

The rise and fall of the adaptive landscape?

Anya Plutynski

Received: 22 December 2006 / Accepted: 16 July 2008 / Published online: 6 August 2008
© Springer Science+Business Media B.V. 2008

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.

Keywords 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 1990), “...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

A. Plutynski (✉)
University of Utah, 260 S. Central Campus Dr. Rm. 341, Salt Lake City, UT 84112, USA
e-mail: Plutynski@philosophy.utah.edu

metaphor in a way that is both coherent and conceptually fruitful.” (Pigliucci and 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.

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 1986). 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, pp. 358–359)

This mechanism was Wright’s “shifting balance” process of evolution. Evolution of populations to novel adaptive gene combinations required “shifts” across adaptive valleys via the three phase process of drift, inbreeding, intra- and interdemec selection. Three diagrams (Fig. 1) represent different kinds of adaptive change; from left to right, D, E, and F represent the fates of small inbred populations,

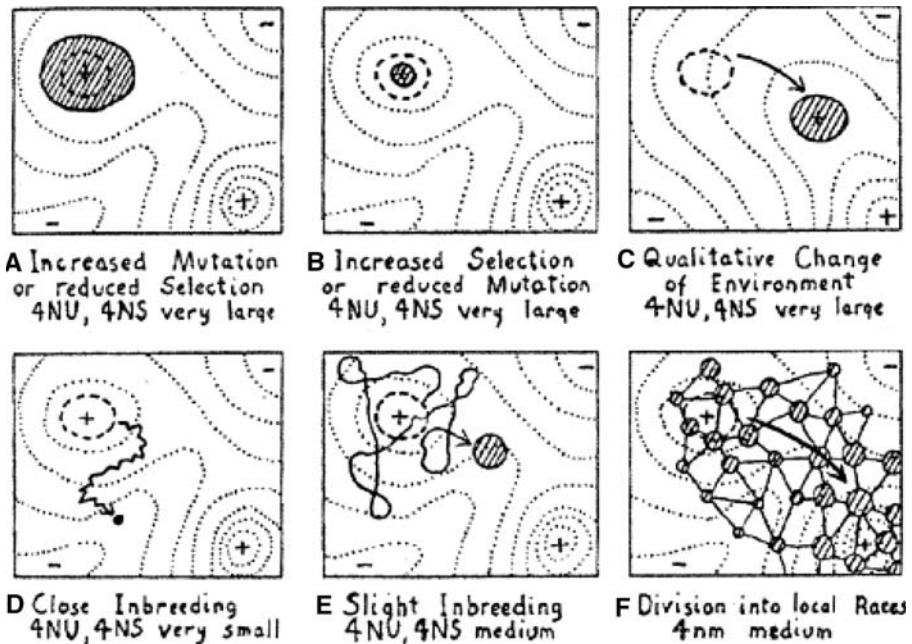


Fig. 1 (a) Increased mutation or reduced selection 4NU, 4NS very large. (b) Increased selection or reduced mutation 4NU, 4NS very large. (c) Qualitative change of environment 4NU, 4NS very large. (d) Close inbreeding 4NU, 4NS very small. (e) Slight inbreeding 4NU, 4NS very medium. (f) Division into local races 4 nm medium

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 Fig. 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 were many

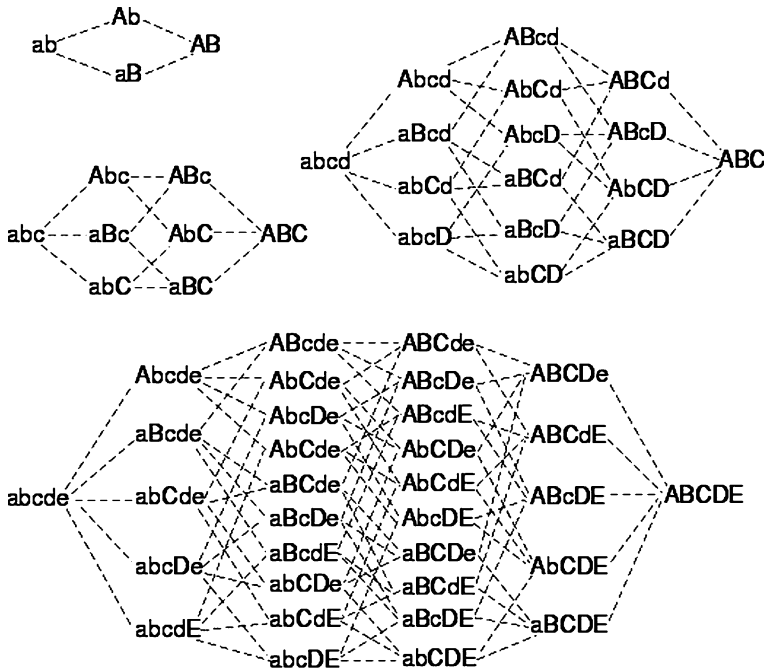


Fig. 2 Wright's representation of increasing dimensions of the fitness landscape

dimensions along which 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)

In short, Wright was very much aware of the limitations of the landscape metaphor. He realized that assumptions he makes for the purposes of representing populations as moving across the landscape—that relative fitnesses are constant in time and that populations are in linkage equilibrium—are violated. Wright acknowledged and explored the consequences of their violation—e.g., for frequency dependent selection—in subsequent papers (1949, 1969). Indeed, in 1969 Wright showed that frequency-dependence can produce situations that cannot be represented by any landscape.

Despite these acknowledged limitations, Wright's image quickly became hugely influential. Dobzhansky used Wright's 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 1937/1951)

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 arguably 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 via drift and intrademic selection, leading to novel gene combinations. 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 in generating non-adaptive differences between species that became popularly associated with Wright (Provine, 1986). 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 1937/1951). 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 1937/1951), (Mayr 1963, pp. 263–264)

Mayr here combines important insights about genetic interaction with speculative views about the extent to which such genetic interaction constrained evolutionary change (e.g., “there must be harmony among all the genes of which a local gene pool is composed”). While he was correct in some part, he appears above to taken the metaphor of genetic interaction or “cohesion” of the genotype to such an extreme that he became rather dogmatic about the necessity for a radical environmental or genetic change for speciation to be possible. Mayr’s 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.

There appear to be many developmental mechanisms and canalizations that prevent gene substitutions from expressing themselves in the phenotype. 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 is 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, popularized 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 led 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. Dobzhansky, as we have seen, represented the landscape as a surface of ecological niches where different species reside, with valleys representing reproductive isolation.

Will Provine (1986) first argued that Wright’s use of the landscape concept was ambiguous and inconsistent. Provine pointed out 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.¹ 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 Fig. 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 (Fig. 4). This is an image of what is called Dobzhansky–Muller incompatibility, where we have two genotypes that are fit in

¹ However, this is not exactly correct. Wright makes assumptions such that when you collapse many dimensions into a few, you get a continuous surface. This assumption was false, but that is a different matter from Provine’s objection.

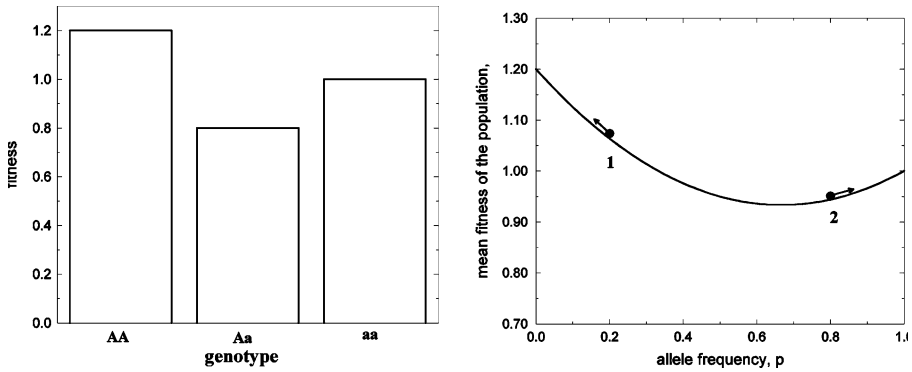


Fig. 3 Landscape for a single locus (Gavrilets 2004)

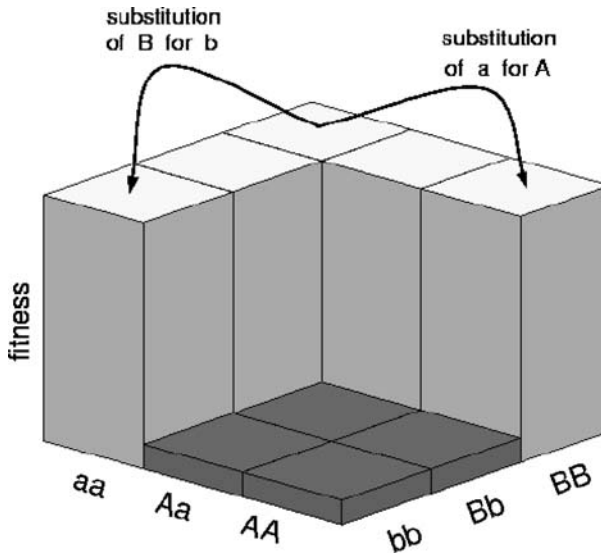


Fig. 4 Landscape for two loci (Gavrilets 2004)

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; a projected trajectory of gene frequency change; 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 the metaphor become apparent. In order to represent populations as

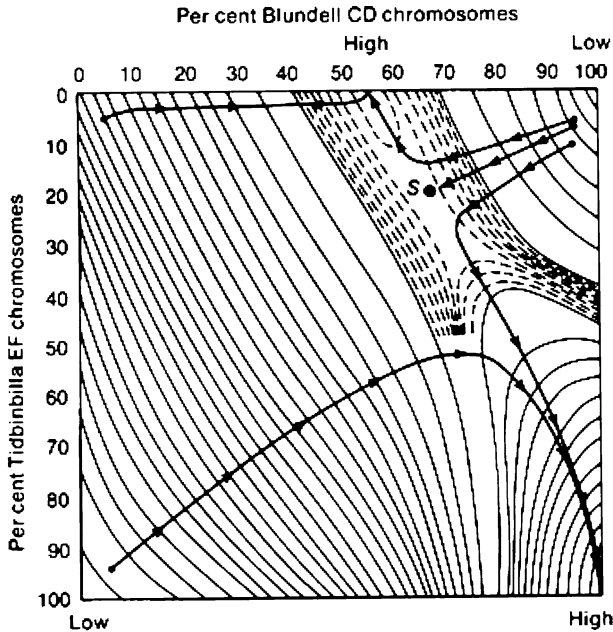


Fig. 5 The theoretical trajectories of gene frequency change in a population of grasshopper (Lewontin and White 1960)

moving across a landscape, Wright needed to make a number of idealizing assumptions: that relative fitnesses remain constant in time, that populations are in linkage equilibrium, and that one can indirectly represent multiple dimensions adequately in two or three dimensions, or that the landscape's surface is "rugged." I.e., he assumes that a 2 or 3D landscape is relevantly similar to a multidimensional landscape.² The "rugged surface" represents how certain genes in combination yield high fitness, separated by "valleys" of gene combinations of lower fitnesses. What happens if these assumptions are violated?

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. Indeed, Wright did consider this. Wright showed (1969) that frequency-dependence can produce situations that cannot be represented in any landscape, rubbery or not.³

Another difficulty is that if multiple alleles contribute to organismic fitness, the landscape will have many more than three dimensions. 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"

² 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.

³ Thanks to Mark Kirkpatrick for bringing this to my attention.

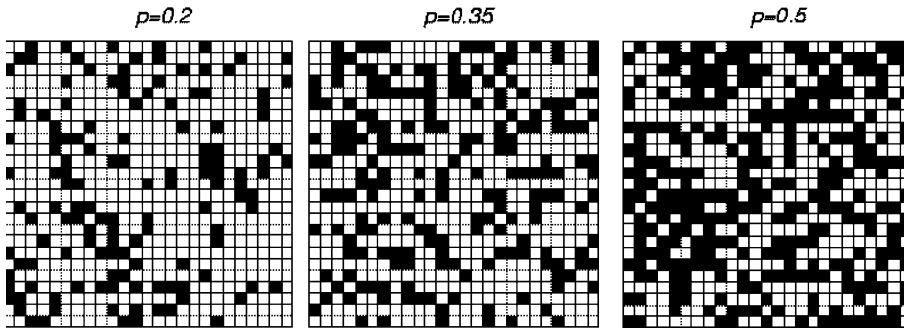


Fig. 6 Gavrilet's Russian Roulette Model, 2004. p = Proportion of black sites (viable genotypes). A "neutral network" is a set of viable genotypes connected via single mutations. As p exceeds a certain threshold, a neutral network extends through the system. Percolation threshold decreases in genotype spaces of high dimensionality

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, Gavrilets argues that there is a high probability that we will get a variety of ridges. Gavrilets calls these "nearly neutral" networks, 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 (Fig. 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.⁴ First, he seems to assume that populations will "hill climb," or increase in fitness. Yet, if we take average population fitness to be the average rate of increase in population size, both Wright and Fisher knew that we should not expect it to increase. 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"?

⁴ Thanks to a reviewer for these comments.

While all of these are legitimate and important questions, what is relevant to the more general question at issue is the following. Gavrillets' reconceptualization of the landscape (and earlier, Coyne, Orr and others' discussions of "ridges" in the landscape) has led many biologists to question some of Wright's, and subsequently, Mayr's presuppositions about genetic interaction and the limits it places on adaptive evolution as well as 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, became enormously influential. Wright's image of the stable, co-evolved gene combinations yielding stable species and populations led many researchers on speciation to equate the problem of speciation as the problem of peak shifting. In other words, the metaphor was a means to framing a hypothesis about speciation; that speciation requires peak shifting. Was this a warranted hypothesis?

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. The hypothesis was mistaken; and, the metaphor proved misleading, but in a constructive way. In other words, the metaphor served as a means for framing and testing a hypothesis about speciation. 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.

To be fair, Wright was well aware of this problem. Wright knew that populations are not always in linkage equilibrium. Moran's example violates this assumption: the population starts in linkage disequilibrium, and it is the decay of linkage disequilibrium by recombination that causes mean fitness to decline. Whenever the landscape involves more than one locus, Wright originally assumed that linkage disequilibrium is negligible. This allows the state of the population to be fully represented by the allele frequencies alone, and implies that recombination won't affect mean fitness or the population's trajectory on the landscape. Of course, recombination is just one of several evolutionary forces that can cause a population's mean fitness to decline. Mutation and migration, for example, can do the same. Wright was also keenly aware of these limitations (see e.g., his 1967 PNAS paper).⁵

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

⁵ Thanks again to Mark Kirkpatrick for pointing this out.

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 and Kaplan, 2006) On the other hand, Ruse (1990) argues that it was a “valuable heuristic.” (Ruse 1990), 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?

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 (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” require construction or visualization of a mechanical model; one must beware of confusing the model and the theory itself. He identified such a weakness with the English temperament: “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 1954, p. 71) In contrast, Campbell, Hesse, Achinstein, Spector, and more recently, Morgan and Morrison (1999), 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:

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)

In other words, for Campbell, the analogy provides a way of extending theory, or setting out the conditions under which the theory may be developed and tested. Analogy provides the "melody," whereby the instrument of the mathematical theory is played. Whatever one thinks of Campbell's account, there is something to be said here about the importance of analogy and metaphor in the history of science. Maxwell, for instance, thought that analogy was enormously important to an

understanding of his theory of gases. Fisher understood his reconciliation of biometry and Mendelism as a product of analogizing evolutionary genetics and statistical mechanics.

Duhem and Campbell are illustrative of two extremes in the debate among philosophers of science in the 1950s and 1960s 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.

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 substantive similarity between properties of the system modeled and an analogue enable the extension of a theory; or, the generation of novel hypotheses, predictions, or suggestions about the properties of the system under study will behave, or so Achinstein has argued:

... 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. (Thus, appeal to the “force” metaphor in discussions of selection and drift may well not be inconsistent with appeals to statistical trends.)
- Analogical thinking is not always merely heuristic, but is often intrinsically tied to the process of explanation and prediction in the sciences.
- Deployment of metaphor and analogy in the sciences is not uniquely problematic; interpretation of analogy is no less problematic, in fact, is arguably less problematic than interpretation of theory absent analogy. Analogy is part and parcel of scientific descriptions.

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. Insofar as it served as a template for testing hypotheses about adaptive change and speciation, it has been a tool for the both explanation and prediction in evolutionary biology. What may be most fair to Wright is to say that the landscape shows how the population responds to selection in the absence of the other forces. Since Wright’s work, there have been several generalizations of his concept that show it’s even more robust than he

realized. These include, for example, its extension to quantitative traits (Lande 1976, 1979), the development of the notion of a quasi-linkage equilibrium (Kimura; Nagylaki; Barton), and the fitness “landscapes” in the area of adaptive dynamics (Metz; Dieckmann). While the adaptive landscape is used as a heuristic by many biologists, it is a quantitative tool for many practicing theoreticians (for a review, see Kirkpatrick and Rousset 2005). Rumors of the demise of the landscape metaphor may be premature!

Surely, it’s not clear that the fitness of whole populations is always adequately represented in three dimensions. Given the variety of different dimensions along which populations can change their genetic constitution, the three dimensional landscape is surely an oversimplification. 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 always 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 tested. 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 (Woody 2004). 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.

There are two ways to view these “problems”—as limitations of the landscape metaphor and reason to reject them, or as respects in which the landscape captures only part, but not all, of the dynamics of evolution in populations. Arguably, the very proposal of the landscape metaphor enabled some of these disanalogies to be discovered. As discussed above, there is a variety of positive ways in which the landscape metaphor influenced research in evolutionary biology.

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.

References

- Achinstein P (1964) Models, analogies and theories. *Philosophy of Science* 31:328–350
 Campbell NR (1920) *Physics: the elements*. Cambridge University Press, Cambridge
 Coyne JA, Orr HA (2004) *Speciation*. Sinauer Associates, Sunderland, Massachusetts
 Dobzhansky T (1937/1951) *Genetics and the origin of species*. Columbia University Press, New York

- Duhem P (1954) The aim and structure of physical theory (trans: Wiener PP). Princeton University Press, Princeton
- Gavrilets S (2004) Fitness landscapes and the origin of species. Princeton University Press, Princeton
- Hesse M (1966) Models and analogies in science. University of Notre Dame Press, Notre Dame, Indiana
- Kimura M (1983) The neutral theory of molecular evolution. Cambridge University Press, Cambridge
- Kirkpatrick M, Rousset F (2005) Wright meets AD: not all landscapes are adaptive. *J Evol Biol* 18:1166–1169
- Lande R (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314–334
- Lande R (1979) Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* 33:402–416
- Lewontin RC (1978) Adaptation. *Sci Am* 239(3):157–169
- Lewontin RC, White MJD (1960) Interaction between inversion polymorphisms of two chromosome pairs in the grasshopper, *Moraba scurra*. *Evolution* 14(1):116–129
- Mayr E (1954) Change of genetic environment and evolution. In: Huxley J, Ford EB (eds) *Evolution as a process*. George Allen and Unwin, Ltd., London, pp 157–180
- Mayr E (1963) *Animal species and evolution*. Belknap Press, Cambridge, MA
- Moran PAP (1964) On the nonexistence of adaptive topographies. *Annu Rev Human Genet Lond* 27:383–393
- Morgan M, Morrison M (1999) Models as mediators: perspectives on natural and social science. Cambridge University Press, Cambridge
- Pigliucci M, Kaplan J (2006) Making sense of evolution: the conceptual foundations of evolutionary biology. University of Chicago Press, Chicago
- Provine W (1986) Sewall Wright and evolutionary biology. University of Chicago Press, Chicago
- Ruse M (1990) Are pictures really necessary? The case of Sewall Wright's adaptive landscapes. In: Fine A, Forbes M, Wessels L (eds) *PSA 1990*. pp 63–77
- Skipper R (2004) The heuristic role of Sewall Wright's 1932 adaptive landscape diagram. In: *Proceedings Philosophy of Science Assoc. 18th Biennial Mtg—PSA 2002: PSA 2002 Symposia*, Milwaukee, WI
- Woody A (2004) More telltale signs: what attention to representation reveals about scientific explanation. *PSA 2002 Proc Philos Sci* 71:780–793
- Wright S (1931) Evolution in Mendelian populations. *Genetics* 16:97–159
- Wright S (1932) The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proc 6th Int Congr Genet* 1:356–366
- Wright S (1949) Adaptation and selection. In: Jepson GL, Simpson GG, Mayr E (eds) *Genetics, paleontology, and evolution*. pp 365–389
- Wright S (1967) “Surfaces” of selective value. *Proc Natl Acad Sci USA* 58:165–172
- Wright S (1969) *Evolution and the genetics of populations, vol 2: the theory of gene frequencies*. University of Chicago Press, Chicago