The Shifting Balance Theory of Evolution

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[1] See accompanying article for details on his life and work.

[2] For readers not familiar with population genetics, it may be helpful to read the boxes in the accompanying article before proceeding.

The Shifting Balance Theory of Evolution is perhaps the most well-known of Sewall Wright's contributions to evolutionary biology[1]. This is probably partly because it is a verbal theory, presented with the aid of heuristic pictures, as opposed to much of Wright's other work in evolution that tended to be rather mathematical. Moreover, this theory was described in many of the most influential books in evolution (written by Dobzhansky, Simpson, and Waddington), published in the middle of the century, that were read by a large number of biologists. Wright himself returned to this theory repeatedly in papers he published (his last paper in 1988 was on this topic), and was very fond of it. The theory itself has been controversial and confusing to many but has, at the same time, also helped many people to think about the evolutionary process in real populations. Ultimately, perhaps, the shifting balance theory has been not so much a rigorous theory, as a picturesque and thought provoking metaphor that has proven helpful in incorporating a spatial dimension into our thinking on evolution.

The shifting balance theory of evolution was first laid out by Wright in two papers in 1931 and 1932. In these papers, Wright argued that the optimum situation for evolutionary advance, in the sense of the population becoming progressively better adapted to its environment, would be when a large population was *'divided and subdivided into partially isolated local races of small size'*. Wright illustrated these views through his concept of a *'field of gene combinations graded with respect to adaptive value'*, nowadays more commonly known as a fitness or adaptive landscape, or a surface of selective value[2]

The Adaptive Landscape

Wright's idea of a fitness or adaptive landscape is a powerful
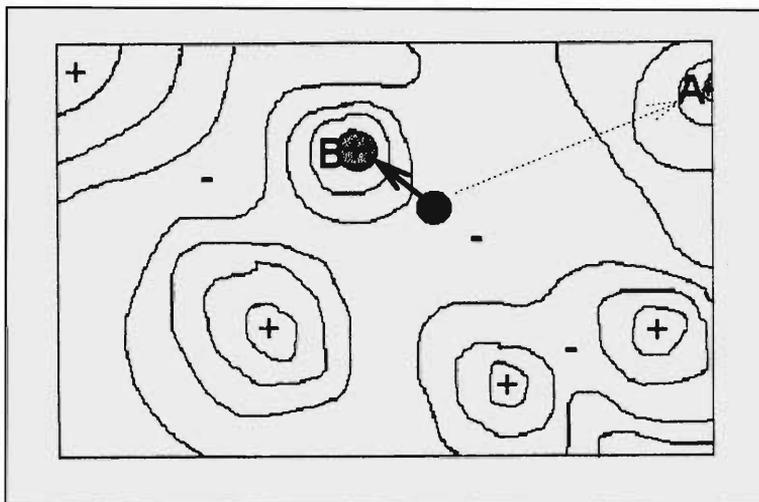
conceptual tool to aid our thinking about evolution, and an example of this conception is shown in *Figure* 1. The two axes represent two out of the potentially many dimensions along which different possible genotypes can be arranged. Thus, in this example, each point on the surface demarcated by the axes represents a particular genotypic combination. A population can therefore be represented, based on the genotypic composition of its members, as occupying a patch on this surface (e.g. the grey shaded patch near the centre of *Figure* 1). Now imagine fitness along a third dimension, perpendicular to the plane of the paper. The lines in the figure connect genotypic combinations that have equal fitness, like contours on a topographical map, and we can think of a fitness or adaptive landscape in three dimensions. The areas marked + represent 'peaks' of high fitness on the adaptive landscape, while areas marked – indicate 'valleys'. The picture shown here can be generalized to a large number of dimensions (n), instead of just two, and we can think of a fitness surface in $n+1$ dimensions on which a population moves as its genetic composition changes in response to evolutionary forces such as selection, mutation, migration, etc.

One important point about the evolutionary process is that, in the vast majority of situations where selection is operating on differences in survivorship rather than reproduction, the mean fitness of a population is non-decreasing. Thus, a population

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under the influence of natural selection will typically only move upward on the fitness surface. Consequently, if there are multiple fitness peaks in the adaptive landscape, a population will evolve so as to eventually climb up the nearest fitness peak. In *Figure* 1, for example, even though peak A may be higher than peak B (i.e. a population with a genetic composition that places it on peak A will have higher mean fitness than a population whose genetic composition places it on peak B), the population in the middle of the picture will evolve to occupy peak B (trajectory shown by the solid arrow). Under the influence of selection alone, there is no way for the population to evolve so as to occupy peak A (trajectory shown by the dotted arrow), even though that is the most fit state for the population. In the metaphorical terminology of the shifting balance theory, the fitness peaks A and B are separated by an adaptive valley which the population cannot cross.

Movement on the Adaptive Landscape

A very large random mating population living in an unchanging environment, Wright reasoned, would eventually reach genetic equilibrium. At this point the population would occupy some region on the fitness landscape, and such an equilibrium population is represented by the dashed circle in the upper left of each panel (a-f) in *Figure* 2. If such a large population experienced an increase in mutation rate (or a decrease in selection intensity), its genetic variability would increase and it would eventually occupy a correspondingly larger area on the fitness landscape, shown by the shaded portion in *Figure* 2a. Similarly, if the mutation rate decreased, or if selection became more intense, the population would become less genetically variable and occupy a smaller area on the fitness landscape (*Figure* 2b). Now imagine what happens if the environment changes, such that genotypes well adapted earlier are rendered less fit, and some hitherto less fit genotypes become more fit in the new environment. This really boils down to a change in the adaptive landscape: what was earlier a peak is now a valley, and a new peak has arisen somewhere else (*Figure* 2c). In nature, the
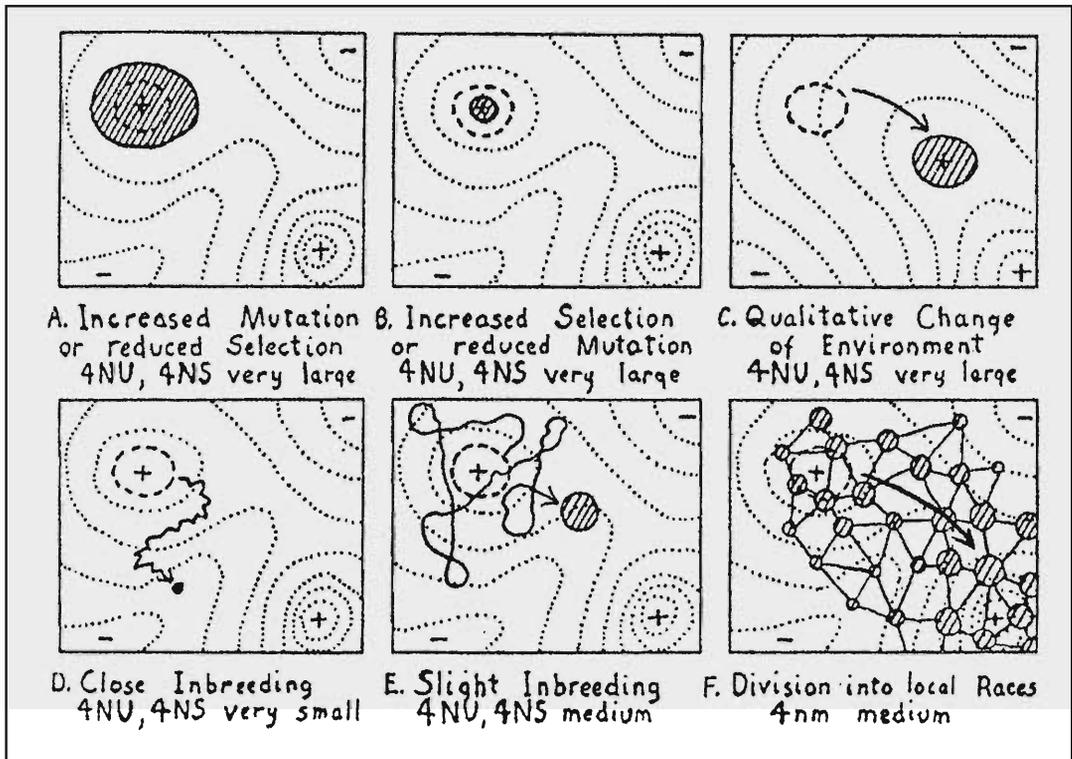
Figure 2. Sewall Wright's conception of the course of evolutionary change in populations of varying size and degree of sub-division into local populations or demes. The original Figure title reads: Field of gene combinations occupied by a population within the general field of possible combinations. Type of history under specified conditions indicated by relation to initial field (heavy broken contour) and arrow'. The labels for the different panels are in Wright's handwriting (from S Wright, The roles of mutation, inbreeding, crossbreeding and selection in evolution, pp 356-366 in Proceedings of the Sixth International Congress of Genetics (D F Jones, ed.), 1932.). N refers to the population size, u is the mutation rate per locus per generation, and s the selection coefficient. Large values of 4Ns or 4Nu indicate that the population is large enough for genetic drift to be negligible, whereas 4Ns, 4Nu very small indicate that drift will predominate as the agent of genetic change in the population over generations.

environment of a population is generally changing, and the question is: what happens then? In Wright's words, '*A species occupying a small field under the influence of severe selection is likely to be left in a pit and become extinct, the victim of extreme specialization to conditions which have ceased, but if under sufficiently moderate selection to occupy a wide field, it will merely be kept continually on the move*'. This kind of evolutionary change, involving a very large

In most situations where selection is operating on differences in survivorship rather than reproduction, the mean fitness of a population is non-decreasing. Thus, a population under the influence of natural selection alone will typically only move upward on the fitness surface.

population continually tracking changes in the environment and, consequently, forever climbing up an adaptive peak which has the nasty habit of changing its position, did not, in Wright's opinion, lead to evolutionary advance. Indeed, this is what is often called the Red Queen effect (after the character in the Alice stories, who ran as fast as she could merely to stay in the same place), wherein a population is continually evolving merely to maintain a given degree of adaptedness to a changing environment.

In a very small population that is isolated from others of the same species, on the other hand, random genetic drift will tend to swamp the effects of natural selection. Such populations will move about randomly on the adaptive landscape (largely downhill, due to deleterious effects of increased homozygosity), eventually lose all genetic variation and be essentially consigned to extinction (*Figure* 2d). Thus, according to Wright, neither very large random mating populations nor very small isolated ones had much scope for continuing evolutionary advance. He next considered the case of a moderately sized isolated population which would undergo drift, but not the severe effects of increased homozygosity (at least not for a very long time). In such cases, he wrote, '*The species moves down from the extreme peak but continually wanders in the vicinity. There is some chance that it may encounter a gradient leading to another peak and shift its allegiance to this*' (*Figure* 2e). Here we have a mechanism – random genetic drift – whereby a population can cross an adaptive valley on the fitness landscape! This is important, for as we have seen, a large population under the influence of selection alone cannot evolve so as to occupy the peak of highest fitness if it happens to be separated from it by an adaptive valley. To quote Wright once again, '*there is here a trial and error mechanism* (i.e. random genetic drift) *by which in time the species may work its way to the highest peaks in the general field*'. However, Wright felt that the rate of evolutionary progress, in terms of how fast the species could move to the highest peak, would be rather slow by this mechanism.

Wright argued that the optimal conditions leading to the greatest rate of evolutionary advance were those where a large population was subdivided into a number of local sub-populations or demes, such that most, *but not all*, matings occurred in a localized manner among members of the same deme (*Figure* 2f). Such subdivision often arises in nature due to geographical barriers to dispersal, or even, in the case of relatively sedentary organisms, because the dispersal of gametes (e.g. pollen) or offspring (e.g. seeds) is not very effective over long distances. In such a scenario, if environments differ from deme to deme, selection pressures may also vary. Then, the movements of different demes on the adaptive landscape will be towards local peaks. Moreover, if the demes are not too large, each deme will also tend to move about randomly on the adaptive landscape due to genetic drift. Unlike in the case of an isolated moderately sized population, however, the movements of demes on the adaptive landscape will be relatively faster under this scenario because of gene flow among demes. Thus, because there are many demes moving about relatively rapidly on the adaptive landscape, there is a good likelihood that one of them will come into the domain of attraction of the highest peak and then climb it. Now consider what the 'highest peak' means: the deme that has occupied this peak has the highest mean fitness, in the Darwinian sense. Thus, this deme will tend to produce more offspring than others (a kind of natural selection between demes rather than between individuals within a deme). These offspring, due to increasing density in their parental deme, are relatively more likely to migrate out and breed with members of other demes. Such interbreeding will then have the effect of altering the genetic composition of other demes, making it more similar to that of the deme on the highest peak. Ultimately, once again in Wright's own words, the deme on the highest peak '*will expand in numbers and by crossbreeding with the others will pull the whole species toward the new position. The average adaptiveness of the species thus advances under intergroup selection, an enormously more effective process than intragroup selection. The conclusion is that subdivision of a species into local races provides the most effective*

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mechanism for trial and error in the field of gene combinations'. Thus, what Wright was emphasizing was that evolutionary change involved a balance between the forces of natural selection (both among individuals within populations, and between local populations), random genetic drift and gene flow (migration), and that the relative contribution of these factors to evolutionary change would vary over time and space; hence the 'shifting' balance.

Wright's writing, as can be seen from some of the quotes above, was not always very clear. Thus, although he himself did not see a serious conflict between his shifting balance theory, and the Fisherian view of evolution in large populations (situations of the kind illustrated in *Figure* 2c), many people came to associate Wright's theory with the view that random genetic drift was a significant alternative to natural selection as a mechanism of evolutionary change. This led to a bitter and acrimonious debate in the literature between Wright and Fisher, Ford and co-workers in the UK: this debate continued even after Fisher's death in 1962. More importantly, the debate sparked some of the best field studies in evolution (some are briefly described in the accompanying article), as supporters of both Wright and Fisher sought empirical evidence favouring their point of view.

Problems with the Adaptive Landscape

Although an evocative and beautiful metaphor, the shifting balance theory of evolution on the adaptive landscape, as described by Wright, suffers from serious problems. One major problem here is: what are the axes? Wright often talked about the axes representing gene combinations, and stated that the number of possible gene combinations was exceedingly large. But what does this mean? If we imagine each axis to represent a locus, then the different genotypes at one locus cannot possibly be treated as a continuous variable. And if the axes have discrete variables along them, then it is completely meaningless to talk of a surface.

On some occasions, Wright viewed the axes as representing

allele frequencies at a locus. In this view, if one considers only biallelic loci, the axes certainly have continuous variables along them. But in this formulation, each point on the surface represents a population, not an individual genotype, and the $n + 1^{th}$ dimension must, therefore, represent population mean fitness. The problem here is that there is not necessarily a one-to-one correspondence between the allelic frequencies of a population and its mean fitness. Population mean fitness ultimately depends upon genotypic frequencies, and allelic frequencies are not a good guide to genotypic frequencies unless many assumptions regarding breeding structure, etc., hold true (formally, allelic frequencies will specify genotypic frequencies, and therefore mean fitness, only if the population is random mating and very large, undergoes no mutation, migration and selection, and is in gametic phase equilibrium).

Another way of depicting the fitness surface is with continuously varying phenotypic characters (e.g. weight, beak length, etc.) on the axes. This formulation, first put forward in 1944 by G G Simpson in his influential book '*Tempo and Mode in Evolution*' was also used later by Wright. The advantage here is that each point on the surface does, in fact, represents an individual, and individuals of somewhat similar phenotype in a population will cluster together on a small patch on the surface. The problem here is that one needs to assume that genotypes and phenotypes have a good correspondence. This is, however, not such a serious problem as, ultimately, fitness is a property of phenotypes even though it is genotypes that get selected. More importantly, it needs to be noted that certain combinations of phenotypes may not be attainable in a single individual due to genetic constraints. In other words, the fitness of certain points in the adaptive landscape demarcated by phenotypic axes is undefined. This is also not a big problem: it just requires some refinement in how we view the adaptive landscape. Indeed, the depiction of the adaptive landscape in terms of phenotypic characters is perhaps the most meaningful and has been used in many studies of evolution in recent years (*Box* 1).

Even 70 years after its conception, Wright's vision of evolution in sub-divided populations continues to spark new empirical and theoretical work today

The Shifting Balance Theory Today

In the final analysis, the shifting balance theory of evolution remains an important contribution to evolutionary biology, despite the several problems discussed in the preceding section. One significant thing about this theory was that it highlighted the importance of population sub-division to evolution and

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Box 1. The Fitness Landscape for a Plant-Pollinator Interaction

Tropical plants of the genus *Dalechampia* produce triterpenoid resins in a specific resin gland in their flowers, and are pollinated by euglossine, megachilid and meliponine bees that collect these resins. The size of the resin gland determines the size of the bee attracted; larger glands attract larger bees and vice versa. Whether a bee actually pollinates the flowers while collecting resin depends upon bee size, and the distance between the resin gland and the stigma, and between the resin gland and the anthers. Scott Armbruster (presently at University of Alaska, Fairbanks) and his co-workers studied bee visits and pollination in 45 populations of 23 species of *Dalechampia*, that differed in resin gland size and the gland-stigma and gland-anther distance. The picture emerging from their studies is that a combination of small gland size and large gland-stigma and gland-anther distance results in lowered fitness, because the smaller bees attracted by small resin glands cannot effectively pollinate flowers in which the stigma and anthers are relatively far from the resin gland. At the same time, resin production is expensive to the plant, diverting resources that could be otherwise used for reproduction. Thus, large resin glands are not of much use if the gland-stigma and gland-anther distances are small: when small bees can do the job of pollination, it is wasteful to allocate resources to making large glands which will attract large bees. Armbruster concluded that the adaptive landscape for flower structure in these species is best described by a somewhat elongated adaptive ridge (*Figure* 3), along which lie matching combinations of gland size and gland-stigma and gland-anther distance that yield high fitness. Similar studies have also been used to predict adaptive landscapes for combinations of beak width and beak depth in red crossbills, based on the characteristics of seeds available for them to feed on in different habitats.
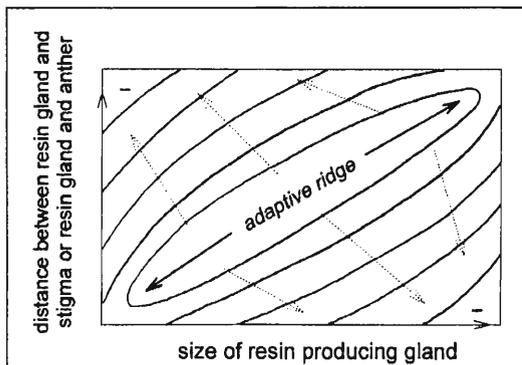
Figure 3. An adaptive landscape for some aspects of flower structure in the tropical genus Dalechampia, predicted by Armbruster. In this landscape, plants with flowers of roughly matching resin gland size and gland-stigma and gland-anther distance are the most fit, resulting in an adaptive ridge which falls off steeply on both sides. Dotted arrows represent the directions in which fitness decreases as one proceeds across the contours, and the minus signs represent adaptive 'pits' of very low fitness [5].

ecology as early as the 1930s. In recent years, studying the ecology and evolution of subdivided populations (now commonly called metapopulations) has become very important, especially from the point of view of conserving biological diversity. Similarly, the theory stressed the importance of breeding structure to population sub-division; a population may not be subdivided due to geography but may still consist of small breeding units. The importance of breeding structure to the ecology and evolution of populations is also an area that is currently receiving much attention. The incorporation of geographical and breeding structure into a view of how selection, drift and local population extinction interact in the course of evolution is the real crux of this theory. In the past decade, John Thompson (working at Washington State University, Pullman) has extended this kind of reasoning to the issue of the evolution of species interactions such as mutualisms and competition in his Geographic Mosaic Theory of Coevolution. Theoretical population geneticists continue to attempt to put the shifting balance theory on a sound mathematical footing, even as experimentalists continue to address the issues of how real adaptive landscapes look, and how populations 'explore' them. Thus, even 70 years later, Wright's vision of evolution in subdivided populations continues to spark new empirical and theoretical work, justifying its place among the most important contributions to evolutionary biology.

Suggested Reading

[1] S Wright, The roles of mutation, inbreeding, crossbreeding and selection in evolution, *Proceedings of the VI International Congress of Genetics* (D F Jones, ed), pp. 356–366, 1932 (reprinted in *Evolution: A Book of Readings*, W C Brown & Co., Dubuque, Iowa, 1967).
[2] S Wright, Surfaces of selective value, *Proceedings of the National Academy of Sciences USA,* 102, 81-84, 1967.
[3] S Wright, Surfaces of selective value revisited, *American Naturalist,* 131, 115–123, 1988.
[4] T Dobzhansky, *Genetics and the Origin of Species,* 3rd Ed. Columbia University Press, New York, 1951. (4th Indian reprint by Oxford & IBH Publ. Co., New Delhi, 1976).
[5] W S Armbruster, Estimating and testing the shapes of adaptive surfaces: the morphology and pollination of *Dalechampia* blossoms, *American Naturalist,* 135, 14–31, 1990.

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