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NEW BIOLOGICAL BOOKS

The aim of this section is to give brief indications of the character, content, and cost of new books in the various fields of biology. More books are received by The Quarterly *than can be reviewed critically. All submitted books, however, are carefully considered for originality, timeliness, and reader interest, and we make every effort to find a competent and conscientious reviewer for each book selected for review.*

Of those books that are selected for consideration, some are merely listed, others are given brief notice, most receive critical reviews, and a few are featured in lead reviews. Listings, *without comments, are mainly to inform the reader that the books have appeared; examples are books whose titles are self-explanatory, such as dictionaries and taxonomic revisions, or that are reprints of earlier publications, or are new editions of well-established works.* Unsigned brief notices, *written by one of the editors, may be given to such works as anthologies or symposium volumes that are organized in a fashion that makes it possible to comment meaningfully on them.* Regular reviews *are more extensive evaluations and are signed by the reviwers. The longer* lead reviews *consider books of special significance. Each volume reviewed becomes the property of the reviewer. Most books not reviewed are donated to libraries at Stony Brook University or other appropriate recipient.*

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ADAPTIVE LANDSCAPES, PHENOTYPIC SPACE, AND THE POWER OF METAPHORS

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A review of
THE GEOMETRY OF EVOLUTION: ADAPTIVE LANDSCAPES AND THEORETICAL MORPHOSPACES.
By George R. McGhee, Jr. Cambridge and New York: Cambridge University Press. $75.00. xii + 200 p.; ill.; index. ISBN: 0-521-84942-X. 2007.

Metaphors play a crucial role in both science in particular and human discourse in general. Plato's story of the cave—about people shackled to a wall and incapable of perceiving the world as it really is—has stimulated thinking about epistemology and the nature of reality for more than two millennia. But metaphors can also be misleading: being too taken with Plato's story has cost philosophers endless discussions about how to access the world "as it is," until Kant showed us that it is just not going to happen, ever.

There are few metaphors in evolutionary biology more powerful and widespread than that of adaptive landscapes—with the exception of course of natural selection itself. The idea of adaptive landscapes was introduced

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by Sewall Wright in 1931, originally presented as a visual aid to get biologists to think about evolution from a genetic perspective without dwelling too much on the underlying math (Wright's advisor knew that many biologists are more comfortable with pictures than numbers, a situation that has not changed much to this day). An adaptive landscape is often represented as a field of gene combinations (genotypes), characterized by "peaks" and "valleys" corresponding to the level of fitness (respectively high and low) of each particular combination of genotypes. The idea is that by drawing two- and three-dimensional "landscapes" of this sort (where one dimension is always fitness) one can begin to visualize how evolution works: if a population finds itself away from a peak, there will be directional selection to move it toward the nearest peak; if, instead, the population already sits near a peak, there will be stabilizing selection to keep it there; and so on.

Wright's advisor was correct: biologists really took to the metaphor and ran with it. Too fast and too far, as it turns out. For the last several decades, "adaptive landscape" (and the closely related, though in fact conceptually distinct "fitness landscape") have been used to model individual genotypes, populations of genotypes, and even phenotypes. Biologists have often implicitly assumed that moving from individuals to populations, or from genotypes to phenotypes, represented straightforward extensions of the metaphor, but that turned out far from being the case. Except in very rare instances, we do not have access to genotype-phenotype "mapping functions" that allow us to move freely between levels, and even going from individual-based models to population-level analyses of landscapes is fraught with both theoretical and empirical obstacles (some of these problems are discussed in detail in Pigliucci and Kaplan 2006). To make things even more dicey, as Richard Lewontin pointed out, adaptive landscapes change all the time: not only for the obvious (but usually neglected) reason that the environment changes (which means that whatever fitness a given combination of genes might have had may not stay the same), but because organisms themselves alter the landscape by virtue of their very own evolution (Lewontin 1978). The image that Lewontin famously presented was of a rubbery landscape that changes shape while populations are trumping on it.

Moreover, Wright knew very well that "real" landscapes are highly multidimensional, not just limited to the two or three dimensions that allow graphical representations. But the assumption had been for a long time that more dimensions, while complicating the quantitative-mathematical aspects of these models, would be characterized by similar dynamics, a crucial point if adaptive landscapes were to play any significant role in evolutionary theory. Alas, work by Sergey Gavrilets (1997) during the past decade has shown that this is not the case: highly multidimensional landscapes display completely different behaviors from low dimensional ones, so much so that old problems such as "peak shifts" (how does a population move from one adaptive peak to another, without having to pass through a maladaptive valley?) actually dissolve in highly dimensional landscapes. It turns out that there are no such things as peaks and valleys, but rather hyperplanes of near-equal fitness, "holey" areas of low fitness, and "extra-dimensional" bypasses allowing populations to go from one area of the landscape to a very distant one without having to cross the middle.

Contrast all of the above with yet another metaphor, this one—as it turns out—much more useful: the idea of "phenotypic space" introduced by paleontologist David Raup in 1966. A phenotypic space is a representation of either a theoretical or an empirical space identified by parameters that define observable phenotypes in a given species or group of species. Raup's famous example is a three-dimensional space defined by the parameters of a growth curve that can generate all possible morphological variants of shell shapes (there are other examples, such as Karl Niklas's simulations of the morphospace of plant architectures). Phenotypic spaces are conceptual tools to help researchers ask (and answer) questions about the distribution of organismic forms, and—particularly—why certain theoretically possible phenotypes do not actually occur, or are found rarely. Because phenotypic spaces ignore the genetic level of analysis, they do not need to rely on hard to obtain knowledge about genotype-phenotype mapping functions; moreover, although phenotypes can of course be very complex, aspects of them can be fruitfully analyzed in a low number of dimensions, which avoids most of the above-mentioned problems with adaptive landscapes.

All of this is necessary to understand the contribution made by George McGhee with his volume, *The Geometry of Evolution: Adaptive Landscapes and Theoretical Morphospaces*. The first third of the book is devoted to Wright-type adaptive landscapes, while the remaining two-thirds deal with Raup-style phenotypic spaces. The author makes a mighty attempt to connect the two and present them as being logically continuous: on the one hand, adaptive landscapes serve to model genetic aspects of evolution, as affected by natural selection, genetic drift, and mutation frequencies; phenotypic spaces, on the other hand, provide us with insights into the interplay between selection and developmental constraints, as well as into the effects of what the author calls "geometrical" constraints (basically, limits on organismal shape imposed by fundamental considerations of biophysics and geometry), and what he refers to as "phylogenetic" constraints (more on this in a moment).

McGhee's program is tempting, but destined to partial failure because of the problems with the whole idea of adaptive landscapes briefly outlined above. The adaptive landscape metaphor is simply too fraught with conceptual problems to be of much use, and it has been since the beginning. Indeed, it is an amazing testimony to the appeal of metaphors to the human mind to see how many biologists still invest a significant part of their time and resources to make sense of adaptive landscapes. This is not to say, of course, that Wright had not identified a significant problem for evolutionary theory to tackle: it is, in fact, interesting to think about what possibilities (and limitations) are imposed on adaptive evolution by what Wright called "the existing field of gene combinations." This is the general question of genetic constraints, which has been tackled by Stuart Kauffman, Sergey Gavrilets, and others, regardless of whether they were using the landscape metaphor or not.

Yet, what McGhee seems to be genuinely interested in, judging from how much discussion he devotes to it in the book, is the concept of phenotypic space. Indeed, that is where tractability is highest, as it is clear from the several intriguing examples that are presented in some detail. For instance, in Chapter 5, McGhee follows up on the work by Raup on ammonoids that he had discussed earlier. Raup had shown that some ammonoid shell shapes are particularly frequent in the fossil record, while others are never found. The question, as always in the study of phenotypic spaces, is: Are the empty areas empty because those forms are selected against? Or because the developmental/genetic system of the organisms in question somehow does not allow them to generate certain forms? Or is this the result of chance events, what Stephen Jay Gould famously referred to as the role of contingency in the evolution of life? One of Raup's graduate students, John Chamberlain, helped by providing an elegant answer to the question in the specific case of ammonoid shells: by experimentally studying the drag coefficient of various shapes, he found that there should be an adaptive peak corresponding to shells with whorl overlap, which have a lower drag coefficient than other forms. Sure enough, the phenotypic space surrounding that peak has been occupied by a large number of actual species of ammonoids, consistent with the conclusion that natural selection for hydrodynamic properties played a major role. The intriguing thing, however, was the existence of a second adaptive peak, apparently empty! What was going on there? It took 40 more years of paleontological research to figure it out, until Saunders, Work, and Nikolaeva showed—based on a much larger database than the one available to Raup and Chamberlain—that, in fact, the second peak has also been colonized by ammonoids during the history of the group. The apparently "empty" space was an artifact of an incomplete fossil record, just as Darwin had predicted to be generally the case.

The kind of results produced by the work on ammonoids, and similar ones detailed by McGhee on bivalves, brachiopods, and plants, constitute the really exciting part of the book. One can see how detective work done by biologists comparing theoretical expectations and empirical findings yields explanations of complex patterns. This is much more than has ever been produced in the study of adaptive landscapes, with one exception: research on the evolution of protein function. But this exception tells us exactly why McGhee's hopes of conceptually conjoining adaptive landscapes and phenotypic spaces are bound to be dashed. In the case of protein function, we have a close proximity between the genetic/coding level of analysis and the phenotypic/functional level, which means that this is one of those exceptional cases where we really can derive detailed information about the genotype-phenotype mapping function. It is this function that allows the conceptual coupling of adaptive landscapes and phenotypic spaces, but it is precisely this function that is missing from most interesting instances of phenotypic spaces.

I hasten to add that I do not think that this limitation is temporary, and that more knowledge of "phenomes" will allow us to investigate any complex instance of the genotype-phenotype mapping function. A case can be made that, generally, we quickly reach what philosophers call "epistemic limits" that are not likely to be transcended either by more data or by more sophisticated analytical techniques. Of course, this is a prediction about where the field will go in the future, and I could be wrong. Nevertheless, it is certainly the case that we are currently very far from producing any interesting genotype-phenotype map except for the case mentioned above. And until (and if) this problem will be resolved it is simply premature to talk about any conceptual unification of adaptive and phenotypic landscapes.

If there is some doubt on whether and how a satisfactory link can be found between the two kinds of spaces discussed in McGhee's book, there certainly is one wrong way to go about it, which is used by McGhee (for instance, in Chapter 7) and that is scattered throughout the literature: treating "phylogenetic constraints" as a category on par with genetic, developmental, functional, and geometric constraints. McGhee (p. 109) recognizes the last three types of constraint, but equates genetic and phylogenetic, which I think leads to endless conceptual confusion for two reasons. To begin with, most authors actually distinguish genetic and phylogenetic constraints, with the first ones referring to limits on phenotypic evolution imposed by the genetic architecture of organisms (pleiotropic and epistatic effects) or by the lack of genetic variation, and the latter identifying "phylogenetic inertia." McGhee explicitly treats genetic and phylogenetic constraint as synonyms, in contrast with established terminology.

Moreover, and more importantly, I think we should abandon entirely the term phylogenetic constraint because it refers to a pattern, not a process. A phylogenetic constraint, in common parlance, refers to the fact that certain characteristics persist throughout the history of a clade, being "inherited" from taxon to taxon. But unlike genetic inheritance, phylogenetic inheritance can be due to a variety of causes, including genetic constraints (in the sense described above), developmental constraints, or even the action of natural selection—what Westoby et al. (1995) referred to as "phylogenetic niche conservativeness." Indeed, the parallel with individual-level inheritance should be illuminating: in the case of individuals, the pattern consists in the similarity of parents and offspring, just like in the case of phylogenetic inertia the pattern is one of species-to-species similarity. But parent-offspring similarity can be explained with more than one operating causal process: for instance, part of it may be due to inherited genetic information, but another part to the fact that parents and offspring often share a similar environment; analogously, species-to-species similarity may be due to similarities in genetic architecture, but also to occupation of similar niches. To complicate things even further, just like gene-environment interactions add to the causal explanation of parent-offspring similarity (or lack thereof), so too the interaction between genetic architecture and realized niche may alter the observable pattern of phylogenetic similarity. I, therefore, propose that we drop entirely the term "phylogenetic constraint," as not indicative of any causal process, and retain "phylogenetic inertia" to describe the pattern we seek to explain.

McGhee's *The Geometry of Evolution* is a must read for anyone seriously interested in phenotypic evolution, despite my reservations on the adaptive landscape metaphor. The book reminds us of why studying phenotypes can be so rewarding, and of how theory and empirical research can be made to blend together in the context of a complex historical science such as evolutionary biology. Just as long as we are mindful of the limits of our metaphors.

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