

## Some Thoughts on “Adaptive Peaks,” “Dobzhansky’s Dilemma”—and How to Think About Evolution

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Theodosius Dobzhansky was one of the most important evolutionary biologists of the twentieth century. Born in Russia in 1900, Dobzhansky came to Columbia University in New York in late 1927 to work in Thomas Hunt Morgan’s famous “fly room”—birthplace of much of modern genetics. He had been trained as a systematist, with an expertise on ladybird beetles.

Dobzhansky’s (1937) first book—*Genetics and the Origin of Species*—was in many ways his best. The book went through two subsequent editions (1941, 1951), expanding and clarifying his own evolving thought. When it came time for a fourth edition, Dobzhansky’s equally renowned colleague Ernst Mayr (personal communication) pleaded with Dobzhansky to change the title—which he did—to *Genetics of the Evolutionary Process* (1970). Excellent as all these works were, though, there is something that still seems fresh as one reads that first book (1937)—where Dobzhansky wrestled for the first time in an extended format with problems of reconciling the genetics of populations with the Darwinian vision of evolution through natural selection.

I remember Dobzhansky’s 1937 work primarily for three reasons—three areas of discussion of evolutionary processes which were novel, even perhaps revolutionary at the time he was writing. First, he was thinking in hierarchical terms: Dobzhansky made it explicitly clear that the rules governing genetic inheritance (“physiological genetics” in his parlance) are different from the rules governing the fate of gene

frequencies within populations (“population genetics”). Selection and drift occur in populations, at least in large measure independent of mutation and the mechanics of parent–offspring inheritance. He also saw that the smoothly continuous states of genetic variation within populations stand in contrast to discrete states of alleles–mutations at the individual level and also in contrast with the manifest genetic discontinuities between discrete, yet closely related, species.

Secondly, Dobzhansky was the first to rethink the importance of geography in setting up the discontinuities between species. Though Mayr (1942) is largely remembered for elaborating the concept of allopatric speciation (see Thanukos 2008, for a review), in reality, it was Dobzhansky who had first resurrected the importance of isolation (primarily geographically induced) in speciation and thus to the evolutionary process in general.

But, thirdly, Dobzhansky was concerned with the maintenance—and selective value—of genetic variation in natural populations. He had become enamored with Sewall Wright’s (e.g., 1931, 1932) imagery of the “adaptive landscape,” using it to frame his discussion of various evolutionary issues.

Wright (born in 1889) was a geneticist based at the University of Chicago (and later at the University of Wisconsin) for most of his long, productive career. He was one of three geneticists (the other two being the Englishmen Ronald Fisher and J.B.S. Haldane) who applied their gifts with mathematics and statistical analysis to evolutionary genetics, essentially founding the field of “population genetics,” and effectively reconciling genetics with the Darwinian theory of evolution through natural selection.

Sewall Wright is perhaps best remembered for his notion of “genetic drift.” He demonstrated mathematically that genes could “go to fixation” (i.e., not be eliminated by

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natural selection) essentially randomly: the genetics of natural populations is not completely determined by natural selection. To make this and related points, Wright proposed the concept of “adaptive landscapes” (see Fig. 1)—where organisms with the “most harmonious” combinations of genes were depicted as occupying the peaks in a landscape—separated by valleys of less harmonious gene combinations from other peaks with other favorable combinations of genes. The problem of evolution—as Wright saw it in the early 1930s—is to maximize the number of organisms in a population on the relatively higher peaks in the field of possible gene combinations.

Wright (especially Wright 1932) quickly extended his use of the adaptive landscape imagery—beginning to see the peaks on his adaptive landscape occupied by entire subgroups of a species: what Wright eventually called “demes,” or local breeding populations. His “shifting balance theory” saw evolution as the outcome of differing histories of the different demes within a species—where demes could merge with one another, bud off from one another, or simply go extinct. Each deme would be expected to have somewhat different mutational histories and, as they are living in a variety of different ecological settings, to undergo different changes through natural selection and through genetic drift.

Dobzhansky—far more experienced as a field biologist than either Fisher, Haldane, or Wright—saw a use for Wright’s adaptive landscape imagery to outline a conceptual framework for understanding how evolution had produced the great diversity of life on earth. Starting in 1937, but especially in his third edition of *Genetics and the Origin of Species* (1951), Dobzhansky had come to see the peaks in the landscape occupied not so much by “harmonious gene combinations” or even by demes (as Wright

initially had) but by entire species. The best-adapted members of a species would be closest to the tip of the peak (or closely adjacent peaks à la Wright)—and the remainder of the genetic variation of the species would be represented by other organisms of the species occupying lower elevations on the slopes of the peak.

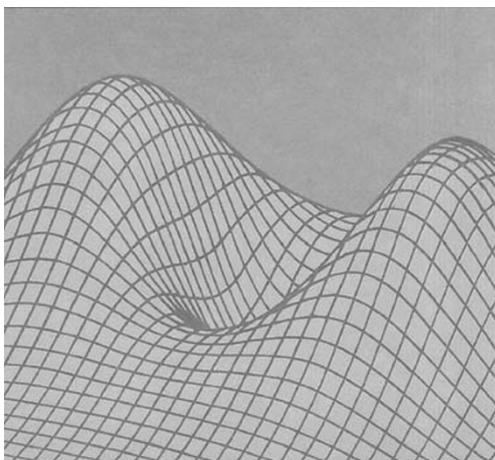
The real difference between Dobzhansky’s and Wright’s usage of the adaptive landscape came when Dobzhansky suggested that the difference between two closely related species reflected their occupation of adjacent peaks of a larger field. Peaks diverge from one another, and evolution (predominantly via natural selection—genetic drift never took its intended full place as an evolutionary process coequal with natural selection in the minds of most evolutionary biologists) would track these divergent peaks—resulting in the evolution of two species from an initial ancestor.

Nor did Dobzhansky stop there: clusters of closely related species form genera and hence are represented as localized clusters of adaptive peaks in what Dobzhansky saw as a larger “range” of mountain peaks. As an example, he wrote that:

The ecological niche occupied by the species ‘lion’ is relatively much closer to those occupied by tiger, puma, and leopard than to those occupied by wolf, coyote and jackal. The feline adaptive peaks form a group different from the canine ‘peaks.’ But the feline, canine, ursine, musteline and certain other groups of peaks form together the adaptive ‘range’ of carnivores, which is separated by deep adaptive valleys of rodents, bats, ungulates primates and others.....The hierarchic nature of the biological classification reflects the objectively ascertainable discontinuity of adaptive niches, in other words the discontinuity of ways and means by which organisms that inhabit the world derive their livelihood from the environment (Dobzhansky 1951, p. 10).

Thus did Dobzhansky explain discontinuities in nature—beginning with species—as a matter of evolution tracking diverging adaptive peaks, a process that has gone on so long that the entire history of life, seen as adaptation to a vast field of different, inherently discontinuous ecological niches, falls out virtually automatically. It is a brilliant use of the landscape metaphor—one that, though not without its problems, still has a decided ring of truth to it.

Dobzhansky’s use of the adaptive landscape as a metaphor for the evolutionary history of life differed somewhat from that of his other famous colleague in New York—George Gaylord Simpson. Simpson (1944) saw major evolutionary events as a matter of populations leaving one adaptive peak for another in the landscape—rather than the peaks themselves diverging and species



**Fig. 1** A three-dimensional depiction of an adaptive landscape with peaks and valleys. For further explication, see text

becoming modified to keep up with the changing field. The landscape imagery was the very basis of Simpson's most famous theory: Quantum evolution—a subject deserving its own *Editor's Corner* in a future issue. Nor is the use of landscape imagery of mere historical curiosity: The Fitness Landscape still is in active use in modern population genetics.

But of the several problems with Dobzhansky's use of the metaphor of the adaptive landscape, one deserves special attention. It is one that Dobzhansky himself recognized and discussed, bearing on the nature, importance, and maintenance of genetic variation in species—a problem I call “Dobzhansky's Dilemma.”

### Dobzhansky's Dilemma

In Wright's adaptive landscape imagery (as used by Wright himself, as well as by Dobzhansky and probably every other evolutionary biologist who has used the metaphor), selection will keep a population (or an entire species, etc.) near the very top of the adaptive peak. Selection relentlessly weeds out the less fit—those less “harmonious” gene combinations, keeping only the best combinations.

Thus selection acts to diminish genetic variation. But that in itself posed a problem for Dobzhansky—for where would that variation come from when environments change (as they inevitably do), altering the position of the peaks, or even splitting those peaks? Adaptive change in evolution requires underlying genetic variation; it is notorious that mutations do not occur just because a species would find them handy when faced with changes in environmental conditions. In other words, Dobzhansky saw an inherent conflict between the short-term benefits of close adaptation of a species to its adaptive peak, on the one hand, and what he called evolutionary *plasticity*—the retention of sufficient genetic variation for future evolutionary change. As he wrote (Dobzhansky 1937, p. 127): “Evolutionary plasticity can be purchased only at the ruthless dear price of continuously sacrificing some individuals to death from unfavorable mutations. Bemoaning this imperfection of nature has, however, no place in a scientific treatment of this subject.”

Hence “Dobzhansky's dilemma”: he felt that there must be some way—some evolutionary mechanism—that would enable a species to retain sufficient genetic variation to allow it to change—to adapt, to evolve—to meet those “rainy day” conditions posed by a fickle environment. There is a reason, in other words, for some of the members of a population lurking down the slopes of the peaks, preserving some of that less-optimal genetic variation. Nor is this problem far-fetched: paleontologists have often noted since the nineteenth century that it is the variable, ecologically diverse species that stand a better chance of

avoiding extinction—relative to narrowly adapted species that are among the first and more numerous of the species succumbing to extinction events.

Evolutionary biologists have persistently confronted the problem of the maintenance of genetic variation—pointing out, for example, that sexual reproduction among diploid organisms (i.e., where there are two sets of chromosomes) shuffles different alleles (forms of a gene). With the exception of identical twins, no two diploid organisms are exactly genetically alike—unlike the case of asexual organisms such as bacteria. Dobzhansky of course explored these notions to explain how genetic variation—and hence evolutionary plasticity—can be maintained.

But—and here is the crux of Dobzhansky's dilemma—biologists (including Dobzhansky himself) have realized that evolution cannot anticipate the future. Evolutionary biologist George Williams (1966), for example, in his book *Adaptation and Natural Selection*, wrote eloquently that natural selection works strictly on the here and now of genetic variation juxtaposed with environmental conditions at the moment. There is no way evolutionary processes such as natural selection or genetic drift can be imagined to be able to anticipate what conditions might be like in the future—no equivalent of opening up a bank account for genes that might just prove handy in the future. To think that evolution can somehow anticipate its own future is *teleological*—imputing a kind of knowledge aforesought to a process that really just sorts out genetically based variation according to what works better than what given the finite nature of the conditions in which a breeding population is living at the moment.

There is a simple lesson here: life is about existence in the here and now. It is about surviving as an organism, meaning for complex multicellular animals, obtaining nutrients, and avoiding the hazards of existence (disease, predation, etc.) that can cut their lives short. The life of an organism may—or may not—also involve reproduction: producing descendants. For these simple acts of living, organisms use the adaptations that have already evolved that they have inherited. The variation within all species, including our own, is an outcome of past history and is maintained either because it is useful or at least not harmful. The idea of DNA repair (where information on one chromosome can be used to change back the mutated information on the paired chromosome) is an example of new thinking that came with the “molecular revolution” that also might help us understand the short-term utility of sexual reproduction and the maintenance of genetic variation—an idea that arrived long after Dobzhansky's career was over.

And, of course, mutation continues to produce more genetic variation every generation. But it is clear that genetic mutation does not occur because evolution might

“need” it sometime down the line. Evolution has no “eyes” for the future. And life is about living, not evolving.

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