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A Shifting Terrain: A Brief History of the Adaptive Landscape

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PART I

Historical Background and Philosophical Perspectives

CHAPTER 1

A Shifting Terrain: A Brief History of the Adaptive Landscape

Michael R. Dietrich and Robert A. Skipper, Jr.

1.1 Introduction

Sewall Wright's graphical metaphor of the Adaptive Landscape is touted as one of the most famous metaphors in the history of biology (e.g. Provine 1986; Ruse 1996; Coyne et al. 1997). In 1932, Wright analogized (the contours of) a physical landscape to a surface whose contours marked differences in fitness. Underlying this fitness surface were the many different possible gene combinations that might be realized. Borrowing representations familiar from topographical maps, Wright's fitness topographies were marked by peaks and valleys corresponding to high and low adaptive value. Populations or individuals could be located on these fitness surfaces and the action of selection pushing and pulling on their different features would help determine their trajectories over time.

Wright developed his Adaptive Landscape metaphor and its diagrams as a way to translate his shifting balance theory from the mathematics of population genetics to a more accessible idiom for the general biologist. The shifting balance theory assumed that genes produced their effects through complex interactions and that subdivided populations created an opportunity for selection to act efficiently as these subpopulations moved through phases of drift and selection (see Chapters 4, 5, and 6 for more detailed discussions of the shifting balance theory). The landscape diagrams also allowed Wright to set up his problem of shifting from one adaptive peak to another (see Chapter 6). While the influence of Wright's landscape analogy is undeniable, similar representations and related ideas had previously been presented. In this chapter, we will first consider the possibility

that the Adaptive Landscape was independently co-discovered, before turning to the conceptual and representational lineages of different forms of the Adaptive Landscape originating from Wright's 1932 representation. We will distinguish between genetic, phenotypic, and molecular versions of the Adaptive Landscape as a way of marking significant moments of change in the history of the Adaptive Landscape concept. The history of these different conceptual lineages supports our claim that one of the chief reasons for the influence and persistence of Wright's Adaptive Landscape metaphor was its plasticity in the hands of different communities of evolutionary biologists and in the face of new forms of data.

1.2 The origins of the Adaptive Landscape

The Adaptive Landscape is commonly thought to have been introduced in Sewall Wright's 1932 paper presented at the Sixth International Congress of Genetics in Ithaca, New York. However, in 1979, J. Wynne McCoy pointed out that fitness curves and their representation as "peaks and valleys" were first introduced by Armand Janet in 1895 (McCoy 1979). Janet was a French engineer with an interest in entomology. Indeed, Janet served as president of the Société entomologique de France in 1911. McCoy makes a compelling case for parallels between Janet's representations of fitness surfaces and that of McCoy's contemporaries, but Janet's ideas have several differences from Wright's, and we argue that Wright's "discovery" of the Adaptive Landscape was independent of Janet's, and certainly more influential historically.

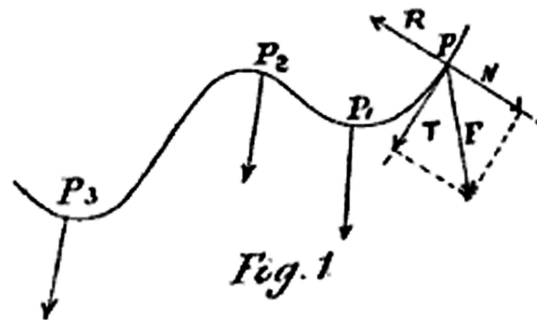


Figure 1.1 Armand Janet's selection surface. Species were represented as occupying different points of equilibrium (P) on the curve. Selection was represented as a vector at each point. The selection vector (F) could be decomposed into two vectors, N , which is normal to the surface, and T , which is tangential to the surface. (Janet 1895.)

At the Third International Congress of Zoology in Leyden, the Netherlands, Janet presented a paper describing the phenotypic change of a species in terms of a point moving along a selection surface (Janet 1895; see Fig. 1.1). The shape of the curve was determined by the external environment of the organism and the population's motion on the curve was directed by multiple forces modeled as a composite vector. In Janet's figure, selection acted like gravity to pull a population to the curves' minima or valleys. A population at a maxima or peak would tend to move toward a valley under the direction of selection.

Janet recognized that populations were variable and so added a measure of complexity to his representation by depicting populations as areas (see Fig. 1.2). The size of the area corresponded to the amount of variability in the population. Populations under strong selection would have narrow valleys and correspondingly smaller areas representing less variability, in contrast to the greater variability possible under weaker selection, depicted as a broader valley.

Moreover, Janet recognized that as environments change so would the shapes of the selective surfaces. So, what was once a valley might become a ridge or a peak. In so far as a phenotype was tracking this environmental change, its position would alter as a result of the changing environment and the force of selection in the new environment. For Janet such environmental transitions must have occurred in the past in order for new species to evolve. These transitional periods would then

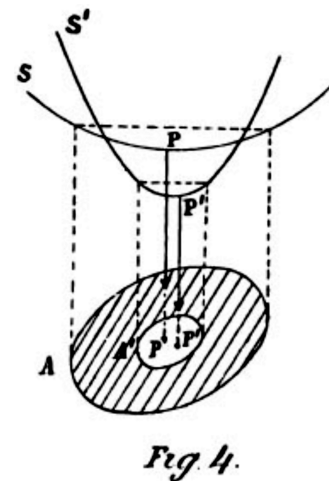


Figure 1.2 Armand Janet's depictions of population variability on a selection surface. Variability in a population was represented by the area (A) occupied by a species (P). The degree of concavity of the selection surface represented the strength of selection. S' represents stronger selection which reduces the variability that can be maintained in the population. Weaker selection represented in the selection surface S allows for greater phenotypic variability. (Janet 1895.)

correspond to transitional species, which would be relatively rare and short lived when compared to the species typical of periods of environmental stability (Janet 1895; McCoy 1979). In terms of his selective surface diagram, points of stability were likely to be found in the valleys and the steepness of the slopes leading to peaks and valleys represented areas of transition where selection would move a population quickly to an equilibrium point. The relative abundance of different species of fossils,

especially the rarity of transitional forms, confirmed for Janet that environmental shifts underlying phenotypic change must be relatively swift.

McCoy's "rediscovery" of Janet was motivated by a paper in the *American Naturalist* published in 1977 by Maurice M. Dodson and Anthony Hallam where they too used a model of selective surfaces to explain phenotypic shifts in a changing environment (Dodson and Hallam 1977). McCoy was confident that Dodson and Hallam arrived at their ideas "in complete ignorance of Janet's paper." Indeed, Dodson and Hallam cite Wright and Simpson with regard to their representations, but not Janet. Regardless of its other virtues, McCoy could not help noting that Dodson and Hallam's paper may have been timely, but was also "out of date, for its argument is over 80 years old!" (McCoy 1979).

Implicit in McCoy's claims that Janet's construct was "recreated" by Wright, Simpson, and Dodson and Hallam is an appeal to recognize Janet as an originator of this diagrammatic form of representing selection. Any meaningful claim for Janet as the originator of the modern Adaptive Landscape concept, however, is undercut by important differences between Janet's and Wright's representations, as well as Janet's almost complete lack of historical influence. Janet's selective surface, coming before the rise of genetics, depicted phenotypic change, where Wright's represented genetic change, subsequently G. G. Simpson would adapt Wright's landscapes to represent phenotypes (see section 1.4). Janet's peaks and valleys represent the inverse of Wright's. Moreover, Janet's representations do not make an explicit analogy to topographic representation as Wright's will later. In fact, Janet's analogy was to forces in mechanics, where Wright's was to traversing hilly terrain. Janet's influence was mediated by his better-known brother, Charles Janet, who was a polymath best known for his reconfiguration of the periodic table (Stewart 2010). Charles referred to Armand's analysis of sudden or saltational changes when trying to explain the evolution of cocoons in ants (Janet 1896). This hypothesis and its references to Armand Janet's selective surface were discussed in William Morton Wheeler's 1904 and 1915 essays on cocoons in ants (Wheeler 1904, 1915). Even Wheeler though

was more interested in Janet's ideas as a kind of mutationism, rather than as a consequence of thinking in terms of Janet's selective surface. In the end, Janet's unappreciated diagram stands in isolation from Wright's independent creation of what we now recognize as a diverse lineage of Adaptive Landscape diagrams. This is not to say that aspects of Wright's Adaptive Landscapes did not have important precursors, as we shall see later in this chapter, but that Janet was not one of those precursors.

1.3 The genetic landscape

Sewall Wright publicly debuted his Adaptive Landscape diagrams in Ithaca, New York at the Sixth International Congress of Genetics in 1932. Wright was an American biologist trained by E. W. Castle at Harvard University in physiological genetics. Prior to his groundbreaking research in evolutionary theory, which he carried out at the University of Chicago and University of Wisconsin, Madison, he worked as a staff scientist for the US Department of Agriculture (Provine 1986). In 1932, at the invitation of Harvard biologist, Edward Murray East, Wright joined R. A. Fisher and J. B. S. Haldane in a session on the newly emerging field of population genetics. Unlike their very mathematically challenging work from the previous 2 years (Fisher 1930; Wright 1931; Haldane 1932), the papers at the International Congress were intended to be accessible to general biologists interested in evolutionary theory.

Wright's principal contribution to evolutionary biology at the time was his 1931 paper "Evolution in Mendelian Populations" (Wright 1931). Wright condensed this long and technical article into his 1932 presentation for the Congress, published in the proceedings as "The Roles of Mutation, Inbreeding, Crossbreeding and Selection in Evolution" (Wright 1932). Rather than explain evolutionary dynamics with detailed mathematical models, Wright developed an analogy between fitness and altitude, between genetic combinations and the features of a hilly, physical landscape. In order to convey his metaphor, Wright offered two different kinds of diagrams. One represented the space of underlying genetic possibilities (see Fig. 1.3) and the

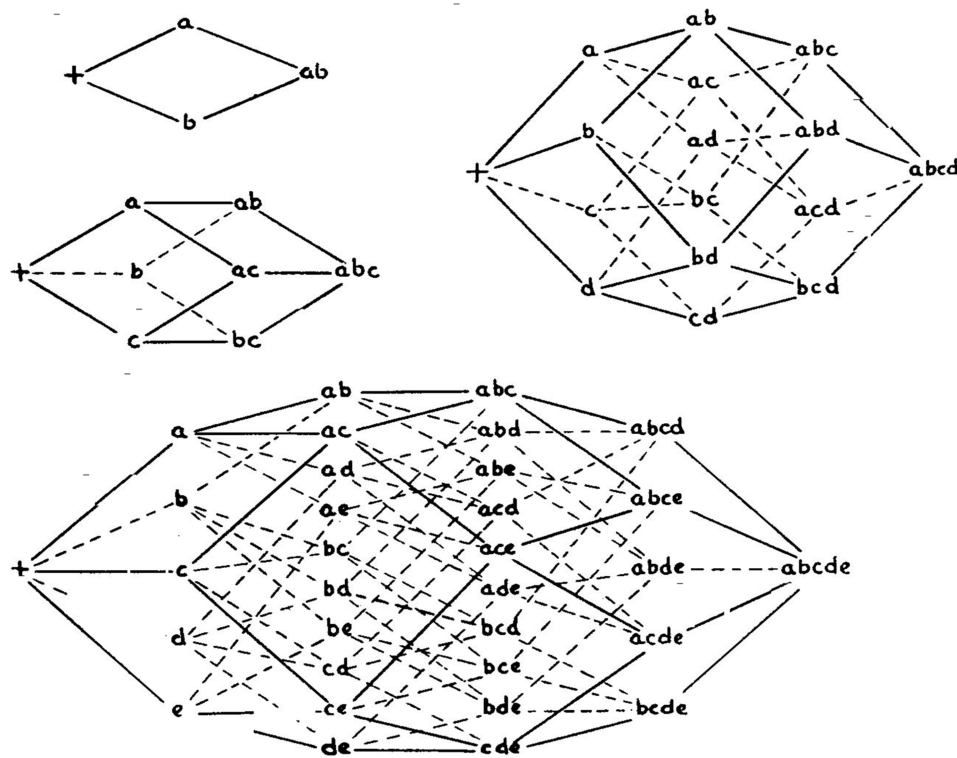


Figure 1.3 Sewall Wright's gene combination network diagrams. Networks of gene combinations or genotypes ranging from two to five loci represented the increasing complexity of all of the one-step transitions composing the space of genotypic possibilities. (Wright 1932.) Genetics by GENETICS SOCIETY OF AMERICA. Copyright 1931 Reproduced with permission of GENETICS SOCIETY OF AMERICA.

other analogized fitness differences to differences in altitude and used a topographic representation to depict those differences (see Fig. 1.4).

The foundation of the genetic version of the Adaptive Landscape is a network of relationships between different gene combinations or genotypes. Wright represented these as a network of single gene differences, where every node represented one possible set of gene combinations and every path between nodes represented one genetic change or difference between the two connected nodes (see Fig. 1.3). Wright offered a simplified image of this genetic space with diagrams showing the increasing complexity of the network as it expanded from two loci to five. Of course, Wright knew that the space of genetic possibilities for any organism in nature were much more complicated, and estimated that the field of gene combinations would number on the order of 10^{1000} (Wright 1932).

Wright used the two-dimensional graphical depiction of an Adaptive Landscape in Fig. 1.4 as a way of intuitively conveying what can only be realistically represented in thousands of dimensions. From its inception then, Wright's landscapes were multidimensional models represented on two dimensions in his figures. The axes of Wright's Adaptive Landscape diagrams are not labeled as such, because we believe that there was no way to provide a metric for the multidimensional network that had been idealized to just two dimensions. The surface of the landscape is typically understood as representing the adaptive value assigned to the underlying gene combinations. So, the vertical axis or height was assigned a measurable value in terms of fitness or relative adaptive value. Peaks on this adaptive topography represented areas of high adaptive value. Valleys represented areas of low adaptive value.

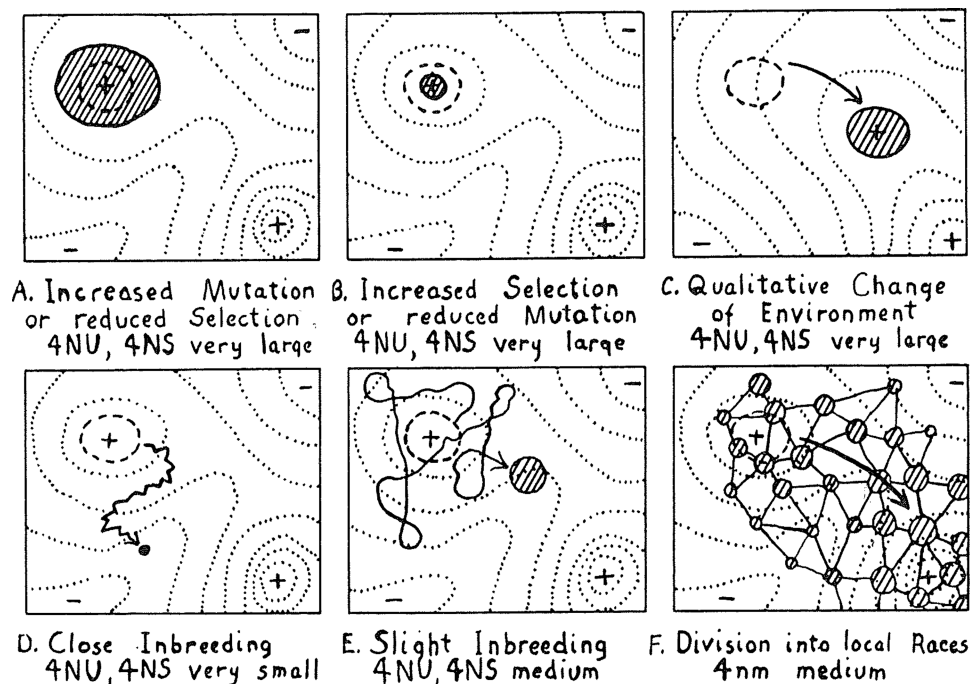


Figure 1.4 Sewall Wright's six-frame Adaptive Landscape diagram. Each frame represents different evolutionary scenarios and their impact on the population in question. Frame C differs from the other five frames in that it represented a changing environment, which would create a dynamic landscape, so the population is shown tracking a moving landscape by the arrow. Frame F represents the dynamics of Wright's shifting balance theory. (Wright 1932.) Genetics by GENETICS SOCIETY OF AMERICA. Copyright 1931 Reproduced with permission of GENETICS SOCIETY OF AMERICA.

Wright had initially presented his idea for the Adaptive Landscape to Fisher in a letter in 1931, where he asked Fisher to:

Think of the field of visible joint frequencies of all genes as spread out in a multidimensional space. Add another dimension measuring degree of fitness. The field would be very humpy in relation to the latter because of epistatic relations, groups of mutations, which were deleterious individually producing a harmonious result in combination. (Wright to Fisher, February 3, 1931 in Provine 1986, p. 272.)

Each peak then would represent a point of harmonious interaction among the genes and the environment that would contribute to evolutionary stability. Fisher doubted that these points of stability could be common. According to Fisher, as the dimensionality of the field of gene combinations *increases*, the number of stable peaks on the surface of the landscape *decreases* (Fisher to Wright May 31, 1931 in Provine 1986, p. 274; Fisher 1941). Rather

than a hilly landscape, Fisher argued that a landscape with a single peak with ridges along it was more likely. On Fisher's landscape, evolution does not require the complex of evolutionary factors of Wright's shifting balance process, but only selection and mutation (see Chapter 4).

In response to Fisher, Wright invoked J. B. S. Haldane's work on population genetics (Haldane 1932; Provine 1986). Haldane had also suggested that populations could be represented as a "multidimensional space" and had worked through the conditions to produce stable equilibria in a two-factor case (Wright to Fisher, June 5, 1931 in Provine 1986). Because Haldane argued that more than one apex in a hypercube or multidimensional space could be stable, Wright interpreted Haldane as holding a middle ground between his view and Fisher's (Wright 1935). Haldane's ideas and Wright's Adaptive Landscape were certainly very similar: both imagined a space of possibilities and a surface with stable equilibria. However, even though Haldane

described his idea in print before Wright's 1932 essay, Wright's correspondence indicates that he had thought of his Adaptive Landscape before reading Haldane's essay (Provine 1986). Moreover, the landscape metaphor itself was absent from Haldane's essay where he opted for a much more complex mathematical argument rather than an analogy that made his theory generally accessible.

In his 1931 and 1932 essays, Wright was trying to describe the ideal conditions for evolution to occur, given specific assumptions about the relationship between Mendelian heredity and the adaptive value of gene complexes. The ideal conditions would produce the fastest rate of evolution to the highest "adaptive peak." Wright believed that these conditions required that populations be subdivided and semi-isolated, and that selection along with random genetic drift and migration operated in a "shifting balance" of phases. Wright tried to capture these conditions in his six-frame Adaptive Landscape diagram (Fig. 1.4). Each frame represented a different evolutionary scenario. When he first published this image in 1932, Wright was predisposed to frame F, which represented shifting balance dynamics mixing drift, selection, and migration among subdivided, semi-isolated populations, as the most efficient and so the most favorable (Wright 1932; Provine 1986). Fisher's work had impressed upon him that the large population in a changing environment represented in frame C was also an important scenario. It is worth emphasizing that frame C represented a dynamic landscape whose peaks and valleys would rise and fall over time like waves on the ocean (Wright 1932, see also Chapter 7). In 1944, as part of the Bulletin of the Committee on Common Problems of Genetics, Paleontology and Systematics, Wright offered the following appraisal of the evolutionary possibilities in his six-frame figure (Fig. 1.4). He wrote,

The cases in which an indefinitely large species is subject to qualitative change of environment (C) or is subdivided into partially isolated local races (F) are stressed as enormously more favorable for evolution than the case of a random breeding population of intermediate size (E) even though this is more favorable than either a small population (D) or an indefinitely large one under the highly improbable

condition of complete panmixia and no change of conditions for selection (or an increase (B) or reduction (A) in severity of selection not associated with any change in the direction of selection). (Wright 1944, p. 34.)

The favorability of the scenario with the large population changing with the environment was a concession to Fisher's views. However, Wright was not convinced that multiple peaks would not occur and that the dynamics of shifting from one peak to another was not a significant problem for evolutionary biology (see Chapter 4).

Despite Fisher's reservations, Wright's landscape was embraced by two key, but very different, proponents of the Neo-Darwinian synthesis, Theodosius Dobzhansky and G. G. Simpson. Simpson would transform the Adaptive Landscape by shifting its basis from genes to phenotypes, discussed in the next section. Dobzhansky would promote Wright's original genetic landscape as a means of understanding the basic processes of evolution.

Dobzhansky was trained in a Soviet tradition of evolutionary biology that emphasized the variability of natural populations. As a student of Iurii Filipchenko, he studied populations of *Coccinellidae* before getting a Rockefeller Foundation fellowship to join T. H. Morgan's famous Fly Group in 1927 (Provine 1986). At Columbia and later Cal Tech, Dobzhansky quickly became a leading figure in *Drosophila* genetics. In collaboration with A. H. Sturtevant and later Sewall Wright, Dobzhansky returned to questions of evolution—taking *Drosophila* genetics from the laboratory to the field. Dobzhansky's 1937 book, *Genetics and the Origin of Species*, articulated a foundational program of research for evolutionary genetics. The theoretical underpinning of Dobzhansky's program was deliberately based upon Wright's shifting balance theory, as Dobzhansky understood it. Because Dobzhansky was not a mathematically expert, his understanding of Wright rested heavily on Wright's non-mathematical 1932 presentation. Accordingly, Dobzhansky's explanation of the shifting balance theory rested heavily on the Adaptive Landscape metaphor (Provine 1986). *Genetics and the Origin of Species* translated and popularized one of the dominant general theories of evolution into a

research program for evolutionary genetics, and served as a foundational publication for the emerging Neo-Darwinian synthesis (Levine 1995; Smocovitis 1996).

The influence of Dobzhansky as a biologist and teacher on twentieth-century biology has been tremendous. Versions of Wright's genetic landscape have appeared in almost every major textbook on evolutionary biology since 1937. Dobzhansky reprinted Wright's diagrams in each of the three editions of *Genetics and the Origin of Species*, as well as in the evolution textbook that he co-authored with Francisco Ayala, G. Ledyard Stebbins, and James Valentine (Dobzhansky 1942, 1951; Dobzhansky et al. 1977). He used the Adaptive Landscape as Wright had—to convey the range of evolutionary possibilities for a range of genotypes and population structures under the influence of selection, drift, mutation, and migration. Even Wright used *Genetics and the Origin of Species* as the textbook for his evolution courses at the University of Chicago from 1937–1954 (Provine 1986). Newer diagrams of the genetic version of the Adaptive Landscape continue to appear in evolution textbooks to this day (Ridley 2003; Barton et al. 2007; Freeman and Herron 2007; Futuyma 2009).

In 1960, one of Dobzhansky's students, Richard Lewontin, transformed the genetic landscape from a depiction of evolutionary possibilities to a graph of measured genetic frequencies and real populations. Lewontin brought an interest in both evolution and statistics to Dobzhansky's laboratory as a graduate student in the early 1950s. This expertise in statistical modeling allowed Lewontin to approach population genetic problems from a more theoretical perspective than Dobzhansky and many others at the time. In Lewontin's words:

While many people like me start with observations in nature and develop theoretical tools to deal with them, which then may become part of the general theoretical apparatus of the field, my way of working has always been the reverse. I start by thinking about some general phenomenon (frequency-dependent selection, multilocus selection, selection in age distributed continuously breeding life histories, etc.), and explore the theoretical dynamics of such systems. (Lewontin to Michael R. Dietrich, October 1, 2010, personal correspondence.)

When he later came across relevant observations, he applied them. According to Lewontin, this pattern of thinking describes his work on Adaptive Landscapes in the late 1950s and early 1960s. At his first job at North Carolina State in the 1950s, Lewontin and his graduate student, Ken-ichi Kojima, worked on two-locus, two-allele models of selection (Lewontin and Kojima 1960). In the late 1950s, M. J. D. White visited North Carolina from Australia and told Lewontin about the chromosomal inversion data that he had been collecting from populations of the grasshopper, *Moraba scurra*. Lewontin realized that White's inversion data fitted the two-locus models that he and Kojima had been developing. Lewontin then applied the *Moraba* data to the two-locus models in papers with both White and Kojima (Lewontin and Kojima 1960; Lewontin and White 1960).

Lewontin's use of Adaptive Landscapes differed from Wright's 1932 presentation in so far as he did not take the Adaptive Landscape to be based on all possible gene combinations and their assumed adaptive values. Instead, Lewontin created a surface based on the frequencies of two different inversions and their fitness values (see Fig. 1.5). In doing so, Lewontin made the Adaptive Landscape into an empirical representation. And with that, Lewontin returned to a second form of Wright's Adaptive Landscape based on gene frequencies, not gene combinations.

When Wright first discussed the idea of the Adaptive Landscape in private correspondence with Fisher in 1931, he proposed that the landscape represent ranges of gene frequencies such that a point or area on the surface would correspond to a population with genes at those frequencies, and the height of the surface would represent the average fitness of the population (Provine 1986). In the version presented in 1932, the surface corresponds to all of the possible gene combinations that might be in individual organisms, and the height of the surface represents the fitness of the individual with that type of genetic combination. He would offer both versions in print in 1939 in a French collection on statistical biology that does not seem to have been widely read (Wright 1939). Wright seemed to shift between these two views, creating ambiguities that have vexed critics ever since (Provine 1986;

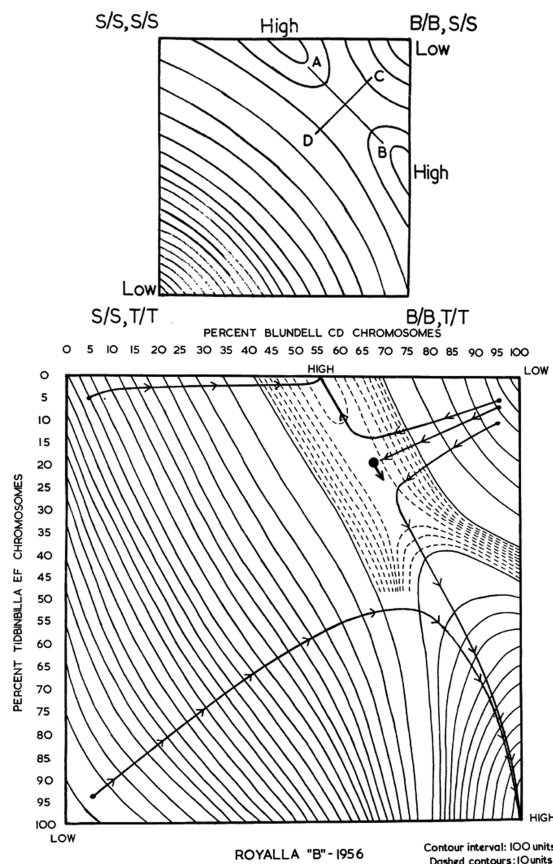


Figure 1.5 Lewontin and White's representation of the Adaptive Landscape and population trajectories for chromosomal inversions in populations of *Moraba scurra*. (a) A generalized version of the Adaptive Landscape with main features identified. (b) A plot of the Adaptive Landscape with current population location and trajectories. Reproduced from Lewontin, R. C. and White, M. J. D. (1960), "Interaction between inversion polymorphism of two chromosome pairs in the grasshopper, *Moraba scurra*," *Evolution* 14: 116–129.

Skipper 2004; Kaplan 2008). That said, Wright did not do what Lewontin and White did in 1960: he did not actually empirically construct an Adaptive Landscape.

Using White's data on chromosomal inversions from different populations, Lewontin calculated an Adaptive Landscape. The x- and y-axes represented the frequency of the *Tidbinbilla* EF chromosomes and the Blundell CD chromosomes in a certain population, such as *Royalla B* in Fig. 1.5b. White had measured the chromosomal composition of this population in 1958. The viability of each of the chromosomal genotypes was then estimated as a ratio

of the actual to the expected number of individuals (Lewontin and White 1960). The graph of the topography was created by allowing the frequency of the *Tidbinbilla* EF chromosomes and the Blundell CD chromosomes to range from 0–1 at intervals of 0.05. With 21 values on each axis, 441 points on the landscape were calculated. An average fitness value was then calculated for each of these 441 points. Topographic lines were then drawn connecting the points with equal mean adaptive values (Lewontin and White called these isodapts, instead of isolines). All of the landscapes calculated in this way showed a ridge with a saddle. The different populations from different years were always located in the saddle of their respective topography. The problem is that saddles are points of instability. Using the Adaptive Landscape as an empirical representation generated a new problem of explaining why the *Moraba* populations would all be found at similar points of instability.

Lewontin and White's genetic landscape lent the representation more reality than it ever had before. But it also opened it to more questioning. Turner and others questioned Lewontin's method for calculating the landscape surface (Turner 1972). Turner's recalculations put the *Moraba* populations on peaks, not saddles. Moreover, as Lewontin and White note, their results raised a number of questions about the adequacy of their model. In 1974, Lewontin would generalize these concerns in terms of the dynamic sufficiency of any two-locus system to describe the evolution of much more complex genetic systems (Lewontin 1974). This problem of representational adequacy, however, did not stop the genetic landscape from being widely used in evolutionary biology, although it does suggest that the Adaptive Landscape was often understood as a heuristic even when it represented measured empirical values (see Chapter 2).

1.4 The phenotypic landscape

Where Dobzhansky brought contemporary genetics to evolutionary thinking in 1937, G. G. Simpson brought paleontology to the mix in his *Tempo and Mode in Evolution*, published in 1944. Having earned his PhD at Yale in 1923, Simpson had rapidly become one of the most prominent paleontologists in the United States. From his position at the

American Museum of Natural History, Simpson's expertise on the evolution and classification of fossil mammals allowed him to articulate a paleontological understanding of evolution compatible with Dobzhansky's genetic approach. *Tempo and Mode* was drafted in the late 1930s and completed after Simpson's service in the Second World War. Where Dobzhansky brought modern genetics to the evolutionary synthesis, Simpson brought paleontological evidence of evolution in deep time and an appreciation for how processes of adaptive change had created patterns of phenotypic change across species.

Like Dobzhansky, Simpson was taken with Wright's Adaptive Landscapes, but as a paleontologist without access to genes, Simpson redrew Wright's diagrams and fundamentally altered their interpretation by casting them in terms of phenotypes (see Chapter 18). Where Wright's diagrams generally represented a selective landscape, Simpson refined the representational vocabulary to denote different forms of selection as topographic patterns. He began by depicting the range of variation in a population as a shaded area. Selection was represented as arrows, which indicated both strength and direction of selection with regard to the population. Selection decreasing population variation was labeled centripetal selection, while centrifugal selection was that which allowed variation to increase (see Fig. 1.6). As in Wright's topographies, the distance between the lines represented the intensity of selection (intensity increases with the slope of gradient).

Simpson then put his phenotypic landscape to work to explain equine evolution (see Fig. 1.7). Simpson divided the *Equidae* lineage into browsers and grazers based on tooth morphology and several other features. Grazing horses evolved from browsing ancestors from the Eocene to the late Miocene. Simpson postulates that in the Eocene the Adaptive Landscape was marked by two distinct adaptive peaks, one for browsing and one for grazing, but only the browsing peak was occupied. As the horses grew bigger, the adaptive peaks moved closer together, because with size came larger tooth crowns, which moved then toward a grazer morphology (Simpson 1944). Asymmetry in the strength of selection on the browsing peak meant that more variants on the grazing side were

allowed to persist. As the two peaks moved closer, this asymmetry resulted in individuals located in the saddle between the two peaks. From the saddle, individuals were under selection to move higher on one of either of the two peaks. The grazing peak was steeper and so individuals climbed it fairly quickly resulting in a relatively sudden appearance of the grazing morphology (Simpson 1944). Later in *Tempo and Mode*, Simpson will use this as a case of what he called quantum evolution, but in doing so will impose his idea of adaptive zones on the Adaptive Landscape (Simpson 1944). Adaptive zones were partitions of the environment that were particularly favorable for certain forms of adaptations. Adaptive zones changed over time as the environment changed, and organisms had to track these changes over time or risk extinction. Simpson's interest in using the Adaptive Landscape to represent changing environments over time follows directly from Wright's depiction of the Adaptive Landscape in frame C, although Simpson was not obligated to large population sizes (see Fig. 1.4).

Wright reviewed Simpson's *Tempo and Mode*, but did not criticize this reinterpretation beyond urging Simpson to consider lower levels of biological organization, such as local populations. The shift to phenotypes was acknowledged as simply "different in point of view" (Wright 1945; Provine 1986).

Simpson's phenotypic landscape was perpetuated in its own lineage of textbooks, especially those written by paleontologists. For instance, Simpson's images were duplicated in G. S. Carter's *Animal Evolution* in 1951, Terrell Hamilton's *Process and Pattern in Evolution* in 1967, and Niles Eldredge's *Unfinished Synthesis* in 1985 and *Macroevolutionary Dynamics* in 1987 (Carter 1951; Hamilton 1967; Eldredge 1985, 1987).

In the 1970s, Russell Lande gave Simpson's phenotypic landscape a mathematical model (Lande 1976, 1979) that broadened its use beyond paleontology (see Chapter 19). In doing so, Lande drew on a tradition of biometrical modeling of phenotypic evolution going back to Karl Pearson. In 1903, Pearson had proposed a mathematical model for the evolutionary selection of two traits in terms of what he called a selection surface or surface of survivals (Pearson 1903). The surface was a way

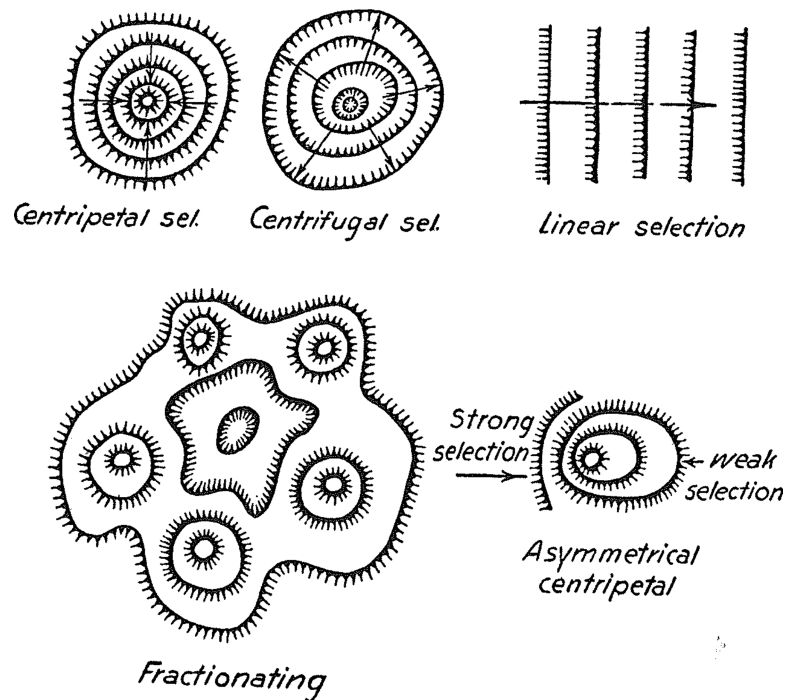


Figure 1.6 G. G. Simpson's reinterpetation of the Adaptive Landscape. Different forms of selection represented as topographic contours. The hash-mark side of a contour line represents a lower area. Tempo and mode in evolution by SIMPSON, GEORGE G. Copyright 1944 Reproduced with permission of COLUMBIA UNIVERSITY PRESS.

of representing the proportions of the population selected as either fit or unfit under different selection regimes. While Wright was familiar with Pearson's mathematically complex papers, there is no evidence that Simpson was. Lande certainly built on the biometrical tradition from Pearson as he developed a mathematical theory for phenotypic evolution and applied it to cases of micro- and macroevolution.

Simpson created a separate lineage of Adaptive Landscape diagrams. Where Wright originated a lineage of genetic landscapes, Simpson reinterpeted the foundation of the Adaptive Landscape in terms of a space of phenotypic possibilities. The foundation of the Adaptive Landscape would be reinterpeted once again with the rise of molecular evolution.

1.5 The molecular landscape

As biology grew increasingly molecular in the 1950s and 1960s, evolutionary biologists began to

consider how these newly discovered sequences of DNA, RNA, and proteins themselves evolved (Anfinsen 1959; Jukes 1966). Reframing evolutionary change in terms of molecular sequences instead of alleles may not seem like a radical reconsideration, but considering networks of proteins and nucleic acids had several important consequences for Adaptive Landscapes.

John Maynard Smith was the first evolutionary biologist to imagine evolution in a space of possible protein sequences (Maynard Smith 1962, 1970). Maynard Smith suggested that in order to imagine how protein evolution proceeds we must imagine a network of proteins, each one mutational step away from the other (Maynard Smith 1970). The question then is how it is possible to evolve from one functional protein to another by natural selection. If natural selection is the only operative means of evolution, then the network must have continuous paths between functional proteins, because a mutation to a non-functional protein would not be favored by natural selection. This would require

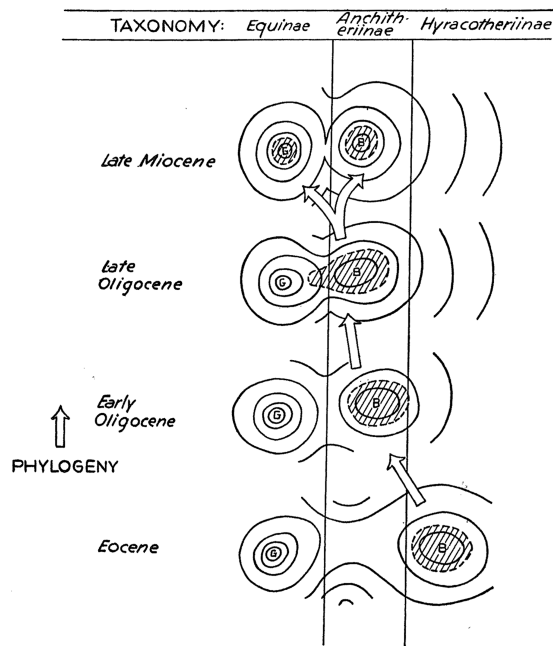


Figure 1.7 G. G. Simpson's changing Adaptive Landscapes for the case of equine evolution. Movement of both a population and the landscape over geological time was used by Simpson to explain patterns of equine evolution in the fossil record. Tempo and mode in evolution by SIMPSON, GEORGE G. Copyright 1944 Reproduced with permission of COLUMBIA UNIVERSITY PRESS.

that a certain proportion of proteins that are one step away be at least as functional as the original protein.

Even as Maynard Smith was imagining protein evolution, molecular evolution was beginning to be understood in very different terms from organismal evolution. In the late 1960s, Motoo Kimura, Jack King, and Thomas Jukes articulated their reasons for thinking that most detected molecular substitutions were not subject to selection, but were instead neutral (Kimura 1968; King and Jukes 1969). The neutral theory sparked an intense controversy over the relative power of natural selection at the molecular level (Dietrich 1994, 1998). This controversy was not an all-or-nothing contest pitting selection against drift. Instead, it was a relative significance controversy, where each side admitted that selection and drift occurred, but the big question was how often did each occur, or, put another way, how much of the genome was evolving neutrally and how much selectively.

In terms of Maynard Smith's model of evolution in protein space, the neutral theory changed the nature of the problem. Maynard Smith asked, "How often, if ever, has evolution passed through a non-functional sequence?" (Maynard Smith 1970). The possibility that many substitutions are neutral, which Maynard Smith acknowledged by citing King and Jukes, allowed him to realize that the "functional" paths may not always lead to higher functionality. The paths could follow equal functionality or neutrality to form a random walk through protein space that circumvented non-functional paths. In terms of Adaptive Landscapes, an idiom that Maynard Smith did not use, every path in protein evolution need not lead uphill.

Molecular evolution and the Adaptive Landscape were more explicitly connected in 1984, when John Gillespie introduced the metaphor of the mutational landscape (Gillespie 1984). Gillespie was a mathematical geneticist and a selectionist partisan in the neutralist–selectionist controversies raging at the time (Dietrich and Skipper 2007). In the mid 1980s, Gillespie was challenging the neutralist mechanism for the molecular clock by proposing a selectionist alternative that depended on episodic bursts of mutations. In order to model the mutational process in DNA sequences, Gillespie proposed a space of nucleotide sequences, each one nucleotide-substitution away from the other. The distance that can be traveled through this molecular landscape depends on the mutational paths from the original sequence that are selectively tractable. So, on the one hand, a set of substitutions may occur in rapid succession if they follow a path of mutations with selective advantage. On the other hand, a much more fit sequence could exist in the sequence space, but if it was two or more mutational steps away and those intermediate steps are through less fit alleles, then that more fit sequence would never be reached (Gillespie 1984). In Gillespie's words, "the mutational structure, in effect, creates innumerable selective peaks in the adaptive topography" (Gillespie 1984). Using this model, Gillespie calculated the time to cross a valley between two adaptive peaks on a selective mutational landscape and drew important implications for the rate of molecular evolution as understood from a selectionist perspective.

Gillespie's model of the mutational landscape did not include neutral mutations. Gillespie did not deny that a model of neutral and selected mutations might be useful and interesting; he was simply involved in a polemic that led him to explore the selectionist alternative to neutrality. If the selectionist molecular landscape was very hilly, the opposite neutral molecular landscape was flat. A molecular landscape that blended selected and neutral changes could still retain its hills and valleys, but would have many new plateaus constituting a neutral space for molecular change. Shifting the foundation of the Adaptive Landscape to a space of nucleotide sequences, thus, has profound effects for the possible topographies (Gavrilets 2004).

1.6 Conclusion

Adaptive Landscape diagrams are often unlabelled giving the impression that the same biological entities underlie every representation. In this brief overview of the history of the Adaptive Landscape in evolutionary biology, we divide representations of the Adaptive Landscape into three historical lineages based on what kind of biological entities were thought to ground the landscape. Although Armand Janet articulated a phenotypic selective surface in 1895, we mark the origin of the Adaptive Landscape with Sewall Wright's 1932 description of a genetic landscape. Phenotypic landscapes quickly re-emerged in 1944 when Simpson reimagined Wright's diagram in terms of organismal phenotypic traits. The molecular revolution inspired a second bifurcation from the genetic landscape when the space of genetic possibilities was reconsidered in terms of the space of possible proteins and nucleic acids. Each of these lineages reaches to the present and is represented by contributions to this volume. Taken together these three different foundations and histories of research and representation have given the Adaptive Landscape a much greater range of application than was imagined by Sewall Wright in 1932. These three different historical lineages reveal the adaptability of the Adaptive Landscape itself and offer one explanation for why the Adaptive Landscape has persisted so long in evolutionary biology.

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