, D. Fogel, Z. Michalewicz.

Wright thus found a conceptual link between a microscopic property of organisms—fitness interactions between genes—and a macroscopic property of evolutionary dynamics—multiple population attractors in the space of genotypes. To illustrate this situation, Wright invoked the metaphor of a landscape with multiple peaks, in which a population would evolve by moving up hill until it reached its local fitness peak. This metaphor of the 'adaptive landscape' is the general term used to describe multiple domains of attraction in evolutionary dynamics.

Wright was specifically interested in how populations could escape from local fitness peaks to higher ones through stochastic fluctuations in small population subdivisions. His was thus one of the earliest conceptions of a stochastic process for the optimization of multimodal functions.

Stuart Kauffman devised the 'NK fitness landscape' model to explore the way that epistasis controls the 'ruggedness' of an adaptive landscape (Kauffman and Levin, 1987; Kauffman, 1989). Kauffman wanted to specify a family of fitness functions whose ruggedness could be 'tuned' by a single parameter. He did this by building up landscapes from multiple 'atoms' of maximal epistasis.

The NK model is a stochastic method for generating fitness functions $F : \{0,1\}^N \mapsto \Re^+$, on binary strings, $\boldsymbol{x} \in \{0,1\}^N$, where the genotype $\boldsymbol{x}$ consists of N loci, with two possible alleles at each locus x_i. (As such, it is an example of a *random field* model elaborated upon in Stadler and Happel (1995).) It has two basic components: a structure for gene interactions, and a way this structure is used to generate a fitness function for all the possible genotypes.

The gene interaction structure is created as follows: The genotype's fitness is the average of N fitness components F_i contributed by each locus i. Each gene's fitness component F_i is determined by its own allele, x_i, and also the alleles at K other epistatic loci (so K must fall between 0 and $N-1$). Thus, the fitness function is:

$$F(\boldsymbol{x}) = \frac{1}{N}\sum_{i=1}^{N} F_i(x_i; x_{i_1}, \ldots, x_{i_K}), \tag{B2.7.2.7}$$

where $\{i_1, \ldots, i_K\} \subset \{1, \ldots, i-1, i+1, \ldots, N\}$. These K other loci could be chosen in any number of ways from the N loci in the genotype. Kauffman investigated two possibilities: *adjacent neighborhoods*, where the K genes nearest to locus i on the chromosome are chosen; and *random neighborhoods*, where these K other loci are chosen randomly on the chromosome. In the adjacent neighborhood model, the chromosome is taken to have periodic boundaries, so that the neighborhood wraps around the other end when it is near the terminus.

Epistasis is implemented through a 'House of Cards' model of fitness effects (Kingman, 1978, 1980): whenever an allele is changed at one locus, all of the fitness components with which the locus interacts are changed, without any correlation to their previous values. Thus, a mutation in any one of the genes affecting a particular fitness component is like pulling a card out of a house of cards—it tumbles down and must be rebuilt from scratch, with no information passed on from the previous value.

Kauffman implemented this by generating, for each fitness component, a table of 2^{K+1} numbers for each possible allelic combination for the $K+1$ loci determining that fitness component. These numbers are independently sampled from a uniform distribution on $[0, 1)$. (See B2.7.2.4 for alternative implementations of this scheme).

The consequence of this independent resampling of fitness components is that the fitness function develops conflicting constraints: a mutation at one gene may improve its own fitness component, but decrease the fitness component of another gene with which it interacts. Furthermore, if the allele at another interacting locus changes, an allele that had been optimal, given the alleles at the other loci, may no longer be optimal. Thus, epistatic interactions produce 'frustration' in trying to optimize all genes simultaneously, a concept borrowed from the field of spin-glasses, of which NK landscapes are an example (Anderson, 1985).

B2.7.2.2 Evolution on NK Landscapes

The definition given by Kauffman for the NK landscape is simply a fitness function on a data structure. The genetic operators that manipulate these data structures in creating variants are not explicitly included in the NK landscape specification. However, nothing can be said about the evolutionary dynamics until the genetic operators are defined. A change in the genetic operator will effectively define a new adaptive landscape (Altenberg, 1994a, 1995; Jones, 1995a, 1995b). The NK structure was defined with the 'natural' operators in mind: bit-flipping mutation, and recombination between strings. The magnitude of mutation and recombination rates also has a fundamental effect on the population dynamics.

One of the main differences between evolutionary algorithms and evolutionary genetics is relative time spent during transient (vs. near-equilibrium) phases of the dynamics. Biological populations have been running a long time, and so their genetic compositions are relatively converged (Gillespie, 1984); whereas in evolutionary algorithms, it is typical that initial populations are random over the search space, and so for much of their dynamics, the populations are far from equilibrium.

The dynamics of nearly converged populations under low mutation rate can be approximated by 'one-mutant adaptive walks' (Maynard Smith, 1970; Gillespie, 1984). The population is taken as fixed on a single genotype, and occasionally a fitter genotype is produced which then goes to fixation. The approximation assumes that the time it takes for the mutant to go to fixation is short compared to the time epochs between substitutions.

In implementing one-mutant adaptive walks, an initial genotype is chosen, and the fitnesses of all of the genotypes that can be produced by a single bit flip are sampled. A fitter variant (or the fittest, in the case of 'greedy' or 'myopic' walks) is selected, and the process is reiterated. When all of the one-mutant neighbors of a genotype are less fit than it, the walk terminates.

Results for One-Mutant Adaptive Walks

The following is a synopsis of the results in Kauffman (1993), Weinberger (1991), and Fontana *et al.* (1993) for one-mutant adaptive walks on NK landscapes.

For $K = 0$ the fitness function becomes the classical additive multi-locus model.

1. There is a single, globally attractive genotype.

2. The adaptive walk from any genotype in the space will proceed by reducing the Hamming distance to the optimum by 1 each step, and the number of fitter one-mutant neighbors equals this Hamming distance. Therefore, the expected number of steps to the global optimum is $N/2$.

3. The fitnesses of one-mutant neighbor genotypes are highly correlated, as $N - 1$ of the N fitness components are unaltered between the neighbors.

For $K = N - 1$, the fitness function is equivalent to the random assignment of fitnesses over the genotype space.

1. The probability that a genotype is a local optimum is $\frac{1}{N+1}$.

2. The expected total number of local optima is $\frac{2^N}{N+1}$.

3. The expected fraction of one-mutant neighbors that are fitter decreases by $1/2$ each step of the adaptive walk.

4. The expected length of adaptive walks is approximately $\ln(N - 1)$.

5. The expected number of mutants tested before reaching a local optimum is $\sum_{i=0}^{\log_2(N-1)-1} 2^i$.

6. As N increases, the expected fitness of the local optimum reached from a random initial genotype decreases toward the mean fitness of the entire genotype space, 0.5. Kauffman (1993) calls this the 'complexity catastrophe'.

For intermediate K, it is found that

1. For K small, the highest local optima share many of their alleles in common. As K increases, this allelic correlation between local optima falls away, more rapidly for random neighborhoods than adjacent neighborhoods.

2. For K large, the fitnesses of local optima are distributed with an asymptotically normal distribution with mean approximately

$$\mu + \sigma \sqrt{\frac{2 \ln(K + 1)}{K + 1}},$$

and variance approximately

$$\frac{(K+1)\sigma^2}{N[K+1+2(K+2)\ln(K+1)]},$$

where μ is the expected value of F_i, and σ^2 its variance. In the case of the uniform distribution, $\mu = 1/2$ and $\sigma = \sqrt{1/12}$.

3. The average Hamming distance between local optima, which is roughly twice the length of a typical adaptive walk, is approximately

$$\frac{N\log_2(K+1)}{2(K+1)}.$$

4. The fitness correlation between genotypes that differ at d loci is

$$R(d) = \left(1 - \frac{d}{N}\right)\left(1 - \frac{K}{N-1}\right)^d,$$

for the random neighborhood model, and

$$R(d) = 1 - \frac{K+1}{N}d + \frac{1}{\binom{N}{d}} \sum_{j=1}^{\min(K,N+1-d)} (K-j+1)\binom{N-j-1}{d-2}$$

for the adjacent neighborhood model.

Results for Full Population Dynamics

Most studies using NK models have investigated adaptive walks on the landscape. A notable exception is the study of Wright's shifting balance process using an NK landscape (Bergman *et al.*, 1995). In this study, the genotypes are distributed on a 1-dimensional spatial array, and mating and dispersal along the array are studied with different length scales. Mutation rates of 10^{-4} per locus per reproduction, and single-point recombination rates of 0.01 or 0.1 per chromosome per reproduction are examined. The NK fitness function is extended to diploid genotypes.

This model produces rich interactions of dispersal distance, recombination rate, and K with the mean fitness that is attained during evolution. For highly rugged landscapes, recombination made little difference in fitness attained, whereas at lower values of K, recombination could either improve or reduce the final fitness depending in a nonlinear way on the other parameters. The results support Wright's original theory: the greater the ruggedness of the landscape, the larger is the improvement in evolutionary optimization provided by population subdivision.

B2.7.2.3 Generalized NK Maps

The epistatic interaction structures described by Kauffman can be seen to be special cases of more general interaction structures. Although Kauffman conceives of each gene as contributing a fitness component, inspection of equation (B2.7.2.7) shows that in fact, the gene and the other K loci that interact with it are all symmetric in their effect on the fitness component. So one can remove the identification of one gene with one fitness component, and conceive of a set of N genes and a set of f fitness components and a map between them. This generalized fitness function is:

$$F(\boldsymbol{x}) = \frac{1}{f}\sum_{i=1}^{f} F_i(x_{j_1(i)}, x_{j_2(i)}, \ldots, x_{j_{p_i}}),$$

where p_i is the number of genes affecting fitness component i (its *polygeny*) and $\{j_1(i), j_2(i), \ldots, j_{p_i}\} \subset \{1, \ldots, N\}$. The index sets $\{j_1(i), j_2(i), \ldots, j_{p_i}\}$ comprise a gene-fitness map, that can be represented as a matrix,

$$\boldsymbol{M} = \left[m_{ij}\right], i = 1 \ldots f, j = 1 \ldots N, \tag{B2.7.2.8}$$

of indices $m_{ij} \in \{0, 1\}$, where $m_{ij} = 1$ indicates that gene j affects fitness component i. The rows of $\boldsymbol{M}$, $\boldsymbol{g}_i = \left[m_{ij}\right]$, $j = 1 \ldots N$, give the genes controlling each fitness component i. The columns of $\boldsymbol{M}$, $\boldsymbol{p}_j = \left[m_{ij}\right], i = 1 \ldots f$, give the fitness components controlled by each gene j. These vectors $\boldsymbol{p}_j$ represent each gene's *pleiotropy*. It is assumed that each gene affects at least one fitness component, and vice versa.

The fitness components F_i can be represented with a single uniform pseudo-random function U:

$$F_i(\boldsymbol{x}) = U(\boldsymbol{x} \circ \boldsymbol{g}_i, \boldsymbol{g}_i, i) \sim \text{uniform on } [0, 1), \tag{B2.7.2.9}$$

where $U : \{0, 1\}^N \times \{0, 1\}^N \times \{1, \ldots, N\} \mapsto [0, 1)$, and $\circ$ is the Hadamard product:

$$\boldsymbol{x} \circ \boldsymbol{g}_i = \left[\begin{array}{c} x_1 m_{i1} \\ x_2 m_{i2} \\ \ldots \\ x_N m_{iN} \end{array}\right].$$

A change in any of the three arguments $i, \boldsymbol{g}_i$, or $\boldsymbol{x}\circ\boldsymbol{g}_i$ gives a new value for $U(\boldsymbol{x}\circ\boldsymbol{g}_i, \boldsymbol{g}_i, i)$ that is uncorrelated with the old. See section B2.7.2.4 for methods of implementing $U(\boldsymbol{x} \circ \boldsymbol{g}_i, \boldsymbol{g}_i, i)$.

Some illustrations of this generalization of the NK model are given in Figure 1. The first two maps are standard Kauffman NK maps, which require that the diagonal be filled. The third is a map that produces a 'block model' of Perelson and Macken (1995). The fourth is an example of a map grown by selective gene addition, a process which produces highly non-generic NK landscapes (see below; Altenberg, 1994b).

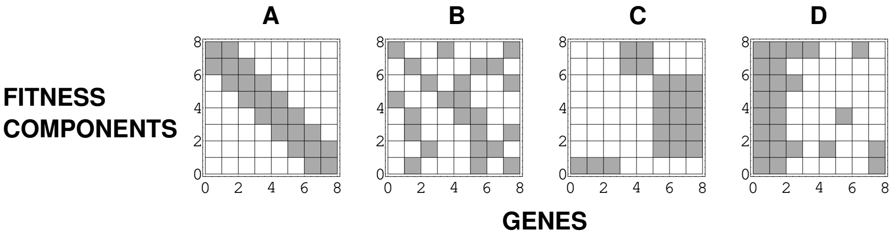

Figure 1: Four different gene-fitness interaction maps. Dark entries are for genes that affect the fitness component. (A) Kauffman's adjacent neighborhood, $N = 8, K = 2$; (B) Kauffman's random neighborhood, $N = 8, K = 2$; (C) Perelson and Macken 'block' map (1995) ; (D) Map evolved through genome growth (Altenberg, 1994b).

The block model presents an opportunity to study recombination operators, which has not yet been utilized in the literature. Recombination between blocks is effectively operating on a smooth landscape, whereas mutation will still experience frustration, to a degree that depends on the size of the block. One can conjecture that a relation could be elucidated between the 'blockiness' of the gene-interaction map and the relative effectiveness of recombination as a genetic operator, as compared to mutation. The blockiness of a generalized NK landscape could serve as another tunable parameter for investigating recombination as an evolutionary strategy.

B2.7.2.4 Implementation Details

Kauffman's algorithm for generating an NK landscape requires storing the values for all of the $2^{(K+1)}$ possible allelic combinations of each fitness component. Since there are N fitness components, this approach requires storage of $2^{(K+1)}N$ numbers. For small K, this poses no problem. But with large K and N, storage and computation become formidable. With 32 genes and $K = 22$, a gigabyte of storage is needed (4 bytes/real $\times$ 32 $\times$ $2^{(22+1)}$). Yet, depending on the evolutionary algorithm used, often many of these numbers will never be called during the run. So one could instead create fitness component values as they are needed, and store them for later access (using, for example, a binary tree structure (Wirth, 1976)).

A simple method (used in Altenberg (1994b)) which requires no storage, but more computation, is to compute fitness components as they are called, using a pseudo-random function:

$$\Psi : \{0, 2^W - 1\} \mapsto \{0, 2^W - 1\},$$

where W is the bit-width of the integer representation . Ψ can be used to implement equation (B2.7.2.9) thus:

$$F_i(\boldsymbol{x}) = 2^{-W}\Psi\{(\boldsymbol{x} \circ \boldsymbol{g}) \wedge \Psi[\boldsymbol{g} \wedge \Psi(i \wedge t)]\},$$

where t is the integer seed of the run, $\wedge$ is the bitwise exclusive-or operator, and the bit strings $\boldsymbol{g}$ and $\boldsymbol{x}$ are represented as integers.

One must be careful in the choice of algorithms for Ψ. Park-Miller random number generators are unsuitable for Ψ, as there are correlations between input bits and output bits. However, the 'pseudo Data-Encryption-Standard' algorithm, *ran4*, (Press *et al.* 1992) works well as Ψ for genomes of length $L \leq 32$, and can be extended for larger genomes.

B2.7.2.5 Computational Complexity of NK Landscapes

The computational complexity of finding the optimum genotype in an NK landscape has been analyzed by Weinberger (1996) and Thompson and Wright (1996). The algorithms they use for the proofs depend only on the epistatic structure of the gene interaction map, and not the statistical assignment of fitnesses.

Weinberger provides a dynamic programming algorithm that finds the optimum genotype of an NK landscape with adjacent neighborhoods for any K. He is also able to reduce the NK optimization problem with random $K \geq 3$ neighborhoods to the well-known 3SAT problem (Garey and Johnson, 1979). Thompson and Wright were able to reduce the NK optimization problem with random $K = 2$ neighborhoods to the 2SAT problem (Garey and Johnson, 1979). These techniques prove the following theorems:

Theorem B2.7.1 (Weinberger) *The NK optimization problem with adjacent neighborhoods is solvable in $\mathcal{O}(2^K N)$ steps, and is thus in $\mathcal{P}$.*

Theorem B2.7.2 (Weinberger) *The NK optimization problem with random neighborhoods is $\mathcal{NP}$ complete for $K \geq 3$.*

Theorem B2.7.3 (Thompson and Wright) *The NK optimization problem with random $K = 1$ neighborhoods is solvable in polynomial time.*

Theorem B2.7.4 (Thompson and Wright) *The NK optimization problem with random $K = 2$ neighborhoods is $\mathcal{NP}$ complete. Moreover, for a generalized $K = 1$ map with no requirement that $m_{ii} = 1$ for all i (in equation (B2.7.2.8)), the NK optimization problem is $\mathcal{NP}$ complete.*

The Fourier expansion analysis of NK landscapes in Stadler and Happel (1995) corroborates the difference between random and adjacent neighborhood models; with adjacent neighborhoods, only the first $K + 1$ Fourier components contribute, while all contribute in the random neighborhood model. Thus, even though adaptive walks on NK landscapes do not show much difference between adjacent neighborhood and random neighborhood models, the computational complexity of these two families of landscapes is quite different.

B2.7.2.6 Application to Coevolution

Kauffman (1993) used the NK model to frame a novel hypothesis about coevolving ecosystems: that they are poised on the 'edge of chaos', exhibiting a form of self-organized criticality (Bak *et al.*, 1988). In his model, Kauffman let the genes of other organisms interact with a gene's fitness component. Hence, evolution of one organism's gene alters the fitness landscapes of other organisms. Kauffman used adaptive walks as the dynamics of the coevolving species. He found that smooth landscapes when coupled together produce chaotic dynamics—the 'Red Queen' hypothesis—that organisms have to evolve as fast as they can just to stay in the same place (Van Valen, 1973), and the average fitness of organisms in the ecosystem is low. On the other extreme, in very rugged landscapes, the likelihood of the species reaching a local equilibrium is very high, but these equilibria are of low average fitness for the ecosystem. There is a threshold level of ruggedness that results in criticality of the dynamics, with a spectrum of 'avalanches' of coevolutionary change, the larger the avalanche, the less frequent. This critical value appears to give the highest average fitness over the ecosystem.

B2.7.2.7 Application to the Representation Problem

The generalized NK model has been applied to the *representation problem* in evolutionary computation: how to represent the objects in the search space so that genetic operators can have a reasonable chance of producing fitter variants when acting on the representation. One method proposed for producing good representations is to evolve the representation itself through a process of selective genome growth (Altenberg, 1994b).

In the model, the gene-fitness map $\boldsymbol{M}$ is built up gene by gene: new genes with randomly chosen connections to the fitness components (i.e. new columns of $\boldsymbol{M}$ with randomly chosen entries $\in \{0, 1\}$) were added to the genome only if they produced a fitness increase. It was found that as more genes were added and the fitness increased, selection for genes with low pleiotropy (affecting few functions) became more intense. An example of an evolved NK map is shown in Fig. 1(D). The fitness peaks of the resulting NK maps were several standard deviations above the fitness distribution for generic NK landscapes with the same interaction maps.

The NK model is thus used as an abstraction for the way representations produce epistatic interactions between genes. It was suggested that the method of selective genome growth which was able to produce highly evolvable NK landscapes might be applicable toward more general representation problems.

Acknowledgements

I thank the Maui High Performance Computing Center for generously hosting me as a visiting researcher.

References

[1] Altenberg, L. 1994a. The evolution of evolvability in genetic programming. In K. E. Kinnear, editor, *Advances in Genetic Programming*, pages 47–74. MIT Press, Cambridge, MA.

[2] Altenberg, L. 1994b. Evolving better representations through selective genome growth. In *Proceedings of the 1st IEEE Conference on Evolutionary Computation. Part 1 (of 2)*, pages 182–187, Piscataway N.J. IEEE.

[3] Altenberg, L. 1995. The Schema Theorem and Price's Theorem. In D. Whitley and M. D. Vose, editors, *Foundations of Genetic Algorithms 3*, pages 23–49. Morgan Kaufmann, San Mateo, CA.

[4] Anderson, P. W. 1985. Spin glass Hamiltonians: A bridge between biology, statistical mechanics, and computer science. In D. Pines, editor, *Emerging Synthesis in Science: Proceedings of the Founding Workshops of the Santa Fe Institute*, Santa Fe, NM. Santa Fe Institute.

[5] Bak, P., C. Tang, and K. Wiesenfeld. 1988. Self-organized criticality. *Physical Review A* 38: 364–374.

[6] Bergman, A., D. B. Goldstein, K. E. Holsinger, and M. W. Feldman. 1995. Population structure, fitness surfaces, and linkage in the shifting balance process. *Genetical Research* 66(1): 85–92.

[7] Fontana, W., P. F. Stadler, E. G. Bornberg-Bauer, T. Griesmacher, I. L. Hofacker, M. Tacker, P. Tarazona, E. D. Weinberger, and P. Schuster. 1993. RNA folding and combinatory landscapes. *Physical Review E* 47(3): 2083–2099.

[8] Garey, M. R. and D. S. Johnson. 1979. *Computers and Intractibility*. W. H. Freeman, San Francisco.

[9] Gillespie, J. H. 1984. Molecular evolution over the mutational landscape. *Evolution* 38(5): 1116–1129.

[10] Jones, T. 1995a. Evolutionary algorithms, fitness landscapes and search. Ph.D. Thesis. University of New Mexico.

[11] Jones, T. 1995b. One operator, one landscape. Working Papers 95-02-025, Santa Fe Institute, Santa Fe, NM 87501.

[12] Kauffman, S. A. 1989. Adaptation on rugged fitness landscapes. In D. Stein, editor, *Lectures in the Sciences of Complexity*, pages 527–618. Addison-Wesley, Redwood City. SFI Studies in the Sciences of Complexity, Lecture Volume I.

[13] Kauffman, S. A. 1993. *The Origins of Order: Self-Organization and Selection in Evolution*. Oxford University Press, Oxford.

[14] Kauffman, S. A. and S. Levin. 1987. Towards a general theory of adaptive walks on rugged landscapes. *Journal of Theoretical Biology* 128: 11–45.

[15] Kingman, J. F. C. 1978. A simple model for the balance between selection and mutation. *Journal of Applied Probability* 15: 1–12.

[16] Kingman, J. F. C. 1980. *Mathematics of Genetic Diversity*. Society for Industrial and Applied Mathematics, Philadelphia, page 15.

[17] Lush, J. L. 1935. Progeny test and individual performance as indicators of an animal's breeding value. *Journal of Dairy Science* 18: 1–19.

[18] Maynard Smith, J. 1970. Natural selection and the concept of a protein space. *Nature* 225: 563–564.

[19] Perelson, A. S. and C. A. Macken. 1995. Protein evolution on partially correlated landscapes. *Proceedings Of The National Academy Of Sciences Of The United States Of America* 92(21): 9657–9661.

[20] Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. 1992. *Numerical Recipes in C: The Art of Scientific Computing. Second Edition*. Cambridge University Press, pages 278–280, 300–304.

[21] Stadler, P. F. and R. Happel. 1995. Random field models for fitness landscapes. Working Papers 95-07-069, Santa Fe Institute, Santa Fe, NM.

[22] Thompson, R. K. and A. H. Wright. 1996. Additively decomposable fitness functions. To Appear.

[23] Van Valen, L. 1973. A new evolutionary theory. *Evolutionary Theory* 1: 1.

[24] Weinberger, E. D. 1991a. Local properties of Kauffman's N-k model, a tuneably rugged energy landscape. *Physical Review A* 44(10): 6399–6413.

[25] Weinberger, E. D. 1996. NP completeness of Kauffman's N-k model, a tuneable rugged fitness landscape. Working Papers 96-02-003, Santa Fe Institute, Santa Fe, NM, First circulated in 1991.

[26] Wirth, N. 1976. *Algorithms + Data Structures = Programs*. Prentice-Hall, Englewood Cliffs, N.J., pages 189–211.

[27] Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. *Proceedings of the Sixth International Congress on Genetics* 1: 356–366.