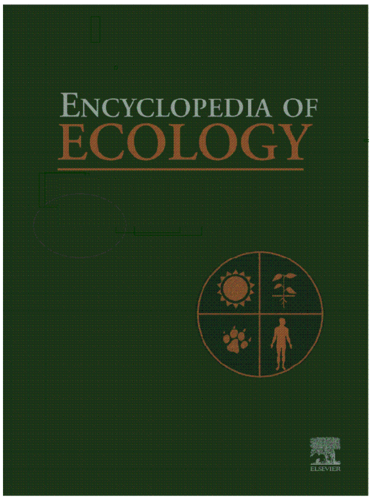

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# Fitness Landscapes

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## Introduction

During the last 70 years Sewall Wright's (1932) metaphor of 'fitness landscapes', which are also known as 'adaptive landscapes', 'adaptive topographies', and 'surfaces of selective value', has been a standard tool for visualizing biological evolution and speciation. Wright's metaphor is widely considered as one of his most important contributions to evolutionary biology. Moreover, the notion of fitness landscapes has proved extremely useful well outside of evolutionary biology (e.g., in computer science, engineering, biochemistry, and philosophy).

A key idea of evolutionary biology is that individuals in a population differ in fitness (because they have different genes and/or have experienced different environments). Differences in fitness that have genetic bases are the most important ones because it is changes in genes that make adaptation and innovations permanent. The relationship between genes and fitness (direct or mediated via phenotype) is obviously of fundamental importance. Wright's metaphor of fitness landscapes provides a simple way to visualize this relationship. Implicitly, it also emphasizes the role of specific biological mechanisms and patterns in evolutionary dynamics.

## Two Types of Fitness Landscapes

The first publication on this topic Wright introduced two different versions of fitness landscapes which Wright himself used somewhat interchangeably, laying the ground for confusion about their exact meaning, dimensionality, and justification.

### Average Fitness of the Population

In one interpretation, which is much more common but sometimes misleading, a fitness landscape is a surface in a multidimensional space that represents the mean fitness of the population as a function of gamete (or allele) frequencies. A population is represented as a point on the surface. This representation can be very illuminating because in some simple population genetic models, the population evolves in the direction of the local gradient in the mean fitness approaching a local 'peak' (i.e., maximum) in a fitness landscape. However, evolutionary dynamics of populations is a very complex process. In general, all relevant evolutionary factors (e.g., natural and sexual selection, random genetic drift, mutation, spatial structure and migration, environmental variability) and their interactions are expected to play important roles. Excluding some special cases (such as one-locus models of constant viability selection), the features and patterns of evolutionary dynamics cannot be captured or predicted on the basis of any single characteristic such as the mean fitness. Indeed, it is well known that the mean fitness of the population does not necessarily increase. Therefore, this version of fitness landscapes is not particularly useful in more realistic (e.g., multilocus) contexts.

### Fitness of Gene Combinations

In the second interpretation, which is a much more fundamental construction, the fitness landscape represents individual fitness as a function defined on the genotype space. The genotype space (i.e., the set of all possible genotypes) can be mathematically represented by the vertices of a (generalized) hypercube or an undirected graph. To construct a fitness landscape one assigns 'fitness' to each genotype in the genotype space. It is useful to visualize each individual as a point in this genotype space. Accordingly, a population will be a cloud of points, and different populations (or species) will be represented by different clouds. Selection, mutation, recombination, random drift, and other factors change the size, location, and structure of these clouds.

## Generalizations

In the classical interpretation, 'fitness' in fitness landscapes is understood as a property of an individual (e.g., viability or fertility) controlled by its genes. More generally, fitness can be an attribute of a mating pair such as a probability of successful mating between a pair of male and female genotypes, or fertility of a mating pair. Moreover, fitness landscapes can be defined for continuously changing ('quantitative') characters such as size, weight, color, or concentration rather than for discrete sets of genes. In this later case, fitness landscape can be defined at the level of a combination of quantitative traits (characterizing individuals or mating pairs) or as the average fitness of the population.

## Canonical Fitness Landscapes

Fitness landscapes for real biological organisms are, in general, unknown. Only recently have direct studies of specific landscapes such as RNA and protein landscapes started to appear. However, some general features of fitness landscapes can be identified using available data, biological intuition, and mathematical reasoning.

### Rugged Fitness Landscapes

Strong artificial selection in a specific direction usually results in a desired response, but as a consequence of the genetic changes brought about by artificial selection, different components of fitness (such as viability or fertility) significantly decrease. Moreover, after relaxing artificial selection, natural selection usually tends to return the population to its original state. These observations stimulated Wright's view of species as occupying isolated peaks in a fitness landscape. Following Wright, fitness landscapes are often imagined as 'rugged' surfaces having many local 'fitness peaks' of different height separated by 'fitness valleys' of different depth (see **Figure 1a**). Fitness peaks are interpreted as different (potential) species, fitness valleys between them are interpreted as unfit hybrids, and speciation is imagined as a 'peak shift'. Fitness peaks are important because of the expectation that natural selection will drive populations towards them. Within the framework of fitness landscapes, adaptive evolution is considered as 'hill climbing'. However, as soon as the population reaches a neighborhood of a local peak, any movement away from it is prevented by selection. It is important to realize that the peak the population has reached does not necessarily have the highest fitness. On the contrary, it is much more plausible that this peak has an intermediate height and that (much) higher fitness peaks exist nearby. Without some additional forces, a population evolving on a rugged landscape will stop changing after a relatively short transient time.

This conclusion leads to two important questions. The first is how fitness can be increased further. The second is how new species can be formed. Within the metaphor of rugged landscapes, both processes are impossible unless a population has a way to keep changing genetically after reaching a local peak. There are two possible solutions. First, additional factors acting against selection and overcoming it at least occasionally can drive the population across a fitness valley. The factor that has received most attention in this regard is random genetic drift. The effects of random genetic drift on the probability of escaping a local peak are considered in an another article (see Limiting Factors and Liebig's Principle). Second, temporal changes in the fitness landscape itself can result in continuous genetic changes driven by selection, with the

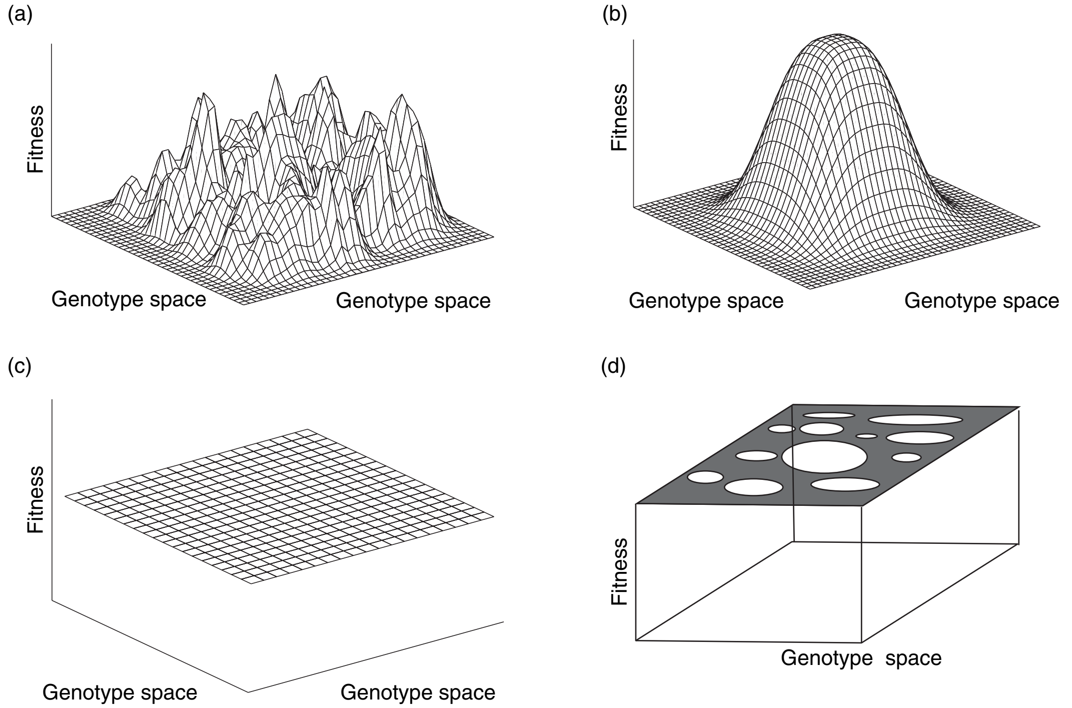

**Figure 1** Four types of fitness landscapes. (a) A rugged landscape. (b) A single-peak landscape. (c) A flat landscape. (d) A holey landscape.

population continuously climbing uphill and chasing a fitness peak that continuously moves away, as implied, for example, in the 'Red Queen' scenario. The metaphor of rugged fitness landscapes is often used within the context of finding an optimum solution out of many possible solutions to complex problems.

## Single-Peak Fitness Landscape

In contrast to Wright, Fisher suggested that as the number of dimensions in a fitness landscape increases, local peaks in lower dimensions will tend to become saddle points in higher dimensions. In this case, according to Fisher, natural selection will be able to move the population to the global peak without any need for genetic drift or other factors. A typical fitness landscape implied by Fisher's views has a single peak (see Figure 1b). This view is based on a belief that (1) there is one perfect combination of genes (rather than a series of more or less equivalent alternative combinations), and that (2) this gene combination (fitness peak) can be found by selection without the need for any additional factors such as genetic drift. It also implies that large populations are the major source of evolutionary innovations because they are more responsive to selection than small populations. Although Fisher's claim proved to be unjustified, his metaphor finds numerous applications, for example, within the context of adaptation or error threshold.

## Flat Landscapes

The major claim of the neutral theory is that most evolutionary changes at the molecular level are neutral (i.e., do not result in changes in fitness). A typical fitness landscape implied by this view is flat (see Figure 1c). The neutral theory explicitly emphasizes the possibility of extensive genetic divergence by stochastic factors in the absence of deterministic forces of selection. There is extensive theoretical literature on the evolutionary dynamics of selectively neutral mutations by random drift.

## Holey Fitness Landscapes

The dimensionality of sequence space can be defined as the number of new sequences (DNAs, RNAs, or proteins) one can get from a sequence by changing single elements of the sequence. Even the simplest organisms known have on the order of thousand genes and on the order of million DNA base pairs. Each of the genes can be at at least several different states (known as alleles). Thus, the dimensionality of genotype space is at least on the order of thousands. It is on the order of millions if one considers DNA base pairs instead of genes. This results in an astronomically large number of possible genotypes (or DNA sequences) which is much higher than the number of organisms present at any given time or even cumulatively since the origin of life. There is an important consequence of this observation. Because of the redundancy in the genotype-fitness map, different genotypes are bound to have very similar (identical from any practical point of view) fitnesses. Unless there is a strongly 'nonrandom' assignment of fitnesses (say all well-fit genotypes are put together in a single 'corner' of the genotype space), a possibility exists that well-fit genotypes might form connected clusters (or networks) that might extend to some degree throughout the genotype space. If this were so, populations might evolve along these clusters by single substitutions and diverge genetically without going through any adaptive valleys.

The huge dimensionality of most biologically interesting fitness landscapes brings some new properties which one does not observe in low-dimensional landscapes (e.g., in 2D or 3D geographic landscapes). In particular, multidimensional landscapes are generically characterized by the existence of neutral and nearly neutral networks (also referred to as holey fitness landscapes) that extend throughout the landscapes and that can dramatically affect the evolutionary dynamics of the populations. A neutral network is a contiguous set of sequences possessing the same fitness. A nearly neutral network is a contiguous set of sequences possessing approximately the same fitness. A holey adaptive landscape is an adaptive landscape where relatively infrequent well-fit (or as Wright put it, 'harmonious') genotypes form a contiguous set that expands ('percolates') throughout the genotype space. An appropriate 3D image of such an adaptive landscape is a flat surface with many holes representing genotypes that do not belong to the percolating set (see **Figure 1d**).

As was discussed above, each of the three classical metaphors of fitness landscapes emphasizes certain features of the landscapes and evolutionary dynamics while neglecting or de-emphasizing others. Wright's metaphor of rugged fitness landscapes emphasizes the existence of multiple high-fitness combinations of genes and the need for stochastic factors to overcome selection for continuous evolution. The metaphor of a single-peak landscape reflects Fisher's belief that there is a single 'best' combination of genes and that selection alone is sufficient for evolutionary change and adaptation. The metaphor of flat fitness landscapes emphasizes Kimura's views on the importance of extensive genetic divergence by mutation and random genetic drift alone. In contrast, the metaphor of holey landscapes illustrated in **Figure 1d** emphasizes the percolating ridges of high-fitness genotypes at the expense of other features of multidimensional fitness landscapes.

Within the metaphor of holey landscapes, local adaptation and microevolution can be viewed as climbing from a hole towards a nearly neutral network of genotypes with fitnesses at a level determined by mutation–selection–random drift balance. The process of climbing occurs on a shorter timescale than that necessary for speciation, clad diversification, and macroevolution. Once a ridge is reached, the population will be prevented by selection from slipping off this ridge to lower fitnesses and by mutation, recombination, and gene flow from climbing to higher fitnesses. Speciation occurs when a population evolves to a genetic state separated from its initial state by a hole. Holey fitness landscapes found numerous applications for studying speciation, innovations, evolvability, and robustness.

## Empirical Data

To date, most empirical information on fitness landscapes in biological applications has come from studies of RNA, proteins, viruses, bacteria, and artificial life. Empirical support exists for the properties of fitness landscapes captured by all three canonical landscape metaphors as well as those reflected in the idea of holey fitness landscapes.

*See also:* Abiotic and Biotic Diversity in the Biosphere; Landscape Ecology; Landscape Planning.

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