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The Fitness Landscape Metaphor: Dead but Not Gone

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Résumé : Dans cet article, je présente une approche sémantique de l'analyse de la fonction de la métaphore du paysage dans la biologie de l'évolution. Le concept de paysage adaptatif a suscité une attention considérable dans la philosophie de la biologie récente. La plupart des auteurs ont considéré ce concept de l'une des deux manières suivantes : en tant qu'outil heuristique, comme partie intrinsèque de modèles mathématiques robustes, ou comme un ensemble définissable d'analogies sur lesquelles les modèles sont basés et testés. Chacune de ces visions conduit à la conclusion que la valeur de la métaphore du paysage dépend seulement du succès des modèles que sous-tend la métaphore, en vue de représenter adéquatement la dynamique de l'évolution. J'essaie de montrer que cette conclusion, ainsi que les visions qui y conduisent, ne tiennent pas compte d'épisodes importants dans l'histoire de la métaphore du langage. Ces visions proviennent plutôt de thèses générales, en philosophie des sciences, quant au rôle des métaphores dans les théories scientifiques. L'analyse sémantique que je propose met en lumière le fait que la fonction première du concept de relief adaptatif, au cours de la synthèse évolutionniste, a été de servir de cadre général d'unification conceptuelle, qui a rendu possible la conciliation de phénomènes empiriques hétérogènes. De ce point de vue, la métaphore du paysage est un outil linguistique-théorique qui ne doit pas être abandonné (et qui ne l'est de fait pas) suite à la falsification des modèles construits et interprétés au moyen de la métaphore.

Abstract: In this paper I present a semantic approach to the analysis of the function of the landscape metaphor within evolutionary biology. The concept of adaptive landscape has drawn a considerable attention in recent philosophy of biology. Most writers have treated the concept in one of the following ways: as a heuristic tool, as an intrinsic part of robustly defined mathematical models, or as a definable set of analogies on which models are based and tested.

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All these views lead to the conclusion that the value of the landscape metaphor depends only on the success of the models, which the metaphor underlies, to adequately represent evolutionary dynamics. I have tried to show that this conclusion, and respectively, the views which imply it, do not account for important episodes from the history of the landscape metaphor. These views rather stem from the general views, in philosophy of science, about the role of metaphors in scientific theories. The semantic analysis which I propose reveals that the concept of adaptive reliefs' primary function during the evolutionary synthesis has been to serve as a general unifying conceptual framework which has made possible the theoretical reconciliation of heterogeneous empirical phenomena. From this perspective, the landscape metaphor is a linguistic-theoretical tool which should not be abandoned (and in fact has not been abandoned) after the falsification of the models which have been built and interpreted by means of the metaphor.

1 Introduction

The concept of adaptive landscape was introduced by Sewall Wright, in the early stages of evolutionary synthesis between Mendelian genetics and Darwinian evolutionary theory. Very briefly, the concept presupposes that the interaction between the evolutionary forces and variation due to genetic factors can be represented in one unified framework as a graphic which shares some features with topographic maps; for instance, the fitness values of genetic combinations or genetic frequencies are gradated, and presented as peaks and valleys. Wright's central idea was that a graphic produced in this manner could serve in exploration of the evolutionary dynamics.

However, the concept of adaptive relief was proven to be problematic and attracted a considerable critical attention. The critics of adaptive relief focused mainly on the fact that Wright had proposed its original concept as an illustrative supplement to his already developed mathematical model of how genetic drift and selection can cooperate to produce evolutionary change. But because of the oversimplified nature of the graphic, speculations based only on it and the concept of adaptive landscape led scientists to investigate pseudo-problems. Thus, according to the critics, the most sensible course would be to abandon the metaphor altogether in favor of some more strict formal investigations.

The proponents of the adaptive landscape metaphor, on the other hand, focused on the fact that the metaphor has been a base for plurality of interpretations some of which have overcome the difficulties of Wright's first interpretation, or have been successfully applied to different evolutionary problems like the explanation of the Cambrian explosion [Marshall 2006] and the theoretical modeling of phenotypic variation [Niklas 1994].

In this paper I suggest a semantic approach to the analysis of the functions of the landscape metaphor within evolutionary biology. It is important to make the clarification that *the adaptive landscape* is an umbrella term. It encompasses *the adaptive landscape metaphor* a metaphoric vocabulary used to interpret the *mathematical models* and the *graphical representations*, that illustrate some features of those models. My focus in this paper will be almost exclusively on this metaphoric vocabulary. I think that most of the analyses of the landscape metaphor mirror the three general views about the role of metaphors in science, namely:

1. Scientific metaphors are ornaments of already well-defined mathematical models. Being such an ornament, the landscape metaphor could be abandoned, without loss of content, in favor of more strict mathematical models.
2. Scientific metaphors play a heuristic function in the first stages of theory development but later become superfluous. As such the landscape metaphor could be abandoned, because the modern synthesis has already reached a more mature stage of development.
3. Metaphors are identical to the models that instantiate them, insofar as all scientific metaphors could be reduced to a set of analogies that could be specified in particular models. As such the landscape metaphor is reducible to a set of loosely based models.

However, none of these general views about scientific metaphors fit the case of the adaptive landscape metaphor. Thus by adopting them the critics of the metaphor fail to account for its primary function: *to serve as a general unifying conceptual framework, which has greatly facilitated the synthesis and which still provides a basis for unifying heterogeneous evolutionary phenomena and explanations.*

In order to clarify my point, I'll first outline the history and the main interpretations of the landscape metaphor. Then I'll present the general views about the role of metaphors in science. I'll try to show that the main critical analyses of the landscape metaphor presuppose the general views about the role of metaphors in science, and as a result they overlook their function as a conceptual framework. Finally I'll present an alternative to the general views about the function of scientific metaphors, and explain why it copes better with the case of the landscape metaphor. According to the view I wish to develop, the primary role of scientific metaphors is to set a unifying conceptual framework. That framework consists of a vocabulary for addressing a reality for which no appropriate descriptive tools have been known so far, and of a general heuristics which permits the unification of previously unrelated phenomena and explanations. As a result, I'll propose, that a functional difference can be drawn between the scientific metaphors and models. Scientific metaphors are neither true nor false. Scientific models which are based on them can themselves be true or false, or adequate or inadequate representations of reality. The conceptual vocabulary is relatively independent from the models which are set forward by it.

2 The landscape metaphor: history and developments

Sewall Wright, publicly presented the landscape metaphor for the first time in 1932, during the 6th International congress on genetics. Wright was asked to present his ideas in a short form, and to keep his mathematical demonstrations at minimum, so he used the metaphor as an illustration to his already developed mathematical model [Wright 1932].

However, the earliest known variant of his landscape metaphor appeared a year earlier (February 3, 1931) in a letter to Fisher [Provine 1986, 271–273].

In this letter Wright discussed his shifting balance theory of evolution, pointing out that the field of gene frequencies can be represented in a multi-dimensional space with an extra-dimension corresponding to fitness. He visualized the multi-dimensional space by the following two-dimensional graphic:

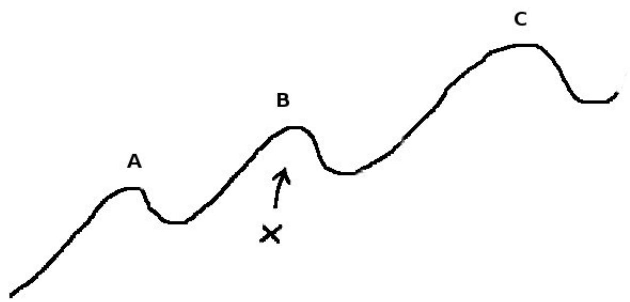

FIGURE 1: 2D adaptive relief, redrawn from Wright's letter to Fisher — February 3, 1931, [Provine 1986, 272]

Wright explained the evolutionary factors that can draw a system of gene frequencies "uphill" (that is toward increased fitness), using the graphic. He outlined 4 factors:

1. Environmental change which is a change in the adaptive relief.

2. Mutations, creating new dimensions and occasionally new paths of advance uphill.
3. Random drift in small populations or exploration of adaptive relief. Incidentally, a population might stumble to a new positive genotype which will become fixed under selection, thus pushing the population uphill.
4. Subdivision of species into many small, not quite completely isolated groups.

One such group can be presented at point B. It will drift between A and C, because of the random sampling (genetic drift). Once it reaches the "slope" of C, the increased fitness will carry it uphill. This will lead to increased number of surviving offsprings and the population will become the major source of migrants to other groups. Since C is the highest peak, it will become the standard for this species. The key concepts of evolution, as envisioned by Wright's shifting balance theory, were already in the letter presented in a rudimentary form with the help of the landscape metaphor. Thus at the next year's congress of genetics, Wright merely articulated the metaphor in a more elaborated form.

There he famously presented the problem of evolution in the following way:

> The 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. In order that this may occur, 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. To evolve, the species must not be under strict control of natural selection. Is there such a trial and error mechanism? [Wright 1932, 360]

The answer which he gives is that the most favorable evolutionary scenario is subdivision of the species in small semi-isolated populations in which selection and genetic drift might co-operate providing conservation for the favorable genotypes and new genetic combinations which might be tested for their adaptive value.

Wright's presentation was a great success and his metaphor became the core of one of the most important works for the synthesis: Dobzhansky's *Genetics and the origin of species* [Dobzhansky 1937, 102–105]. Dobzhansky was a "field" biologist as opposed to Wright's theoretical approach. These two scientists found convenient to use the "landscape" metaphor to communicate their own research. Their collaborative scientific work could be used as an example of the spirit of the synthesis as well as an illustration of the communicative role of the landscape metaphor.

The interpretations of the metaphor increased. Literally every major figure during the synthesis adopted some understanding of the adaptive landscape that fitted his views on evolutionary dynamics.

Fisher, for instance, adopted a single peak adaptive relief because he suspected that as the dimensions increase, the local peaks in lower dimensions will tend to become saddle points in higher dimensions. In this case, natural selection will be able to move the population to the global peak without any need for genetic drift or other factors. Even though, situations with a single global peak that can be reached by selection alone proved to be exception rather than the rule, the single peak-metaphor still remains a useful model for studying problems such as the levels and the structure of genetic variation maintained by mutation [Gavrilets 2004, 38].

The landscape metaphor played also an important unificatory role during the synthesis. This point could be exemplified by the work of Simpson who also used the metaphor in his *Tempo and mode of evolution*, but he interpreted the landscape not as constructed from genotypes or genetic frequency, but from phenotypic traits. His project was to unify (or reduce) paleontology with population genetics [Simpson 1944], [Gould 2002, 528–531]. His interpretation also might serve to exemplify the point that on the onset the landscape metaphor was not confined to a single model or theory but proliferated to other fields like paleontology.

However, Wirght's idea did not remain unproblematic. Wright used the concept to present an adaptive landscape populated by genetic combinations and genetic frequencies. He used the two variants of the adaptive landscape as interchangeable although they are not wholly mathematically compatible [Gavrilets 2004, 69–76].

Further theoretical studies of Wright's model had also shown another problem. If the adaptive landscape contains peaks and valleys, the problem of peak-shift proves to be solvable only in very limited circumstances, thus it could not be the general mechanism of species formation as Wright envisioned it [Gavrilets 2004, 69–76].

In a more influential paper, Coyne, Barton & Turelli showed that the shifting balance theory does not have any compelling empirical support. On the contrary the authors claim that most of the cases which Wright interpreted as a support to his theory are better explained by Fisherman's mass selection [Coyne, Barton *et al.* 1997, 664].

However the falsification of the original shifting balance theory has not led to the abandonment of the adaptive landscape metaphor. And this fact supports the view that, the concept of adaptive landscape is largely independent from its particular interpretations.

In a recent study Sergey Gavrilets re-interpreted the concept of adaptive landscape in order to mend the flaws in Wright's original model. He presented the adaptive relief as a multidimensional surface which could be graphically represented as a flat holey plane. In his variant, fitness is normalized between zero (nonviable) and one (viable). Thus the genotypes of equal or nearly equal fitness form a "net" through the genotypic space. The "holes" represent parts of the genotypic space where there are more densely situated deleterious mutations with fewer viable combinations among them. The process of species formation is presented as a movement on the neutral net. Because the simple shifts in the genotype will eventually lead to sexual isolation. Gavrilets' variant overcomes the peak-shift problem which plagued earlier interpretations [Gavrilets 2004, 100–114].

The landscape metaphor did not remain confined only in population genetics. As we have already stated, one of its earliest incarnations was made by Simpson to designate phenotypic variation. This interpretation remains in circulation today and has been re-rejuvenated by the work of Niklas to model morphological diversity in plants [Niklas 1994].

Expounding on the work of Niklas, Marshall applies the concept of adaptive landscape explicitly as a conceptual framework which unifies in one consistent picture the existing explanations of Cambrian explosion [Marshall 2006, 355–384]. In short, he utilizes the phenotype variant of the adaptive landscape to demonstrate that the rapid diversification of forms is caused by the interaction between the variations due to the existing genetic basis for bilateral development, with the increased number of needs the organisms had to satisfy as a result from the development of complex ecological interactions, such as predation.

This short and by no means complete survey of the interpretations of the landscape metaphor is sufficient to demonstrate its rich history and its prolific applications to quite different problems within evolutionary biology.

The preliminary conclusion which we might draw is that all those interpretations would not be possible if the landscape metaphor was related only to Wright's shifting balance theory.

The methodological critics of the adaptive landscape concept, however, presuppose that scientific metaphors are reducible to a set of analogies, or are mere ornaments facilitating understanding. Thus they focus on the problematic aspects of Wright's notion of fitness landscape and his shifting balance theory or on the problems of constructing precise graphics of evolutionary mathematical models. The general conclusion which they draw, in most cases, is that the concept of adaptive landscape could be abandoned in favor of rigid mathematical models. I shall try to demonstrate that these views are misled by the general understanding about the functions of scientific metaphors. Thus my next task will be to overview the understandings about the functions of scientific metaphors that have dominated philosophy of science in the last years.

3 Metaphors in science

According to the substitution view, which is one of the general views about scientific metaphors, metaphors have no serious place in scientific discourse. They can be used only as rhetoric ornaments, or for educational purposes.

The reason behind it is that metaphorical statements are literally false thus expressing a deviation of meaning. The consequence is that they can't be vigorously verified as declarative statements of facts. If metaphors are ever to be found in scientific texts, it must be possible in any moment to substitute them with literal paraphrases, without any loss of content.

With the fall of classical positivism, however, this view was abandoned in favor of the substantial view. The roots of the substantial view lie in the work of Max Black and it was later developed mainly by Richard Boyd and Marry Hesse. According to it, metaphors could have a positive place in science because:

1. They are introduced to address new aspects of reality which are the aim of the investigation and for which no literal descriptions yet exist; thus metaphors fill "vocabulary gaps".
2. They are a source of analogies which can be precisely investigated by setting them in scientific models.

The position of Max Black [Black 1993, 19–42] is that the primary function of scientific metaphors is heuristic. The metaphor lets its referent to be investigated as a projection of implications common for the literal meaning of the phrase. In this way, some possible features of similarity and analogy between the second and the primary subject of the metaphor become apparent. Since those features might be typically in the background when the object is referred to by the literal expression, or there might be no suitable literal expression to begin with, metaphors can give an irreplaceable insight on how things really are.

The drawback is that the complex of common implications is not limited in any way, so the metaphor trades its fixed meaning for open-endedness. According to Black, this proves to be a limitation in scientific discourse because its central aim is exactly the opposite: the formation of empirically testable sentences. In this case the conclusion that Black draws is justified: metaphors can be used only in the initial phases of theory construction as a heuristic tool. Later they must be replaced by strict testable models.

Richard Boyd builds up on that but he emphasizes that there are important cases of metaphors in relatively mature sciences. His thesis is that some metaphors have a theory constructive function [Boyd 1993, 481–533]. He tries to find what kind of mechanisms might let metaphors to persist in theory development beyond the initial heuristic phase.

Boyd suggested that metaphors are usually born as a consequence of an "informed guess", a suggestion of analogies between a known system and the system which is to be investigated. Thus metaphorical open-endedness is not always a limitation. It expresses the need for precise fit between scientific language and the causal structure of the world. Boyd's position is that the investigation of analogies and similarities will eventually reveal the real categories of phenomena, which will be expressed as metaphor's open-endedness is exhausted. As scientific research progresses, the metaphor "dies", because all the aspects of similarity and analogy have been explained. The result is a precise description of the phenomena via the vocabulary introduced initially by the metaphor.

It is important to note that scientific metaphors can also be rejected on the basis that the aspects of similarity and analogy relevant to the theory are to be found incorrect, or that the metaphor will be found to have no unique referent. We may conclude that Boyd's view is that metaphors have substantial heuristic role.

The addition which Marry Hesse [Hesse 1970] does to the substantial view is that the metaphor's function is reducible to that of scientific models. In turn, models can be summarized as a list of positive, negative, and neutral analogies. The negative analogies are features of dissimilarity, positive analogies are features of similarity, and neutral analogies are features of phenomena that are yet to be investigated. Scientific models owe their predictive power to the latter.

In the next paragraph I demonstrate that the present views are mirrored by the methodological critiques of the landscape metaphor and that's why these critiques could not adequately account for the actual usage of the landscape metaphor in evolutionary biology. According to my analysis, the metaphor has been mainly used as a conceptual framework facilitating the unification of heterogeneous evolutionary phenomena. This function could be explained only if we accept the idea that scientific metaphors do not relate to a fixed secondary meaning. The "open-endedness" of the landscape metaphor made possible the advance of new interpretations after the falsification of the primary model of Sewall Wright.

4 The critics of the landscape metaphor

The first serious critique of the landscape metaphor mirrored the substitution view. It was made by Provine in his biography of Wright [Provine 1986, 308–317]. There he defended the idea that the only function the adaptive landscape concept have is to facilitate understanding of Wright's formal model. But since there exist at least two variants of the metaphor that can be expressed with the same graphical representation and discussed in the same terms (the adaptive landscape constructed by grading genetic combinations and genetic frequencies) and those variants are not completely mathematically equivalent, the metaphor taken by itself leads to a confusion.

Provine argued further that the graphical representations of the adaptive landscape populated by genetic combinations are even more confusing, because the genetic combinations are discrete entities, and the graphic represents them on a continuous surface. Thus he concluded that since Wright's shifting balance theory is already well-defined in precise mathematical terms, it does not depend on the usefulness of the landscape metaphor.

This critical position is further developed by Jonathan Kaplan. According to him, Wright's main idea was that the interpretations based on the graphics alone can help to reach important conclusions about evolutionary dynamics [Kaplan 2008, 627]. However, the errors in constructing the graphic of the adaptive landscape and the verbal speculation based on the metaphor led biologists to investigate pseudo-problems like the "peak-shift problem".

Kaplan also discussed the model of Gavrilets, which aims to mend the flaws in Wright's shifting balance theory. He notes that interpretations based solely on the graphics or on verbal speculations with his interpretation could also lead to erroneous conclusions, because the graphics and the supporting concepts of the adaptive landscape again are oversimplifications of his otherwise rigid formal model. Thus he concludes also that:

> it is time to give up the pictorial metaphor of the landscape entirely and rely instead on the results of formal modeling, however difficult such results are to understand in "intuitive" terms. [Kaplan 2008, 625]

A more positive interpretation of the adaptive landscape as a rhetoric tool is due to Jean Gayon [Gayon 1998, 321–355]. According to him the metaphor in its original form has been developed by Wright mainly, as a rhetoric tool, to criticize Fisher's fundamental theorem. Wright never intended the "adaptive landscape" as a center to a rigidly defined mathematical model. Thus he never precisely defined the "peaks" in a parameter space, which he expressed as formed both of "gene combinations" and "gene frequencies". Wright's main aim was to show that since multiple adaptive peaks could represent multiple possible adaptive optima, Fisher's fundamental theorem explained only the behaviour of the populations when they are already in the vicinity of an adaptive peak. Thus Wright's own shifting balance theory presented a more general view of speciation.

The critique of the metaphor based on the idea that it has only ornamental value could be met by the actual history of the metaphor in which, as we have seen, the concept received multiple interpretations some of which are not related directly to the graphical representations and have a clear explanatory power. For instance, in Marshall's analysis of the causes for the Cambrian explosion, the concept of adaptive landscape is used to order the existing explanations in one unified framework. Moreover, the concept itself could not be erroneous or flawed; but its interpretations in particular models could be good or bad representations of the evolutionary dynamics. Finally the notions of "peaks", "valleys", "random walks", "changes in the relief" in fact could be defined in a mathematically precise matter, as recent formal research in evolutionary algorithms shows [Richter 2010, 409–447].

The idea that scientific metaphors function as heuristic tools in the case of the landscape metaphor is exemplified by the analyses of Michael Ruse and Massimo Pigliucci.

According to Ruse, the concept of adaptive landscape is not necessarily related to Wright's mathematical model because it has found numerous interpretations during the synthesis [Ruse 1996, 75]. These interpretations, in turn, were possible because of the metaphor's open-endedness, which served as a heuristic basis for inferring testable hypotheses.

In a more recent work Pigliucci makes an overview of the interpretations of the metaphor, having in mind the same idea—that the metaphor's interpretations should be judged according to their heuristic value; but the actual tools that bring significant scientific results are the underlined mathematical models [Pigliucci 2013, 26–32].

The view of Max Black as an approach to the functions of the landscape metaphor is more susceptible to its many interpretations. As a result the analysis of Ruse and Pigliucci is historically more accurate. But by focusing only on the heuristic function they overlook the fact that the concept of adaptive landscape provides a vocabulary and an approach in modeling and explaining the complex phenomena of evolution.

Both views, that the adaptive landscape concept is a heuristic tool or a rhetoric ornament, have in common the idea that the underlined mathematical models are somehow the most important vehicle of scientific progress. This idea disregards the fact that there is no other way to make the assumptions and consequences of mathematical models intelligible, but using additional concepts, explaining their precise place and meaning in the general theory. Any mathematical model in evolutionary biology represents some relationship between magnitudes of known evolutionary factors. Without a general conceptual framework which unites them, the mathematical models can't be clarified and united. The concept of genotype space which is the essence of the landscape metaphor is an example of such a framework. It presents a pattern for the analysis of the relationships between the forces which "shape" the genotype space—natural selection, genetic drift, mutation, migration, sexual isolation etc. In turn, those relationships can be presented more rigidly by landscape based models.

The third approach treating scientific metaphors as a source of analogies on which models are based finds place in the work of Anya Plutynski, Robert Skipper, Michael Dietrich and Brett Calcott.

Anya Plutynski explicitly bases her analysis on the Hesse's views about scientific metaphors [Plutynski 2008, 617]. Plutynski defends the position that a complex phenomenon as species formation could be investigated only with the help of idealized models which focus only on some of the relevant factors. The landscape metaphor presented such an approach, and has played a heuristic function during the synthesis, because it proposed an analogy which could be tested. The peak shift problem was rooted in the similarity between adaptive landscape and geographic relief. It presupposes the existence of adaptive peaks which require the populations to traverse "areas" of lower fitness or adaptive valleys. The analogy between the fitness landscape and the geographic relief is obvious: in mountains we must always pass valleys in order to reach new peaks.

However the peak shift problem proved to be based on a negative analogy. The reason why the landscape metaphor was not falsified, according to Plutynski, is that Gavrilets' variant still provides new "neutral analogies"—the dynamics on his neutral relief could prove to bring new insights on evolution. The conclusion she makes is that since evolutionary biology at present does not have a new better approach to investigate the relationship between individual adaptation and genetic frequencies, the claims for the removal of the metaphor are hastened.

This point is further exemplified by the work of Robert Skipper & Michael Dietrich. According to them the adaptive landscape metaphor serves a heuristic function, which depends on the analogy with actual hilly landscapes and their representation as topographical maps [Skipper & Dietrich 2013, 18]. This in turn permits the graphic representation to have a dual function: a didactic function for the underlined mathematical model and a heuristic function for imagining how the represented system might behave [Skipper & Dietrich 2013, 23].

This type of analysis has one limitation: by focusing on analogies, we disregard the fact that some of the successful interpretations of the adaptive landscape concept are not at all based on examination of literal similarities. Gavrilets' variant does not display any meaningful metaphoric similarities. His interpretation of the adaptive landscape concept is defined mostly by his formal model. Thus the metaphoric terms which he employs as holes and neutral networks do not designate analogies but are details of his formal model. The metaphor itself does not provide a correct approach or accurate description of evolutionary phenomena based on analogies and similarities.

In this case it seems possible to examine the landscape metaphor as a group of weakly related models and to avoid the whole semantic debate about the function of scientific metaphors. The position of Brett Calcott follows similar ideas. According to him, the landscape metaphor is simply a family of models which address different evolutionary problems. In his view, no interpretation could claim universal validity or application [Calcott 2008, 640]. The idea that adaptive landscape models have a limited validity is close to the idea that I wish to develop in the next paragraph: that the landscape metaphor functions as a unifying conceptual framework. According to Calcott, the only difference between scientific models and scientific metaphors is based on the degree of accuracy in defining the meaning of scientific metaphors and defining what models signify. Since both can be more or less precisely defined, the difference between them could be neglected. Thus the landscape metaphor could be analyzed as a group of loosely based models. However, we should bear in mind that if evolutionary models use radically different conceptual apparatuses, their unification under a general theory will be very difficult. Calcott's analysis could serve to show that models aim at solving particular problems. The common conceptual vocabulary that is their base has a wider unificatory role.

5 The landscape metaphor as a conceptual framework

As we have seen so far, all the methodological critiques of the landscape metaphor presuppose one or another general view about scientific metaphors. Neither of the adopted general views, however, can adequately account for the history of the concept of adaptive relief or for its current uses.

The radical shifts in interpretation concerning different problems like population dynamics (Wright's original study), species formation (Gavrilets) and phenotypic variation (Simpson, Niklas and Marshall) are possible only if the concept of "fitness landscape" is taken to be relatively independent from the model which was first exemplified with its help. This in turn signifies that the concept of adaptive landscape is not confined to a rhetoric figure which illustrates a formal model, nor to a particular heuristic pattern, or to a set of testable analogies.

The reason for the prolific use of the metaphor in modern evolutionary theory, I think, is that the concept of adaptive landscape provides an invaluable unifying conceptual framework which could be specified to accommodate various evolutionary models which unify several previously separately studied evolutionary phenomena in order to investigate their relationships. Moreover, the concept was used in its more loose non-mathematically defined form to construct unified explanations of concrete evolutionary episodes like the evolution of the horse [Simpson 1944, 89–93] and the Cambrian explosion (Marshall). The latter are additional examples of metaphor's more general usage which is relatively independent from any concrete mathematical models.

Further evidence in support to this view is the recent theoretical research into evolutionary algorithms [Richter 2010], which has shown that the adaptive landscape could be defined in a mathematically precise matter in its more complex form as a dynamic adaptive landscape. Thus the theoretical research in dynamic systems could be integrated successfully within the adaptive landscape framework. Of course models using evolutionary algorithms on the adaptive landscape remain largely theoretical but their development might be a step in the right direction of the analysis of the evolutionary dynamics of real biologic populations.

Finally a recently published volume [Svensson & Calsbeek 2013] dedicated to the many applications of the adaptive landscape, has made plain the fact that the adaptive landscape has not outlived its usages and it is perhaps an indispensable element in some fields of evolutionary biology such as evolutionary genetics, ecological theory of adaptive radiation and ecological speciation.

For our purposes however the history of the development of the adaptive landscape metaphor can be used to draw a new conclusion about some theory-constructive scientific metaphors. Their primary function is to set a unifying conceptual framework. That framework consists of a vocabulary for addressing a reality for which no appropriate descriptive tools have been known so far; and of a general heuristics which permits unification of previously unrelated phenomena and explanations. This view implies that there is a functional difference between scientific metaphors and models. Scientific metaphors are neither true nor false. Scientific models which are based on them can themselves be true or false, or adequate or inadequate representations of reality. That means that the conceptual vocabulary is relatively independent from the models which are set forward by it.

The landscape metaphor is a good example for such a conceptual framework. It was introduced during the early stages of the evolutionary synthesis when it served as a heuristic tool. But it did not only provided a graphical representation and a model of evolutionary dynamics but a common dictionary for describing relations between evolutionary phenomena (such as variation and inheritance) which were previously treated as unrelated by the early and confronting theories of genetics and evolutionary biology.

Keeping such a common framework is important. If we use several unrelated models each with its specific vocabulary addressing different evolutionary problems such as morphological diversity and species formation, the unification under one theory will be harder, if possible at all. But if we use a common conceptual framework to interpret all the different models that have been suggested, the achievement of unification and consensus will be significantly easier.

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