The Uncertain Perils of an Invisible Landscape

Evolutionary biologists are familiar with the concept of an adaptive landscape, but it may be that, as originally presented, the landscape is illusory

SOMETIMES IN SCIENCE a simple phrase or diagram appears to be so cogent an encapsulation of an important truth that it takes on almost mythological proportions. And it sometimes happens too that in being raised to this greater stature, the phrase or diagram assumes a meaning that cannot be justified by the initial formulation. "Survival of the fittest" is perhaps the most famous example.

Drawing on more recent sources—but again in the territory of evolutionary biology—William Provine believes he has identified something amiss with a powerful diagrammatic representation of a key intellectual idea in population genetics. While recently preparing a biography of the late Sewall Wright, Provine, a professor of the history of science at Cornell University, realized that there was something not quite right about a famous concept in evolutionary biology: that of the adaptive landscape.

Wright's adaptive landscape, which was published first in 1932, essentially gives a picture of how a species' fitness varies as a result of modifications in its genetic makeup: it is a contour map on which peaks on the surface of the landscape represent genetic makeups that confer high fitness; valleys are locations of lower fitness. A population would be seen as a "cloud" of dots hovering somewhere near a peak, each dot representing a single individual. Wright used this representation to illustrate how genetic change might come about in a population through moving from one peak to another—his famous shifting-balance model (see box).

"Hundreds of published papers refer to the surfaces," Provine wrote in Wright's biography. "I travel to many universities and centers where population genetics is taught, and at most places graduate students talk as if natural populations lived on fitness surfaces rather than on the earth's surface in ecological settings." Wright's famous figures, which illustrate various possible journeys across the adaptive landscape, must be the most frequently published diagrams in the history of evolutionary biology, with the possible exception of Darwin's branching tree from the *Origin*.

The problem, contends Provine, is that, as originally formulated, the adaptive landscape is an illusion: the axes of gene combinations, and one for fitness, do not translate into any kind of fitness surface. For Wright's surface to be mathematically real, the x and y axes must be continuous variables, not discrete entities as is the case with gene combinations. "By no stretch of the imagination can Wright's famous diagrams of the 1932

William B. Provine

Sewall Wright. *His shifting-balance theory transformed population genetics.*

paper be constructed by his method of utilizing gene combinations," says Provine. "The diagrams represent a nicely continuous surface of selective value of individual genotypic combinations; the method Wright used to generate this surface actually yields an unintelligible result."

A few years after the first publication Wright produced another version, in which the axes were now gene frequencies in populations, not gene combinations in individuals. This version of the adaptive landscape had the dual advantages of being mathematically translatable into a real surface, and being relatable to Wright's strictly statistical treatment of population genetics. "But," says Provine, "this conception of the fitness surface has difficulties also."

One difficulty is this. A single set of gene frequencies in a population can be produced by many different gene combinations in individuals within the population. As a result, a single set of gene frequencies can have many different fitnesses, and a single fitness figure must be an average of these.

Despite what Provine sees as the inherent flaw of the first version of the adaptive landscape and its inevitable mathematical incompatibility with the second, Wright continued to use both, depending on the circumstances. "When he was trying to illustrate his qualitative shifting-balance theory of evolution, he tended to use the individual fitness surface, switching to the populational surface when he wanted to become quantitative and relate his equations to the surface."

Provine developed his criticisms during the final stages of preparing Wright's biography, and the two men discussed the issue many times. Wright conceded that on the face of it there were problems, but, in a public reply published in the *American Naturalist* shortly before he died earlier this year, he said: "I think [Provine] was looking for something more mathematical than was intended." Wright was referring specifically to the gene combinations version of the adaptive landscape, which he described as being of "symbolic" not literal value.

Wright explained that he devised the famous diagrams when asked to present at the Sixth International Congress on Genetics in 1932 a "brief, nonmathematical account" of his views on evolution, which had been published in mathematical form a year earlier. Describing the enormous mathematical complexity of dealing with the possible combinations of many gene loci he said: "An intelligible representation depends on some enormous simplification."

"I agree with that," Provine told *Science*, "but he doesn't say how you enormously simplify a mathematical presentation of a surface that doesn't mean anything. I'm not sure you can do that."

Wright did concede that he had recently become "somewhat dissatisfied" with the two-dimensional representation of what is in fact a multidimensional process. As a result he suggested of the adaptive landscape that: "The contours should be considered as merely symbolic of the complex pattern to a greater extent than before. However, I did not arrive at any changes that should be made in the diagrams as presented."

Provine admits that the adaptive landscape has "tremendous intuitive appeal," but is concerned that "far from helping people understand what is happening in the evolution of natural populations, it could actually have been misleading."

Provine has attracted a good deal of sharp comment for his criticisms of Wright's adaptive landscape, not only because, in its more mathematical formulations at least, the concept has been enormously influential in shaping modern population genetics, but also because of its elevated, mythological status. "Allegiance to the surfaces is intense," Provine comments.

Nevertheless, most population geneticists admit that in a limited manner, Provine is correct. "There is no question that if one attempts to take what Wright did literally, there is no surface there, because there are no numerical coordinates," observes Thomas Nagylaki of the University of Chicago. "The criticisms are essentially right, but they lack a certain perspective," says Richard Lewontin of Harvard University. Russell Lande of the University of Chicago suggests that although Provine's criticisms are sound, "he is taking an overly historical view."

Lewontin says that, despite the problems of the pictorial versions of the adaptive landscape, the concept has been of great heuristic value. "It illustrates a number of qualitative features, a key one of which is the existence of multiple adaptive peaks," he says. "It is often very difficult to convey the notion that, even under identical selective conditions, a population can wind up at many different genetic constitutions, depending on the initial conditions."

Anyone who is sufficiently sophisticated with complex differential equations would know this, says Lewontin, "but for most biologists Wright's adaptive landscape is a good way of seeing that point." Another crucial point illustrated by the adaptive landscape is that in the evolution of natural populations you do not separate selection from random processes. Depending on the initial conditions—such as population size, mutation rate, and selection coefficient—you can visualize a population wandering over an adaptive surface, eventually coming to rest temporarily at or near a new peak. "I can't think of a better metaphorical device than this," says Lewontin.

Provine emphasizes that his criticisms in no way detract from Wright's shifting-balance theory, which he describes as one of the few "really robust theories of evolutionary change." The criticism is solely of a pictorial representation that, although tremendously appealing, is mathematically unintelligible and therefore potentially misleading.

■ Roger Lewin

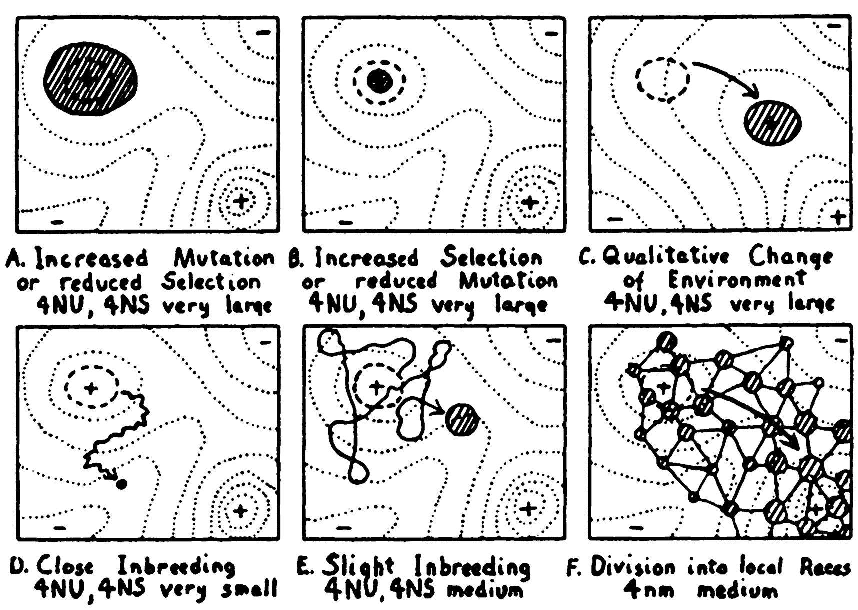
Journeys on a Selective Surface

Sewall Wright depicted his adaptive landscape as a contour map in which the peaks represented gene combinations of high fitness, and valleys of low fitness. In his classic 1932 paper, Wright presented the famous sextet, reproduced below, the aim of which was to illustrate pictorially his otherwise mathematical shifting-balance theory.

A real population can be represented on this hypothetical landscape as a more or less tightly clustered cloud of points, each point being an individual's genotype. A population usually will be distributed at or near an adaptive peak, the result of selection. In the figures below the population occupies one adaptive peak while a peak of higher selective value lies unoccupied nearby. In figure A, Wright shows how the original distribution of a population on the landscape (dashed circle) expands if the rate of mutation increases or the selective force decreases (hatched area). Conversely, a decrease in mutation or an increase in selection will cause the population to "climb" the peak, reducing its area of distribution on the adaptive landscape (figure B). Figure C shows how, with a change in environment, the contours of the landscape will shift: the population then tracks the moving adapative peak.

In the bottom three figures the population is represented as being very small, in figure D so small that it wanders off the adaptive peak as a result of genetic drift, and probably goes to extinction. In E, genetic drift is balanced by selection: the population remains viable, but wanders over the adaptive landscape. The last figure, F, encapsulates the shifting-balance theory. Here, the population is divided into small local populations, each of which therefore experiences a good deal of genetic drift. Occasionally, one of these populations will acquire a superior genotype, and will act like a magnet on surrounding populations, pulling their gene frequenices toward its own. As a result, the population may be pulled across the saddle that separates the two adaptive peaks, whereupon mass selection brings the population under the control of the higher peak. The process can then be repeated with the next circle of local populations.

"This shifting-balance process is enormously more effective than the preceding process (figure E)," says Wright, "both because many local populations are exploring the field of gene combinations more or less independently and because the rate of change of each one (under favorable conditions) is much greater. . . . With a thousand local populations, each exploring the field a thousand times as rapidly, the rate of evolutionary advance will be a million times as great. It also seems, intuitively, to be enormously more rapid than any process not involving differentiation of small local populations." Key to the shifting-balance theory is the combination of random drift and subsequent selection among genetically differentiated groups, something that Wright claims was often overlooked. ■ R.L.



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 medium
F. Division into local Races 4nm medium

ADDITIONAL READING

W. P. Provine, *Sewall Wright and Evolutionary Biology* (Univ. of Chicago Press, Chicago, 1986).

S. Wright, "Surfaces of selective value revisited," *Am. Nat.* **131**, 115 (1988).