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## CHAPTER 2

# Sewall Wright's Adaptive Landscape: Philosophical Reflections on Heuristic Value

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

## 2.1 Introduction

Sewall Wright's 1932 Adaptive Landscape diagram is arguably the most influential visual heuristic in evolutionary biology, yet the diagram has met with criticism from biologists and philosophers since its origination. In our view, the diagram is a valuable evaluation heuristic for assessing the dynamical behavior of population genetics models (Skipper 2004). Although Wright's particular use of it is of dubious value, other biologists have established the diagram's positive heuristic value for evaluating dynamical behavior. In what follows, we will survey some of the most influential biological and philosophical work considering the role of the Adaptive Landscape in evolutionary biology. We will build on a distinction between models, metaphors, and diagrams to make a case for why Adaptive Landscapes as diagrams have heuristic value for evolutionary biologists.

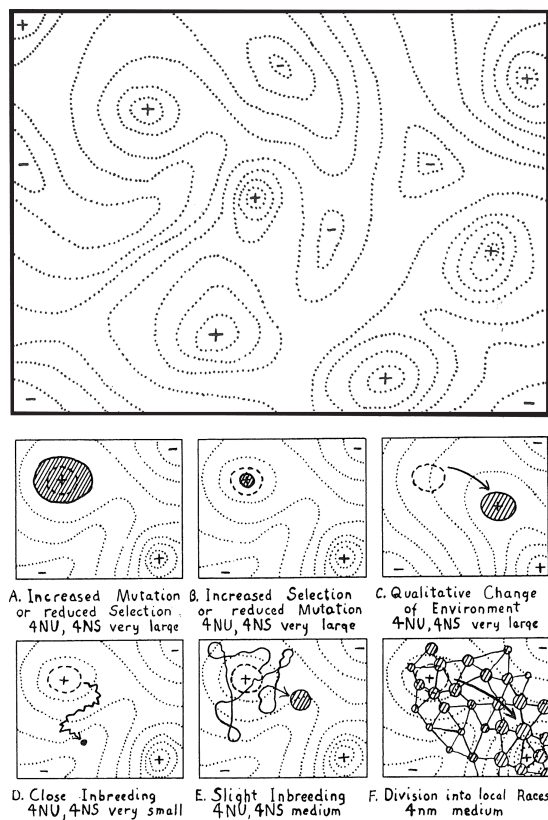
## 2.2 Sewall Wright's Adaptive Landscape

E. M. East invited the architects of theoretical population genetics, R. A. Fisher, J. B. S. Haldane, and Sewall Wright, to present their work at the 1932 Sixth International Congress of Genetics. They were to present compact and accessible forms of their seminal but mathematically intimidating work on evolutionary theory. Wright's principal evolutionary paper was his 1931, "Evolution in Mendelian Populations" (Wright 1931). The paper Wright delivered at the congress in 1932 was, basically, a distillation of the 1931 paper, and was pub-

lished in the proceedings as "The Roles of Mutation, Inbreeding, Crossbreeding and Selection in Evolution" (Wright 1932). The Adaptive Landscape was first publicly presented in the 1932 paper.

Wright's aim in the 1931/1932 papers was to determine the ideal conditions for evolution to occur given specific assumptions about the relationship between Mendelian heredity and the adaptive value of gene complexes (Wright 1931, 1932). In Wright's 1932 paper, he used the Adaptive Landscape diagram to demonstrate his solution (see Chapter 5).

According to Wright (1932), accurately representing the population genetics of the evolutionary process requires thousands of dimensions. This is because the field of possible gene combinations of a population is vast (approximately  $10^{1000}$ ). Wright used the two-dimensional graphical depiction of an Adaptive Landscape in Fig. 2.1a as a way of intuitively conveying what can only be accurately represented in thousands of dimensions. Wright's interpretation of his diagrams is confusing, as we will discuss later in this chapter. The surface of the landscape is typically understood as representing populations with each point on the landscape representing a unique combined set of allele frequencies. Each point or population is then graded for adaptive value. Presumably, populations with very similar sets of alleles at similar frequencies will have similar adaptive values and so the adaptive surface will show relatively gradual transitions from low to high adaptive value, although this is not a necessary condition. The surface of the landscape is very "hilly," says Wright, because of epistatic



**Figure 2.1** Wright's (1932, pp. 161–163) key figures. (a) Wright's Adaptive Landscape diagram. (b) Diagrams depict evolution occurring on the Adaptive Landscape under alternative assumptions. Genetics by GENETICS SOCIETY OF AMERICA. Copyright 1932. Reproduced with permission of GENETICS SOCIETY OF AMERICA.

relations between genes, the consequences of which (for Wright) are that genes adaptive in one combination are likely to be maladaptive in another. Given Wright's view of epistasis and the vastness of the field of gene combinations in a field of gene frequencies, Wright estimates the number of adaptive "peaks" separated by adaptive "valleys" at  $10^{800}$ . Peaks are represented by "+"; valleys are represented by "-."

The Adaptive Landscape diagram sets up Wright's signature problem, viz., the problem of peak shifts (see Chapter 6). That is, given that the Adaptive Landscape is hilly, the ideal conditions for evolution to occur must allow a population to shift from peak to peak to find the highest peak. Otherwise, a population would remain fixed at the

nearest local peak regardless of its adaptive value. In Wright's 1931 paper, he demonstrated mathematically the statistical distributions of genes under alternative assumptions of population size, mutation rate, migration rate, selection intensity, etc. In the 1932 paper, the graphs displaying the results appear, and he uses them in combination with the landscape diagram to argue for his three-phase shifting balance model of the evolutionary process (window F in Fig. 2.1b) as the solution to his problem of peak shifts via assessments of alternative models of the process (windows A–E in Fig. 2.1b). Wright's view was that his "shifting balance" process of evolution satisfied the ideal conditions for evolution to occur. Evolution in the shifting balance process occurs in three phases: Phase I—random genetic drift causes subpopulations semi-isolated within the global population to lose fitness; Phase II—selection on complex genetic interaction systems raises the fitness of those subpopulations; Phase III—interdemic selection then raises the fitness of the large or global population.

### 2.3 Models, metaphors, and diagrams

Wright's 1931 exposition of his shifting balance theory relied on a series of mathematical models. When he presented his work for a general biological audience in 1932, he chose to describe the elements, behaviors, and consequences of these models by developing a metaphor and interpretations of a series of diagrams. These different entities, i.e. models, metaphors, and diagrams, are recognized by philosophers of science and some biologists as having importantly different features and significantly different roles in the manufacture of scientific knowledge.

Diagrams are visual representations that use spatial configurations within an image to convey information (Perini 2004, 2005). Understanding how the form of a representation assigns meaning or content is a major topic among scholars interested in visual representation (Lynch and Woolgar 1990). Extracting the meaning of some images may involve interpreting an image symbolically in terms of conventions that associate a particular form and a particular meaning. For other images, their meaning can be interpreted in terms of the

resemblance of the form to the object represented. For propositionally-oriented philosophers though, images are one of many forms for conveying information and so seem like they ought to be replaceable by linguistic descriptions (Ruse 1996; Perini 2005). Other philosophers eager to explain why images are so prevalent in science, see them as a particularly concise and effective way of communicating complex information, such as the functional relationships between different molecular structures to form the active site of an enzyme (Perini 2005).

Models, like many diagrams, are extralinguistic representations. However, the relationships between the variables and parameters of a model are articulated linguistically and mathematically (Lloyd 1988). Philosophers advocating the semantic approach to theories have developed a sophisticated understanding of the features of biological models in terms of rules of coexistence, interaction, and temporal succession for the variables and parameters in any particular type of model. In other words, the semantic approach views theories as models describing the many different relationships between a set of variables and parameters. An important feature of the semantic approach is its natural understanding of models in contemporary biology (Lloyd 1988). Richard Lewontin, for instance, defines a scientific model as a set of entities with corresponding quantities that are connected to each other by rules of transformation (Lewontin 1963, 1974).

Two of the central virtues of scientific models are that they allow scientists to make very precise claims about relationships between variables in the models and that they allow scientists to make precise claims about which empirical entities are represented by which features of that model. Metaphors by contrast depend on an analogy between two objects or two systems (Hesse 1966). A metaphor is an accurate analogy in so far as its components and relationships correspond to the object and relationships with which it is meant to be compared. A metaphor is didactically useful, however, in so far as it allows us to understand those elements and

relationships better by way of analogy (Lewontin 1963). The didactic function of the Adaptive Landscape as a metaphor depends on our familiarity with actual hilly landscapes and their representation as topographical maps.

We are convinced that the metaphor of the Adaptive Landscape has been didactically useful in generating novel theoretical and empirical paths of inquiry. In the remainder of this essay, we justify our claim by evaluating influential criticisms of the usefulness of the metaphor, analyzing a series of criticisms of Wright's version of the Adaptive Landscape, and describing the way in which we understand the didactic role of the metaphor.

## 2.4 Questioning value of the Adaptive Landscape diagram

There is considerable agreement among biologists and philosophers that Wright's particular version of the Adaptive Landscape is flawed. Roughly, this agreement revolves around the extent to which Wright's evolutionary assumptions in fact underwrite a hilly landscape of the sort depicted, and therefore the problem of peak shifts, that he thought is so central to evolutionary biology. Among these same biologists and philosophers, however, is sharp disagreement about the heuristic value of the Adaptive Landscape diagram. Some, notably William Provine (1986) and Jonathan Kaplan (2008), argue that Wright's Adaptive Landscape ought to be abandoned as a visual representation of the evolutionary process because confusions surrounding its interpretation have led scientists down fruitless paths of inquiry.<sup>1</sup> Others, such as Michael Ruse (1996), Robert Skipper (2004), and Anya Plutynski (2008), argue that in spite of the technical problems with Wright's diagram and the fact that as a heuristic it may lead scientists astray, the Adaptive Landscape metaphor has led and will continue to lead scientists down fruitful paths of inquiry. We endorse this latter position in the following critical analysis of the Adaptive Landscape metaphor. We begin with those who adopt the former view.

<sup>1</sup> Pigliucci and Kaplan (2006) and Pigliucci (2008) come very close to this view.

Provine (1986), Wright's biographer, harshly criticized Wright's view of the Adaptive Landscape. Provine argues that Wright interpreted the diagram in two main ways. First, Wright (1932, 1977) interpreted the diagram as the multidimensional field of *all possible gene combinations* graded for their adaptive value. Call this the *genotype interpretation*. Second, Wright (correspondence to Fisher, 3 February 1931 in Provine 1986; Wright 1939, 1978) interpreted Fig. 2.1a as the multidimensional field of *joint frequencies of all genes* in a population graded for their adaptive value. Call this the *population interpretation*.

According to Provine (1986), Wright's genotype interpretation of the diagram is mathematically incoherent and the two interpretations are incommensurable. Provine claims that on the genotype interpretation each axis of the graphic is a gene combination. But, Provine argues, there are no gradations along the axes, no indications of what the units along the axes are, and no point along them to indicate where a gene combination is to be placed. Given this, Provine concludes that there is no way of generating the continuous surface represented in Fig. 2.1a. On the population interpretation, Provine argues, each point on the surface represents a population, and the entire surface is of mean population fitness rather than genotype fitness. Each axis is now graded between 0 and 1 for gene frequency; the result is a continuous surface. However, Provine claims, there is no way to plot genotype fitness values on the surface of gene frequencies; one is attempting to plot individual haplotypes onto a surface of which the points are populations. The result is a surface that collapses into a single point because the axes are incompatible. For these reasons, Provine concludes that Wright's Adaptive Landscape diagram does not successfully illustrate the shifting balance process and, so, must be abandoned.

Wright (1988) responded to Provine's criticism by uncritically claiming that Provine confused a metaphor for a mathematical model. Ruse (1996) develops the criticism and rightly disagrees with Provine: *even if* Wright's interpretation of the diagram *is* incoherent (meaning that it does not accurately represent Wright's mathematical model), it may *still* be a valuable heuristic. Ruse thinks

that Provine's assessment of the heuristic value of Wright's diagram is too conservative. Heuristics are devices that are used to generate paths of inquiry whether those paths are fruitful or not. The fact that Wright's interpretation of the diagram does not cohere with his mathematical models is beside the point. Rather, because uses of the diagram have a track record of generating fruitful paths of inquiry, it is a valuable heuristic. Ruse cites T. Dobzhansky (1951), G. G. Simpson (1953), G. Ledyard Stebbins (1969), and C. H. Waddington (1956) as having used the Adaptive Landscape to produce apparently positive results: Dobzhansky used the landscape to illustrate the shifting balance process, Simpson used the landscape to illustrate species and speciation, and Waddington used the diagram for his own illustrative purposes in population genetics. Moreover, the biological work we discuss later in this essay includes instances of the heuristic used to produce positive results, as we will see (briefly) (see Chapter 1). Provine's doubts about the heuristic value of the Adaptive Landscape diagram are misplaced.

Kaplan (2008) argues that the Adaptive Landscape metaphor in general ought to be abandoned. Kaplan lists a number of complaints about the diagram, e.g. it is not explanatory in the way a mathematical model is, the diagram does not map onto a relevant mathematical model, it is imprecise, it lacks a univocal heuristic role, and it has done more to confuse than to enlighten. But the main point of Kaplan's argument is that the diagram is no longer useful given the continued growth in computational power that we are experiencing with respect to scientific modeling. That is, there is no need for a simplified landscape diagram when biologists have access to computational power that will allow them to build models that will more precisely do the work that the landscape diagram is meant to do. Kaplan then recommends biologists abandon the diagram in favor of computational models.

Many of Kaplan's complaints are familiar. Indeed, the Adaptive Landscape diagram has led biologists astray, it is not explanatory in the way that a mathematical model is, it is imprecise, and so on. We think these criticisms are misplaced. One certainly expects mathematical models

to be explanatory, precise, etc. But, in the vein of Wright's and Ruse's arguments against Provine, these demands are misdirected when aimed at the landscape diagram. Wright developed the Adaptive Landscape in an effort to defend his shifting balance process in an intuitive, informal way using a simple, unlabeled topographical map as a metaphor for the mean fitness of populations. It is wrongheaded to expect such a heuristic to meet the standards of a mathematical model. Rather, as we described above, we expect positive analogies from metaphors, but we also expect negative analogies (Hesse 1966). Nothing Kaplan has said in criticizing the landscape diagram addresses it as a metaphor. After all, the diagram may not meet the expectations we have for mathematical models, but that does not mean the diagram does not meet expectations properly construed. The review of biological work in section 2.5 we think demonstrates that the diagram is heuristically valuable.

Finally, it is not at all clear that Kaplan's suggestion to abandon the landscape diagram in favor of complex mathematical models is reasonable. Certainly the suggestion is not descriptive of the way many if not most population geneticists practice, though there are exceptions. And, at any rate, we do not think there is good reason to think that the computational power that is available to biologists is sufficient to yield a biologically realistic population genetics model. Idealizations and simplifications are the norm and will no doubt continue to be the norm.

We think Provine's and Kaplan's reasons to reject the Adaptive Landscape diagram are poor. Both seem to think that the diagram must play the role of an explanatory model, and because it cannot do that, it is a defective scientific tool. For Provine, the diagram is simply a failure. For Kaplan, the diagram has led scientists down fruitless paths of inquiry. On our view, not all aspects of scientific models are explanatory; some are metaphorical (Lewontin 1963). These metaphorical elements play heuristic roles in scientific theorizing. And heuristics are rules of thumb, i.e. strategies that work well sometimes but not always. We now consider a patchwork of biological work that suggest that the Adaptive Landscape metaphor is a valuable heuristic

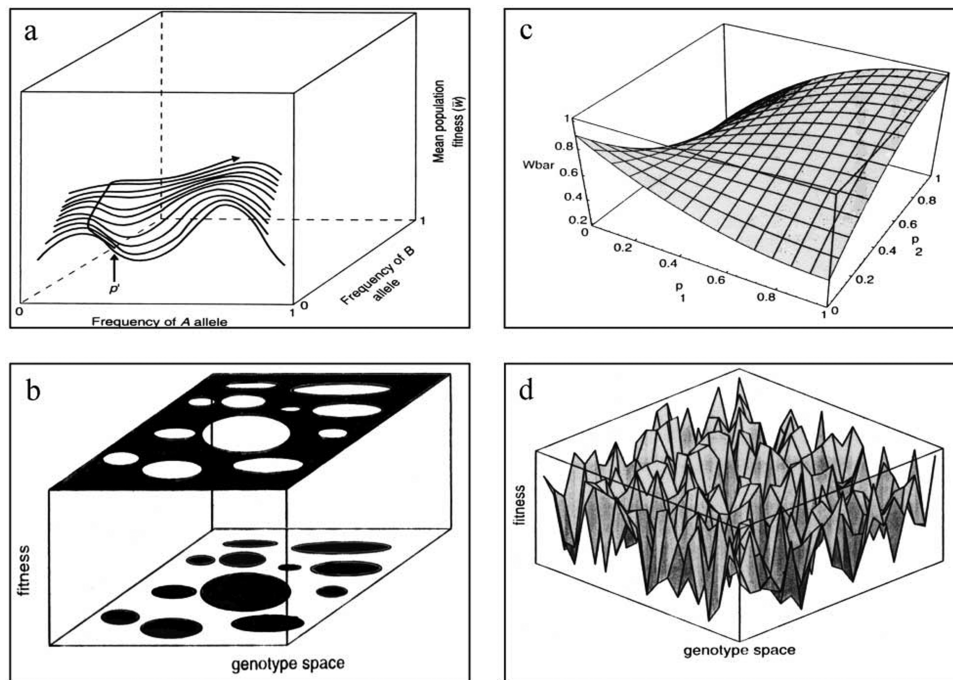
in spite of the flaws in Wright's particular view of it (cf. Plutynski 2008).

## 2.5 The case for heuristic value

Fisher immediately pointed out the central problem for Wright's version of the diagram. Fisher and Wright discussed the landscape metaphor in correspondence prior to the 1932 presentation (Wright correspondence to Fisher, 3 February 1931 in Provine 1986, pp. 271–273; Fisher correspondence to Wright, 31 May, 1931 in Provine 1986, p. 274). According to Fisher, the Adaptive Landscape diagram is flawed because, in fact, as the dimensionality of the field of gene combinations in the field of gene frequencies *increases* the number of stable peaks on the surface of the landscape *decreases* (see also Fisher 1941). Thus, claims Fisher, representation of the mean fitness of populations in multiple dimensions will not result in a *hilly* landscape, but one that is a single peak with ridges along it. As a consequence, evolution on the landscape does not require the complex of evolutionary factors of Wright's shifting balance process, but only selection and mutation. Fisher's informal critique of Wright was taken up perhaps most influentially by P. A. P. Moran (1964), A. W. F. Edwards (1994), and Jerry Coyne et al. (1997). Mark Ridley (1996) developed an Adaptive Landscape diagram based on Fisher's critique, reproduced in Fig. 2.2a (see Chapter 4).

Sergey Gavrillets (1997, 1999, 2004) has criticized Wright's version of the landscape. On Gavrillets's view, the Adaptive Landscape in multiple dimensions will not have adaptive peaks and valleys. Instead, the landscape will be the holey one depicted in Fig. 2.2b. That is, the higher the number of possible gene combinations in a field of gene frequencies, the higher the number of incompatible combinations in that field. The incompatible gene combinations cause reproductive isolation within populations, which cause genetically-driven speciation events. The holes represent locations of incompatible combinations of genes and replace the peaks. Gavrillets's argument, as he recognizes, is based on a set of specific assumptions that must be relaxed in fundamental ways if his theoretical intuitions are to be tested empirically. Gavrillets assumes that (1) fitnesses of gene





**Figure 2.2** Four Adaptive Landscape diagrams, resulting from critiques of Wright's 1932 diagram. (a) Ridley's (1996, p. 219) depiction of a Fisherian landscape. *Evolution*. 2nd edition. Copyright 1997. Reproduced with permission of Wiley-Blackwell. (b) Gavrillets's (1999, p. 309) depiction of the holey landscape. *Trends in Ecology and Evolution*. Copyright 1997. Reproduced with permission of Elsevier. (c) Coyne et al.'s (1997, p. 647) simplified Wrightian landscape. Reproduced from Coyne, J., Barton, N., and Turelli, M. (1997), "Perspective: A Critique of Sewall Wright's Shifting Balance Theory of Evolution", *Evolution* 51: 643–671 (d) The Kauffman and Levin (1987, p. 33) rugged Adaptive Landscape. *The Journal of Theoretical Biology*. Copyright 1987. Reproduced with permission of Elsevier.

complexes are generated randomly; (2) fitnesses are generated independently; and (3) fitness values are either 0 or 1. Nevertheless, Gavrillets (1999) has discussed the evolutionary dynamics of speciation on holey landscapes as driven by random genetic drift, mutation, recombination, and migration. Indeed, Gavrillets points out that Wright's apparently restrictive combination of drift, mass selection, interdemic selection, and migration is not necessary to traverse the Adaptive Landscape if Gavrillets is correct. There are, after all, no adaptive valleys between peaks to pass through.

A series of papers by collaborators working on the genotype–phenotype map problem have raised an issue against Wright's version of the landscape diagram that is related to that of Gavrillets (e.g. Fontana and Schuster 1998; B. Stadler et al. 2001; P. Stadler 2002). The basic claim here is that a discontinuous landscape surface is more likely than a continuous one. The argument, however, is different. Roughly, the argument is that taking seriously

the developmental processes involved in going from genotype to phenotype in evolution, one will discover that there are many phenotypes inaccessible from genotypes, resulting in discontinuities on the surface of the landscape. The argument is rooted in computational work on the biophysical genotype–phenotype model defined by the folding of RNA sequences into secondary structures. The RNA sequences are considered to be genotypes, and the role of the phenotype is played by the structure of the molecule. Based on this model, a general, mathematical theory of landscapes has resulted, reaching far beyond the informal use of topographical map-making that Wright used in 1932. Despite the implications for Wright's landscape, apparently a landscape on which to depict evolutionary trajectories in population genetics based on the general landscape theory is not immediately forthcoming due to constraints on computational power.

Although there are serious problems for Wright's view that he can transform a hilly landscape in

two dimensions into a hilly landscape in thousands of dimensions, the notion that there are simple cases of hilly landscapes persists (e.g. Coyne et al. 1997, p. 647). Indeed, in simple and rather restrictive cases, i.e. two loci cases assuming complete dominance at each locus, Wright's landscape has been given some plausibility (e.g. Lande 1976, 1979; Coyne et al. 1997) (Fig. 2.2c). Further, Kauffman and Levin (1987) responded to problems for Wright's view of the landscape by developing "rugged Adaptive Landscapes" as a way of understanding the fitness of gene combinations given simple Wrightian epistatic gene interaction (Fig. 2.2d). In Kauffman and Levin's *NK* model, the fitness contribution of each of  $N$  loci depends in a random way on  $K$  other loci. The parameter  $K$  describes the degree of epistasis. If  $K = 0$ , then an Adaptive Landscape with one peak results. But as  $K$  increases, the number of peaks on the landscape increases and the mean fitness of the nearest peak decreases toward that of an entirely random genotype. Typically, the result is a rugged Adaptive Landscape. Kauffman and Levin's work has been applied in biochemistry (e.g. Fontana et al. 1989, 1991, 1993), and interestingly that work is a principal ancestor of the genotype–phenotype mapping work discussed earlier. Kauffman (1993) extends the use of rugged Adaptive Landscapes in his work on complexity and on artificial life modeling.

Notice that these biologists do not view the landscape diagram as a failed heuristic. Rather, each critically evaluates the foundational assumptions of the other out of which a new Adaptive Landscape metaphor is created, along with new, arguably fruitful paths of inquiry. This pattern of contrasts can be seen across all of the cases discussed, but consider the contrast between Fisher's single-peak landscape and Wright's hilly landscape. The single-peak landscape reflects Fisher's view that there is one optimal gene combination, which can be found by the combination of mutation and selection. Wright's hilly landscape reflects his emphasis on the evolutionary effects of epistatic gene interaction.

For Wright, genes adaptive in one combination will be maladaptive in another. The consequence of such epistasis was, for Wright, a hilly Adaptive Landscape. More generally, depending on the basic genetic assumptions in a model, whether it is Fisher's, Wright's, Coyne's, Gavrillets's, etc. the corresponding surface of selective value will take different forms. Indeed, it is important to note that it is the set of core genetic assumptions embedded in a population genetics model rather than assumptions about the balance of evolutionary causes that go toward shaping the surface of an Adaptive Landscape. Given that, it seems plausible that while, for example, Wright's shifting balance process is dependent on his version of the Adaptive Landscape, the landscape is in no way dependent upon the shifting balance process (cf. Ruse 1996; Coyne et al. 1997).

Ultimately, we think the cases we have discussed demonstrate that these biologists find the heuristic useful. Next, we describe the way in which we think the Adaptive Landscape metaphor has been a valuable heuristic.

The diagram is used importantly as a model evaluation heuristic (Skipper 2004). Indeed, we think it is clear that Wright used the Adaptive Landscape diagram as a visual heuristic to evaluate the *dynamical behavior* of population genetics models of evolutionary processes constructed with alternative assumptions to demonstrate his own. The dynamical behavior of a mathematical model refers to the way(s) in which some system being described by the model change(s) according to changes in the model's state(s).<sup>2</sup> The dynamical behavior of such a model in population genetics includes, for example, the changes in the mean fitness of a population against the parameters that hold the measured intensity of specific evolutionary factors such as population size, migration rate, selection, mutation, etc. and describes the ways that the states of the model change. The Adaptive Landscape diagram, as a simplified visualization of common, core assumption of all the models, is where the

<sup>2</sup> Our "dynamical behavior" should not be confused with Lewontin's (1974) "dynamical sufficiency." Lewontin's dynamical sufficiency refers to a model's empirically being demonstrated to contain all of the relevant parameters, etc. required to describe evolutionary change. And Lewontin outlines a specific and probably unattainable view of "sufficiency." "Dynamical behavior" is a practical specification of one way to assess a much more modest notion of sufficiency.



evaluation of the behaviors of the models takes place; the diagram is the heuristic with which the evaluation is being made. A model is positively evaluated in case a model system described by it can traverse the landscape, shifting from one adaptive peak to the highest adaptive peak.

Wright assesses the dynamical behavior of evolutionary systems described by six alternative models, i.e. windows A–F in Fig. 2.1b. Each window is a piece of the larger Adaptive Landscape in Fig. 2.1b. What Wright does is to visually depict the dynamical behavior of a model system on the landscape. Consider window A in Fig. 2.1b. Here, Wright sets up a model with the following assumptions: populations are very large and panmictic, mutation rate is high, selection intensity and mutation rate are low. Depicting that model by way of Wright's landscape, the model system will not be able to get to the highest adaptive peak because it will not be able to traverse the hilly surface—it will not be able to move from its initial position to a higher peak. Wright repeats this process in windows B–F, demonstrating how the dynamical behavior of the various mathematical models changes as the assumptions change. Only the model sketched in window F succeeds in traversing the heuristic landscape; that is the model Wright interprets as describing the shifting balance process.

Ultimately, Wright's evaluative strategy, using the landscape diagram, led him to his view that evolution is a process that includes a constellation of factors. That is, out of his evaluation of alternative evolutionary hypotheses, driven by the landscape diagram, Wright was led to his shifting balance process: the evolutionary factors delineated in the shifting balance process are necessary for traversing the Adaptive Landscape. Now, Wright's own heuristic use of the diagram is problematic because of a flaw in his interpretation of it. However, critics who have pointed out Wright's flaw have then gone on to create landscape diagrams of their own for the same sorts of assessments. And they further use the landscape to assess the dynamical behavior of alternative population genetics models. Indeed, Ridley (1996), using his version of the Fisherian landscape, shows that Wright's shifting balance process is unnecessary for traversing the landscape:

The models that describe the shifting balance process overdetermine the process that is required given the surface of the landscape. Gavrillets (1997, 2004) shows, using his holey landscape, that neither Wright's nor Fisher's mechanisms are necessary to traverse the landscape. In Gavrillets's case, Wright's shifting balance process is unnecessary because there are no peaks. And Coyne et al. (1997) show that, in simple cases, Wright's three-phase evolutionary process is one among many possible mechanisms for traversing a hilly landscape. The Adaptive Landscape diagram is valuable, in spades, as a heuristic for evaluating the dynamical behavior of evolutionary models (Skipper 2004).

## 2.6 Conclusion

In spite of the fact that Wright's Adaptive Landscape diagram is one of the most influential visual heuristic in evolutionary biology, there has been considerable confusion about whether it is actually valuable in that role. We have argued that the confusion about the heuristic value of the diagram is rooted in misunderstandings about models and metaphors. The landscape diagram is not a mathematical model; it is a visual metaphor intended to represent the ways in which a system described by a mathematical model may behave. Broadly, metaphors play a didactic and not explanatory role in scientific theorizing. The Adaptive Landscape plays that didactic role as a model assessment heuristic. Understanding the diagram in this way makes it clear why the Adaptive Landscape has been so influential.

## References

- Coyne, J. A., Barton, N. H., and Turelli M. (1997). Perspective: A critique of Sewall Wright's shifting balance theory of evolution. *Evolution*, 51, 643–671.
- Dobzhansky, T. (1951). *Genetics and the Origin of Species*, 3rd edn. Columbia University Press, New York.
- Edwards, A. W. F. (1994). The fundamental theorem of natural selection. *Biological Reviews of the Cambridge Philosophical Society*, 69, 443–474.
- Fisher, R. A. (1941). Average excess and average effect of a gene substitution. *Annals of Eugenics*, 11, 53–63.
- Fontana, W., Greismacher, T. Schnabl, P. Stadler, F., and Schuster P. (1991). Statistics of landscapes based on free

- energies, replication and degradation rate constants of RNA secondary structures. *Monatshefte für Chemie*, 122, 795–819.
- Fontana, W., Schnabl, P., and Schuster, P. (1989). Physical aspects of evolutionary optimization and adaptation. *Physical Review A*, 40, 3301–3321.
- Fontana, W. and Schuster, P. (1998). Continuity in evolution: On the nature of transitions. *Science*, 280, 1541–1455.
- Fontana, W., Stadler, F., Tarazona, P., Weinberger, E., and Schuster, P. (1993). RNA folding and combinatorial landscapes. *Physical Review*, E 47, 2083–2099.
- Gavrilets, S. (1997). Evolution and speciation on holey adaptive landscapes. *Trends in Ecology & Evolution*, 12, 307–312.
- Gavrilets, S. (1999). A dynamical theory of speciation on holey adaptive landscapes. *American Naturalist*, 154, 1–22.
- Gavrilets, S. (2004). *Fitness Landscapes and the Origin of Species*. Princeton University Press, Princeton, NJ.
- Hesse, M. (1966). *Models and Analogies in Science*. Notre Dame University Press, Notre Dame, IN.
- Kaplan, J. (2008). The end of the Adaptive Landscape metaphor? *Biology and Philosophy*, 23, 625–638.
- Kauffman, S. (1993). *The Origins of Order: Self-Organization and Selection in Evolution*. Oxford University Press, New York.
- Kauffman, S. and Levin, S. (1987). Towards a general theory of adaptive walks on rugged landscapes. *Journal of Theoretical Biology*, 128, 11–45.
- Lande, R. (1976). Natural selection and random genetic drift in phenotypic evolution. *Evolution*, 30, 314–334.
- Lande, R. (1979). Effective deme sizes during long-term evolution estimated from rates of chromosomal inversion. *Evolution*, 33, 314–334.
- Lewontin, R. (1963). Models, mathematics, and metaphors. *Synthese*, 15, 222–244.
- Lewontin, R. (1974). *The Genetic Basis of Evolutionary Change*. Columbia University Press, New York.
- Lloyd, E. A. (1988). *The Structure and Confirmation of Evolutionary Theory*. Greenwood Press, New York.
- Lynch, M. and Woolgar, S. (Eds.) (1990) *Representation in Scientific Practice*. MIT Press, Cambridge, MA.
- Moran, P. A. P. (1964). On the non-existence of adaptive topographies. *Annals of Human Genetics*, 27, 383–393.
- Perini, L. (2004). Convention, resemblance and isomorphism: understanding scientific visual representations. In G. Malcolm (ed.) *Multidisciplinary Approaches to Visual Representations and Interpretations*. Elsevier, Amsterdam, pp. 39–42.
- Perini, L. (2005). Explanation in two dimensions: Diagrams and biological explanation. *Biology and Philosophy*, 20, 257–269.
- Pigliucci, M. (2008). Sewall Wright's Adaptive Landscapes: 1932 vs. 1988. *Biology and Philosophy*, 23, 591–603.
- Pigliucci, M. and Kaplan, J. (2006). *Making Sense of Evolution: The Conceptual Foundations of Evolutionary Biology*. University of Chicago Press, Chicago, IL.
- Plutynski, A. (2008). The rise and fall of the Adaptive Landscape? *Biology and Philosophy*, 23, 605–623.
- Provine, W. B. (1986). *Sewall Wright and Evolutionary Biology*. University of Chicago Press, Chicago, IL.
- Ridley, M. (1996). *Evolution*, 2nd edn. Blackwell Science, Inc., Cambridge, MA.
- Ruse, M. (1996). Are pictures really necessary? The case of Sewall Wright's 'Adaptive Landscapes'. In B. Baigrie (Ed.) *Picturing Knowledge: Historical and Philosophical Problems Concerning the Use of Art in Science*. University of Toronto Press, Toronto, pp. 303–337.
- Simpson, G. G. (1953). *The Major Features of Evolution*. Columbia University Press, New York.
- Skipper, Jr., R. A. (2004). The heuristic role of Sewall Wright's 1932 Adaptive Landscape diagram. *Philosophy of Science*, 71, 1176–1188.
- Stadler, B. M. R., Stadler, P., Wagner, G., and Fontana, W. (2001). The topology of the possible: Formal spaces underlying patterns of evolutionary change. *Journal of Theoretical Biology*, 213, 241–274.
- Stadler, P. (2002). Fitness landscapes. In M. Lässig and A. Valleriani (eds.) *Biological Evolution and Statistical Physics*. Springer-Verlag, Berlin, pp. 187–207.
- Stebbins, G. L. (1969). *The Basis of Progressive Evolution*. University of North Carolina Press, Chapel Hill, NC.
- Waddington, C. H. (1956). *Principles of Embryology*. Macmillan, New York.
- Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, 16, 97–159. Reprinted in W. B. Provine (1986). *Sewall Wright: Evolution: Selected Papers*. University of Chicago Press, Chicago, IL, pp. 98–160.
- Wright, S. (1932). The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the Sixth Annual Congress of Genetics*, 1, 356–366. Reprinted in W. B. Provine (1986). *Sewall Wright: Evolution: Selected Papers*. University of Chicago Press, Chicago, IL, pp. 161–177.
- Wright, S. (1939). *Statistical Genetics in Relation to Evolution*. [Actualités scientifiques et industrielles, 802. Exposés de Biométrie et de la statistique biologique XIII.] Hermann & Cie, Paris. Reprinted in W. B. Provine (1986). *Sewall Wright: Evolution: Selected Papers*. University of Chicago Press, Chicago, IL, pp. 283–341.

- Wright, S. (1969). *Evolution and the Genetics of Populations*, Vol. 2: The Theory of Gene Frequencies. University of Chicago Press, Chicago, IL.
- Wright, S. (1977). *Evolution and the Genetics of Populations*, Vol. 3: Experimental Results and Evolutionary Deductions. University of Chicago Press, Chicago, IL.
- Wright, S. (1978). The relation of livestock breeding to theories of evolution. *Journal of Animal Science*, 46, 1192–1200. Reprinted in W. B. Provine (1986). *Sewall Wright: Evolution: Selected Papers*. University of Chicago Press, Chicago, IL, pp. 1–11.
- Wright, S. (1988). Surfaces of selective value revisited. *American Naturalist*, 131, 115–123.