

Regular Article
The Rise and Fall of the Adaptive Landscape?
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Abstract:

The discussion of the adaptive landscape in the philosophical literature appears to be divided along the following lines. On the one hand, some claim that the adaptive landscape is either “uninterpretable” or incoherent. On the other hand, some argue that the adaptive landscape has been an important heuristic, or tool in the service of explaining, as well as proposing and testing hypotheses about evolutionary change. This paper attempts to reconcile these two views.

Key words: adaptive landscape, heuristic, metaphor, model, Sewall Wright

Evolution is an extremely complex process, involving many factors – the genetic constitution of populations, the changing environment, developmental patterns and processes in organisms, and the variety of interactions between all three. In order to make progress in investigating such a complex process, biologists begin their investigations of the most difficult problems of evolution by developing models that are founded on idealizing assumptions. Biologists have deployed a variety of idealized models, as well as metaphors and analogies in service of this aim. The aim of this paper is to provide a historical overview of one such metaphor, the adaptive landscape metaphor. A variety of historians and philosophers of biology have weighed in on the adaptive landscape metaphor. According to these authors, the landscape metaphor is “mathematically uninterpretable.” (Provine, 1986), a “valuable heuristic.” (Ruse, 1996), “...a theory evaluation heuristic for evaluating the dynamical behavior of population genetics models,” (Skipper, 2004), and according to two recent authors, “it may in the end be impossible to articulate the metaphor in a way that is both coherent and conceptually fruitful.” (Pigliucci & Kaplan, 2006)

At first glance, all these views may seem at odds with one another. The aim here will be to show how the above views might be reconciled. The metaphor will first be described, its history briefly reviewed, the key assumptions of the metaphor discussed, and finally, it will be shown how the above authors’ views are not so contradictory as it may first appear.

1 What is an adaptive landscape?

The first published image of the landscape was in 1932, in a paper delivered at the Sixth International Congress of Genetics. Wright, along with Haldane and Fisher, the founders of theoretical population genetics, were invited to convey to a non-mathematical audience some of the key elements of their views. Wright's landscape was meant to illustrate the argument(s) in a 1931 survey paper, which summarized the key elements of his "shifting balance" theory of evolution. Wright's shifting balance theory was his solution to the problem of adaptive evolution. He envisioned a three-phase process, by which populations could climb from one less optimal adaptive peak to a higher adaptive peak on the fitness landscape. A central background assumption of Wright's was that most adaptations were products of many genes in combination, and that interactions between genes significantly constrain evolutionary change. Epistasis, or genetic interaction, was, he thought, pervasive in most populations; most traits were due to many genes in combination, and so, most changes in these combinations would lead to an organism being less fit. These assumptions were empirically founded on Wright's early research on physiological genetics. His work on path analysis, the diagrammatic representation of gene expression, grew out of research in the inheritance of coat color in guinea pigs, which was dependent upon many genes in interaction (see Provine, 1989). Wright was also influenced by research at the USDA on selection for desirable traits in agricultural species. It seemed to Wright that selection as a mechanism of adaptive change would run up against certain limits. Populations eventually get "stuck" at a

suboptimal fitness (measured, in this case, by oil content in corn, for instance), change in which required novel evolutionary circumstances. Wright explains:

The central problem of evolution as I see it is that of a mechanism by which the species may continually find its way from lower to higher peaks in such a field... there must be some trial and error mechanism on a grand scale by which the species may explore the region surrounding the small portion of the field which it occupies. (Wright, 1932, p. 358-59)

This mechanism was Wright's "shifting balance" process of evolution. Evolution of populations to novel adaptive gene combinations required "shifts" across adaptive valleys viz. the three phase process of drift, inbreeding, intra- and inter-demic selection. Three diagrams (Figure 1) represent different kinds of adaptive change; from left to right, D, E, and F represent the fates of small inbred populations, intermediate sized groups with less inbreeding, and division into semi-isolated groups, what he thought was the optimal for evolution.

The three phases of shifting balance process of evolution were:

Phase I: Random drift (or, sampling error) in small populations allows an "exploration of the adaptive topography."

Phase II: Natural selection increases the frequency of favorable gene combinations found in phase I.

Phase III: Interdemic selection (selection between groups), in which the groups characterized by the best gene combinations send out the most migrants, and eventually, export the most well-adapted gene combinations to the entire population.

Wright was cautious about introducing this simplifying metaphor of evolutionary change. He wrote that accurately representing the genetics of populations would require thousands of dimensions; the field of possible gene combinations, he thought, was vast (10^{1000}), so, representing the adaptive values of all these combinations could not possibly be accomplished in a two, or even three dimensional landscape (see Figure 2). These

comments were in part a response to Fisher, who in correspondence with Wright, (1931) raised concerns about the adaptive landscape metaphor. Wright, in reply, acknowledged that there was many dimensions along with selection could change the genetic composition of a population. As Wright wrote, in response to Fisher:

In regard to the theoretical point which you raised, I appreciate that with increase in the number of dimensions the chance that one might pass by a continuously upward path from one point to another increases...(letter to Fisher, 1931, cited in Provine (1986), p. 310)

Nonetheless, Wright's image quickly became hugely influential. Dobzhansky used his two-dimensional image to picture the distribution of species in adaptive space. He imagined that each species resided on a separate adaptive peak, separated by valleys of reproductive isolation:

...Each living species may be thought of as occupying one of the available peaks in the field, of gene combinations. The adaptive valleys are deserted and empty. Furthermore, the adaptive peaks and valleys are not interspersed at random. "Adjacent" adaptive peaks are arranged in groups, which may be likened to mountain ranges in which the separate pinnacles are divided by relatively shallow notches. (Dobzhansky, 1951)

Notice, Dobzhansky is shifting the application of Wright's image to speak of whole species as opposed to individuals or populations as resting atop adaptive peaks.

Dobzhansky had a significant influence on Ernst Mayr's views on speciation, the origin of two or more species from a single common ancestor. One of the key mechanisms of speciation, according to Mayr, was via founder effect, the isolation of a small "founder" population and the subsequent divergence of this population from its parent population. Mayr (1954) proposed that speciation frequently occurs when a small group of founders migrates to a new habitat or island. The "founder effect" model capitalized on the general belief in the importance of genetic drift popularized by Wright.

The founder emigrants could only take a fraction of available genetic variation to their new home (genetic drift as in shifting balance phase I). These genes would undergo a selection-driven "genetic revolution" or reorganization of the genome (as in phase II). Mayr believed that a genetic revolution took place, in part, because the new population was also exposed to unusual environmental conditions, yielding rapid divergence and speciation.

However, Mayr's grasp of the genetics underlying this process was dubious. Mayr spoke of the "unity of the genotype" as what made each species and population distinct, and characterized by its own distinct adaptations:

Work in population and developmental genetics has shown... that the thinking of beanbag genetics is quite misleading. To consider genes as independent units is meaningless from the physiological and evolutionary viewpoint. Genes not only act... but also interact... It had long been known that a gene which adds to fitness in its normal genetic background may be deleterious or even lethal when placed on a different genetic background (Dobzhansky, 1937). Such a shift in the selective value of a gene is not an isolated phenomena... This interaction has been described,... in the statement: every character of an organism is affected by all genes and every gene affects all characters. The result is a closely knit functional integration of the genotype. With recombination producing in every generation new assortments of genes (new genotypes), which in turn have to form well-balanced and fully viable phenotypes, it is evident that the integration has to extend beyond the level of the individual. There must be harmony among all the genes of which a local gene pool is composed. This gives the local population its cohesion and makes it a significant level of interaction. Whatever phenotypic variation may be observed in a local population is not in conflict with this basic unity, because all the genotypes in a population are products of the same gene pool (Dobzhansky, 1951, 1955b). (Mayr, 1963, pp. 263-4)

This view was influenced by Lerner's *Genetic Homeostasis*, as well as Waddington's views on genetic contributions to development (1955). Mayr was convinced that each gene interacts with *every* other gene in development. While Mayr's views on the extent of interaction may today seem an extreme view, this assumption was

very much in the air at the time. Citing Goldschmidt and Waddington, Mayr argued:

It is obvious not only that such an interacting system is highly sensitive but also that it permits numerous feedbacks and systems of regulation. The students of development have various terms for these regulatory powers, such as buffering, canalization, and developmental homeostasis. These terms apply to models that help us to visualize the action of genes in the developmental process.... We refer to various textbooks and essays on epigenetics for further details on the physiology of differentiation of the tissues and organs in relation to gene action. (Goldschmidt, 1955, Waddington, 1956a...)

There appear to be many developmental mechanisms and canalizations that prevent gene substitutions from expressing themselves in the phenotype (Waddington, 1957). This constancy of the genotype is by no means fully understood, but it is, no doubt, one aspect of the general phenomenon of the unity of the genotype.

Mayr frequently shifts from a discussion of the integration of the genotype at the level of the organism to integration at the level of the entire population. Mayr's reasoning was as follows: if the genotype of individual organisms are functionally integrated in the sense that each gene interacts with all other genes in the construction of a phenotype, and genes are shared in a population via recombination, then it must be the case that the entire population shares genes that interact, as he says, "harmoniously". Throughout his 1963 book, the "unity of the genotype" is sometimes taken to refer to the genotype of a particular individual organism, and sometimes to the genotypic constitution of species. Mayr slips fluidly between the two, as if the first implies the second as a matter of deductive logic.

Mayr's influential work on speciation, along with Dobzhansky's important book on genetics and speciation, lead to the notion that speciation required some special process of traversing a valley of low fitness, a "genetic revolution." Founder effect and peak shifting thus became linked in the evolutionary literature. One of the assumptions of much of the literature on speciation from the 1960s until as late as the 1980s was that

if one could understand how peak shifting was possible, one could understand how founder effect worked at a genetic level. Was this assumption justified? Here are some of the key assumptions attendant upon this way of framing the problem:

- i. That populations are composed of individuals whose genes are highly “coadapted”.
- ii. That generating more fit gene combinations requires that a population pass through gene combinations of lower fitness.
- iii. That species in some sense rest “atop adaptive peaks,” due to the coadaptation of their collection of genes.
- iv. That speciation requires a “peak shift” and a “genetic revolution” – due primarily to drift, followed by the origin of new, more adaptive gene combinations.

All of these assumptions were subsequently questioned in the biological literature.

However, we should not fault Dobzhansky or Mayr alone for assuming these things to be so. In part, Wright’s inconsistent use of the metaphor could have lead to some of the confusion.

One source of the confusion is that Wright sometimes took the surface of the landscape to represent the field of gene combinations graded for adaptive value (the genotype model), and sometimes to represent the mean fitnesses of whole populations graded for adaptive value (population interpretation) (Skipper, 2004, Provine, 1986). In other words, on one interpretation, we can think of the surface as representing the variety of possible gene combinations, and on another, we can think of the surface as representing the average fitnesses of whole populations, whatever this might mean. Wright imagined also that whole species rest atop adaptive peaks; where, the valleys in this case represented reproductive isolation. Again, Wright assumed that these were all due to gene combinations of low fitness. One can also represent the landscape as a surface of ecological niches where different species reside, or as representing the

fitnesses of different phenotypes.

Will Provine (1986) first pointed out that Wright's use of the landscape concept was ambiguous and inconsistent. He argued that, on the genotype interpretation, it is unclear what exactly the units along the axes are supposed to be. Provine claims that the surface would have to be discontinuous. And, further, Provine argued that it is impossible to translate the genotypic landscape into a surface representing the average fitness of whole populations. He wrote:

[Wright's] construction does not in fact produce a continuous surface at all. Each axis is simply a gene combination; there are no gradations along the axis. There is no indication of what the units along the axis might be or where along the axis the gene combination should be placed...Thus ...the most popular of all graphic representations of evolutionary biology in the 20th century, are meaningless. (Provine, 1986, p. 310)

Provine is (partially) correct: For single genotypes, (see Figure 3), it is possible to translate a graphical representation of fitnesses for a single genotype and for a whole population of individuals. However, the translation is more difficult if we consider more than one genotype.

Consider the following example (Figure 4). This is an image of what is called Dobzhansky-Muller incompatibility, where we have two genotypes that are fit in certain combinations but not in others. This is a case where one can traverse the landscape along certain "ridges" but not others. Figure 5 is an image of the fitness landscape for an actual empirical case of the same; based on actual genotype frequencies found in the field for a grasshopper with two kinds of chromosome. In this image, there are two peaks represented by dense contour lines, and a saddle between them. So, it is possible to translate from one or two loci to a fitness surface. The problem becomes much more difficult, however, as we imagine many more loci in combination.

It's when we take the metaphor to higher and higher dimensions that some of the difficulties with Wright's thinking become apparent. Wright makes a number of assumptions about the landscape: that it is static, that one can indirectly represent multiple dimensions adequately in two or three dimensions, or that its surface is "rugged" - I.e., he assumes that a 2 or 3D landscape is relevantly similar to a multidimensional landscape.¹ The "rugged surface" represents how certain genes in combination yield high fitness, separated by "valleys" of gene combinations of lower fitnesses. Are all these things true? What happens if we consider larger numbers of genes in combination?

Lewontin (1978) has pointed out that the environment does not remain fixed. As populations of organisms change, they affect one another, and modify their environment, and the environment itself is, of course, constantly changing. He suggested that we envision a "rubbery" landscape which organisms themselves modify over time. And, if multiple alleles contribute to organismic fitness, the landscape will have many more than three dimensions; the fitness landscape is a hypercube.

Sergei Gavrillets, in a series of papers and a recent book (2004) has expanded upon Fisher's earlier criticism of Wright. Starting with the observation that the dimensionality of "genotypic space" is on the order of millions, he argues that the metaphor of the rugged landscape will have to be adapted. We ought to think of the landscape as a hyperspace, with many more than three dimensions. Further, as we increase the number of dimensions of the landscape, thereby representing the large number of genes that contribute to fitness, there is a high probability that we will get a variety of ridges, which can be traversed. Gavrillets calls these "nearly neutral" networks,

¹ Or, according to a reviewer: "when you collapse lots of dimensions into a few, you'd get a nearly continuous surface." Thanks for these comments.

a contiguous set of sequences of genotypes possessing very nearly the same fitness. They are contiguous in the sense that any two sequences in a set can be connected by a chain of one-step allele or sequence changes. He developed what he calls a “Russian Roulette” model to illustrate this. Consider a two-dimensional lattice (Figure 6); with squares painted black and white representing genotypes that are either viable (black) or inviable (white) (thus, “Russian Roulette”). “ p ” is the proportion of black sites. As p exceeds a certain threshold, a neutral network extends through the system. The percolation threshold decreases in genotype spaces of high dimensionality. Gavrilets explains:

As we increase the number of dimensions of the landscape, the probability of ridges connecting high fitness genotypes increases; I.e., there is a strong possibility that high-fitness genotypes form networks that extend throughout the genotype space (we can get substantial genetic divergence without going through adaptive valleys) (Gavrilets, 2004)

There are a number of reasons one might question Gavrilets’ model.² First, he still speaks of populations as occupying positions in the adaptive landscape; but what is meant by mean population fitness? How ought we to measure this, and ought we to expect it to increase? Indeed, if we take it to be the average rate of increase in population size, both Wright and Fisher knew that we should not expect it to increase. Moreover, there’s no clear mapping of genotypic space to this notion of mean fitness. Second, he substitutes one metaphor for another; what are the “ridges”? What do they represent? And, how ought we to conceive of their connections between “peaks”?

While all of these are legitimate and important questions, what is relevant to the more general question at issue is the following. Gavrilets’ reconceptualization of the landscape (and earlier, Coyne, Orr and others’ discussions of “ridges” in the landscape)

² Thanks to a reviewer for these comments

has lead many biologists to question some of Wright's, and subsequently, Mayr's presuppositions about genetic interaction and the limits it places on modes of speciation. Let's return to Wright's central background assumption: that evolution requires traversing adaptive valleys. This assumption, along with the imagery of peak shifting as a means not only of adaptive change, but speciation, became an enormously influential one. In particular, Wright's image of the stable, co-evolved gene combinations yielding stable species and populations lead many researchers on speciation to equate the problem of speciation as the problem of peak shifting. Was it a warranted assumption?

Using both a one-locus, two-allele models, and multilocus models, theoretical biologists have been able to demonstrate that the probability of stochastic transitions between fitness peaks (peak shifting via drift) is very low. Even for very small populations, with relatively shallow valleys, the chance of a peak shift via drift is very small. This is because the chance of such a shift occurring decreases with population size and depth of valley, but the waiting time to a peak shift grows exponentially with the product of the population size and the depth of valley.

Perhaps the most important objection to peak shift models is that the chances of such shifts are small and, even if they do occur, they yield only trivial reproductive isolation... the probability of a peak shift is proportional to the size of population and depth of valley... the deeper the valley, the smaller the chances of a peak shift...[and] the less gene flow there is. The lesson is clear, while deeper valleys yield greater reproductive isolation, they are less likely to be crossed." (Coyne and Orr, 2004, p. 395)

In other words, the scenario Wright envisions in shifting balance is very implausible.

Small populations are more likely to go extinct than to drift into the vicinity of a more adaptive peak.

In short, the theoretical assumptions supporting the argument for founder effect, one of the most widely taught and well-known models of speciation, is flawed. This is not to say that founder effect does not occur, it simply does not likely occur via the genetic mechanisms that Mayr imagined for it. Looking back, Kimura remarked that the founders of the synthesis were perhaps overzealous; the claims about the genetics of adaptation and speciation were largely unsupported by empirical evidence.

Led by the *Zeitgeist*, a great deal was said about how gene pools of the species are organized and how they change in evolution. However, these were inferences based on observations at the phenotypic level, and in reality, there was no way of actually knowing what is going on in evolution at the level of the internal structure of the gene. As mentioned already, much importance was claimed for epistatic and heterotic gene interactions in fitness. Such terms as integrated gene complex, genetic revolution, cohesion of the gene pool, as well as genetic homeostasis were introduced and accepted by some. But, in my opinion, they were more rhetorical than scientific. (Kimura, 1983, p. 22)

In another striking paper critiquing the adaptive landscape, P.A.P. Moran demonstrated that under a wide variety of circumstances, selection will not drive populations up adaptive peaks, indeed, it can sometimes drive populations down into valleys. As mentioned above, the average fitness of a population (understood as rate of increase) can decrease rather than increase over time for any number of reasons; for instance, when fitnesses are frequency dependent.

In sum, there are a variety of different complaints that one might raise about the adaptive landscape:

1. The adaptive landscape, for both genotypes and whole populations, is not three-dimensional, but multidimensional. As one increases the number of dimensions, one of the central assumptions of Wright – that one cannot arrive at a higher adaptive peak without traversing a valley – turns out to be defeated. That is, as the number of dimensions of the landscape increases, the number of ways one might traverse the landscape without lowering fitness increases substantially.

2. The landscape is most likely not static; it changes in time, either because of changes in the environment, or changes in the actual genetic constitution of the population.
3. As Moran pointed out in 1964, a population in the vicinity of an adaptive peak may not necessarily climb such a peak. Average population fitness can decrease for any number of reasons. Indeed, “populations do not in general tend to maximize their mean fitness if the latter is dependent on more than one locus” (Moran, 1964) (i.e., most of the time). This challenges both Wright’s and Fisher’s views; for, Wright thought that in phase three, population in the vicinity of a new adaptive peak would necessarily climb that peak, and Fisher assumed much the same. But Moran’s discussion challenges all this. Both Fisher and Wright assumed that relative fitnesses depend upon a single variable (the frequency of certain alleles), and that they do not change in time. But, average population fitness frequently depends upon more than one variable that changes in time, e.g. the case of frequency dependent genotypic fitness. The fitness of a population is by no means directly related to the frequencies of various genes.

In light of these objections, some biologists (e.g. Moran) have rejected the notion of adaptive landscapes, in particular, for representing population level change. Others (Gavrilets, 2004), have reformed the concept to consider the possibility of multiple dimensions. Provine writes that the landscape metaphor is “mathematically uninterpretable.” (Provine, 1986) And, more recently, Pigliucci and Kaplan argue that “it may in the end be impossible to articulate the metaphor in a way that is both coherent and conceptually fruitful.” (Pigliucci & Kaplan, 2006) On the other hand, Ruse (1990) argues that it was a “valuable heuristic.” (Ruse, 1996), and Skipper expands on Ruse, explaining that the landscape is “a theory evaluation heuristic for evaluating the dynamical behavior of population genetics models.” (Skipper, 2004) May all these arguments be made consistent?

2. Models and Analogies in Science: Some Lost but not Forgotten History of Philosophy of Science:

What to make of these (apparently) divergent views? I will argue here that there are grains of truth in all of them. First, Provine, Kaplan and Pigliucci are correct (in part). The landscape metaphor is founded on serious misconceptions. However, if we take challenging the assumptions of the metaphor itself playing a role in theory evaluation, then Ruse and Skipper are correct. These apparently competing interpretations of the metaphor are not irreconcilable. One key to understanding how and why these views can be reconciled can be found in the infrequently cited work of Mary Hesse. (Hesse, 1966)

Philosophers of science going back to Duhem have debated the use and abuse of metaphor and analogy in science. Duhem, Braithwaite, Brodbeck, and Nagel all argued that the use of analogy in science had pernicious effects. Duhem wrote that only "Weak minds" such as those of the English require construction or visualization of a mechanical model; one must beware of confusing the model and the theory itself: "The Englishman... finds the use of the model so necessary to the study of physics that to his mind the model ends up being confounded with the very understanding of the theory." (Duhem, 1917, p. 71) In contrast, Campbell, Hesse, Achinstein, Spector, and more recently, Morrison and Morgan, have argued that analogies and metaphor have been central to prediction and explanation.

Hesse's classic (1966) book is an imagined dialogue between a Duhemian and a Campbellian. We might imagine Provine and Kaplan and Pigliucci as Duhemians, and Skipper and Ruse as Campbellians in the exchange over the adaptive landscape. According to Duhem, mechanical models may play at best a meager and problematic role in the progress of physics. Duhem's view did not go unchallenged. In *Physics, the*

Elements, Campbell comes to the defense of the British. He argues that analogies are not mere aids to theory construction, but are essential to explanation and prediction.

Campbell's argument is the following. He took theories to consist in a set of propositions divided into two groups. The first set of propositions, the "hypotheses" are statements incapable of proof or disproof by themselves, or, usually mathematical assumptions simply "defined by postulate." For instance, the sentences "x, y, and z are independent variables," or "a is a constant," would count as the "hypotheses." The second set of propositions, the "dictionary," supplies the theoretical concepts with an interpretation, or defines the theoretical variables and constants and their relations. From these two sets of propositions taken conjointly, an empirical law may be deduced. In a thought experiment intended to disprove the Duhemian, Campbell describes two examples of such "physical theories." The first example is a set of mathematical propositions plus rules for their interpretation that he invents, from which he deduces a (fictional) phenomenal law. The second is Boyle's theory of gases. The first, he says, is not a theory at all: "Any fool" he argues, "can invent a logically satisfactory theory to explain any law."(Campbell, 1920, p. 259) What makes theory "satisfactory," according to Campbell, is that it displays an analogy. A simple set of propositions alone, from which may be deduced a phenomenal law, does not provide an explanation.

In order for a theory to be "valuable," according to Campbell, its laws must "display an analogy" with some known laws. Or, in order to understand some phenomenon in virtue of a theory, we have to understand the hypotheses of the theory in terms of some substantive analogy between the properties of the phenomena to be explained and the properties of some known system: as between the particles of a gas in

motion and a number of infinitely small and highly elastic bodies contained in a cubical box. A theory, to be explanatory, must provide an account of what mechanical properties are the causal basis of the system studied, not simply proffer logically connected propositions from which the phenomenal properties of a system may be deduced.

According to Campbell, to think of analogies as mere aids to theory construction is misguided. Analogies are absolutely essential to the theory being at all meaningful or explanatory:

Analogy, so far from being a help to the establishment of theories, is the greatest hindrance. It is never difficult to find a theory which will explain the laws logically; what is difficult is to find one which will explain them logically and at the same time display the requisite analogy. Nor is it true that, once the theory is developed, the analogy becomes unimportant. If it were found that the analogy were false it would at once lose its value; if it were presented to someone unable to appreciate it, for him the theory would have little value. To regard analogy as an aid to the invention of theories is as absurd as to regard melody as an aid to the composition of sonatas. (Campbell, 1920, p. 130)

Duhem and Campbell are illustrative of two extremes in the debate among philosophers of science in the 1950's and 60's over the role of models in science. On the one hand, the understanding of what models are and how they function was viewed in the context of rational reconstruction of scientific theorizing as a deductive system. A model, on this view, is simply another interpretation of the axioms of some theory, such that model and theory bear a formal relationship to one another in virtue of their common logical structure. Philosophers such as Braithwaite, Nagel and Brodbeck thus contended that the concept of "model" in the empirical sciences may be understood in a single sense, akin to that given in mathematical logic. On the other hand, philosophers such as Hesse, Achinstein, and Spector investigated the nature of analogical models and how they

function in the context of how scientists in fact speak about and use models; i.e., their focus was on the practice of science, and the dynamics of scientific change.

In *Models and Analogies in Science*, Hesse makes an important advance in the discussion by introducing a distinction between “positive,” “neutral” and “negative” analogies. She constructs an imaginary debate between a Duhemian and a Campbellian. “When we take a collection of billiard balls as a model for a gas,” explains the Campbellian, “we are not asserting that billiard balls are in all respects like gas particles.”(Hesse, 1966, p. 8) Positive analogies are just those properties of billiard balls, for instance, that we do want to ascribe to molecules in our statistical model of the properties of a perfect gas. Negative analogies are those respects in which we take it that billiard balls do not resemble gases; for instance, properties such as “hard and shiny” are predicated of billiard balls but not of particles of a gas. Neutral analogies are the most important aspects of a model; these are the respects for which we do not know whether or not the model and the system under study are positively or negatively analogous. In the early stages of theory construction, most of the analogies will be “neutral”; that is, the respects in which the model is like the world are largely unknown. As a theory advances, neutral analogies may be converted into positive or negative analogies. In this respect, Hesse incorporates an appreciation of the dynamics of theory change that Nagel and Braithwaite lack. In Hesse's view, the neutral analogy is “that feature of the model which are its growing points.” Or, it is only in virtue of posited substantive similarities between the theoretical object and the model that a theory may suggest hypotheses, or suggest avenues for growth.

I wish to suggest that appeal to “neutral” analogies in the history of biology were important aspects of their theoretical program. Argument from analogy, where scientists make substantive identities between object modeled and the analogue, is a key tool in the process of generating predictions. Assertion of mere formal analogy, or identity of structure between logical structure of the propositions of the theory and model, may not lead to novel, predictive, and theory-extending suggestions about the properties of the system under study in the same manner. For this, assertions of substantive similarity between properties of the system modeled are required, or so Achinstein has argued:

From an identity in logical form of two sets of statements, nothing can be inferred about the credibility of individual statements in one set from a knowledge of the truth of the statements in the other set. For the credibility, or plausibility, of a set of postulates must be determined by an appeal to content and cannot be ascertained by reference to logical form alone.

.... Those analogies in which objects are described having certain properties physically similar to properties of entities in the theory can provide a plausible foundation for additional theoretical postulates. For if two types of objects are described as physically similar in certain respects this furnishes a basis for supposing that further similarities may be discovered. Such reasoning constitutes an argument from analogy. (Achinstein, 1964, p. 347)

Hesse, Achinstein and Spector thus argued that substantive analogies between properties of the system under study and of some other - often more familiar - system enable scientists to make predictions and extensions of theory.

I take some of the key insights of these latter day proponents of analogy in the sciences to be the following:

- Analogies may be false in some respects and true in others; in Hesse's words, there are positive, negative and neutral respects in which our theory and analogue bear resemblances to one another. It follows that there need not be a conflict in deploying two different analogies in our scientific description; while they may contradict one another in some respects, these respects are not

necessarily the respects in which an analogue can be positive or neutral - the “growing points” of the theory.

- Analogical thinking is not always merely heuristic, but is often intrinsically tied to the process of explanation and prediction in the sciences.
- In light of the above, a theory may not be the same theory when stripped of its analogies.
- There are no unique problems in the deployment of metaphor and analogy in the sciences. Analogy is part and parcel of scientific descriptions.

3. Return to the Present Debate:

In sum, there is no doubt that analogical thinking surely may lead scientists astray. However, it may also lead to substantive predictions, tests, and advances in understanding. It is often in virtue of posited substantive similarities between the theoretical object and the model that a theory is predictive. Moreover, insofar as there are positive, negative and neutral respects in which our theory and analogue bear resemblances to one another, there need not be a conflict in deploying two different analogies in our scientific description; while they may contradict one another in some respects, these respects are not necessarily grounds for treating the theories as contrary.

As a model of adaptive change within populations, the three dimensional landscape has historically been enormously useful. Surely, it's not clear that the fitness of whole populations is adequately represented in three dimensions. Given the variety of different dimensions along which populations can change their genetic constitution, the three dimensional landscape is inadequate. Nonetheless, Wright's metaphor at least suggested a substantive analogy that could be tested, and was found wanting (e.g., for the case of speciation via peak shifting). So, the landscape made possible tests of Wright's

presuppositions: that adaptive change required decline in fitness. The positive, negative, and neutral features of the model are thus:

Positive: Individual fitnesses may be mapped as a function of gene frequency.

Negative: However, population fitnesses do not, in general, increase as a function of allele frequencies, fitness landscapes for whole populations are not static, and are multidimensional.

Neutral: Exploring the multidimensional landscape could yield novel insights into speciation...

Scientific representations are always representations only in some respect or to some degree. The only difference between a mathematical representation (formalism) and the analogical model is that the former has explicit rule-based structure; certain inferences are licensed and not others as a matter of the form of the equations. The value of a representative scheme is determined by its ability to support certain kinds of inferences; e.g. to support hypotheses and predictions that may be falsified. Representations meet the epistemic aims of some domain and can come to shape these aims. As a science makes progress, the representational framework determines which questions are worth asking and how one should go about investigating such questions. Success of a representation or explanation is thus a pragmatic matter; it is dependent on the aims of a particular community. Thus, whether or not to regard the landscape as useful or problematic will hinge in part upon the aims of practitioners, and whether and how their

attempts to generalize this framework lead to useful new predictions in new domains.

In sum, there are at least four purported problems with Adaptive Landscapes:

1. That the landscape is static, rather than changing.
2. That populations in the vicinity of an adaptive peak will tend to “climb” to a new fitness optimum. Average population fitness can decrease. As Moran (1964) pointed out, “populations do not in general tend to maximize their mean fitness if the latter is dependent on more than one locus” (i.e., most of the time). Wright had to assume that relative fitnesses depend upon a single variable (the frequency of certain alleles), and that they do not change in time. But, average population fitness frequently depends upon more than one variable that changes in time, e.g. the case of frequency dependent genotypic fitness. Selection does not necessarily drive populations toward peaks of the landscape described by the mean fitness function.
3. When fitnesses are frequency dependent, it is not necessarily possible to translate dynamic equations into a landscape that represents the force of selection.
4. Generally speaking, the fitness of a whole population is not a direct function of the frequencies of genes in the population.

However, there is a variety of positive ways in which the landscape metaphor influenced research in evolutionary biology. For instance, the study of peak shifting and founder effect; using both a one-locus, two-allele models, and multilocus models, theoretical biologists have been able to demonstrate that the probability of stochastic transitions between fitness peaks (peak shifting via drift) is very low.

In sum, the views of the Duhemians (Kaplan and Piglucci, as well as Provine) on the one hand, and the Campbellians (Skipper and Ruse) can be reconciled. The metaphor does have a variety of disanalogies with the patterns and processes it was intended to illuminate. However, these may usefully be “discharged” in the context of hypothesis testing and prediction. The metaphor has been enormously fruitful at generating questions for further inquiry, and providing substantive hypotheses that have been subject to test. Campbell, and his advocate, Hesse argued that what makes models and analogies useful was the dynamical character of theories; a theory is not static, but is always being

extended and modified to account for new phenomena. Without the analogy, the extensions will be limited. The formal model gives one a framework to build upon, but the advantage of the analogy is that it provides a variety of not entirely rule-bound ways to extend and test the model.

Fisher and Wright used different analogies to speak about the systems they studied, and their disagreements often took place in terms of the proper choice of analogy. Their choice of analogy was in part governed by perceived similarities between properties of the two systems, informed by different background assumptions about the genetic structure of populations. Without sufficient empirical knowledge about the genetic structure of populations, they used analogy to suggest different hypotheses. These analogies are now integrated into population genetic theory. Surely, they have limitations and are being emended, but in the early stages of evolutionary theory, it was difficult to even conceive of evolving populations in population genetic terms without some sort of vision of the field of gene combinations – lumpy, holey, or what have you. Perhaps we do not need to choose.

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