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Sewall Wright, shifting balance theory, and the hardening of the modern synthesis

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ABSTRACT

The period between the 1940s and 1960s saw the hardening of the modern synthesis in evolutionary biology. Gould and Provine argue that Wright's shifting balance theory of evolution hardened during this period. But their account does not do justice to Wright, who always regarded selection as acting together with drift. This paper presents a more adequate account of the development of Wright's shifting balance theory, paying particular attention to his application of the theory to the geographical distribution of flower color dimorphism in *Linanthus parryae*. The account shows that even in the heyday of the hardened synthesis, the balance or interaction of evolutionary factors, such as drift, selection, and migration, occupied pride of place in Wright's theory, and that between the 1940s and 1970s, Wright developed the theory of isolation by distance to quantitatively represent the structure of the *Linanthus* population, which he argued had the kind of structure posited by his shifting balance theory. In the end, Wright arrived at a sophisticated description of the structure of the *Linanthus* population, where the interaction between drift and selection varied spatially.

> "The problem presented by distribution of blue and white flowered plants [in the population of *Linanthus parryae*] is not as simple as a decision between two sharply distinct alternative[s]: control by selection or by random drift. Selection may be involved in diverse ways, there are different sorts of random drift to be considered, and selection and random [drift] may be combined in any degrees and may conceivably interact to produce a more heterogeneous pattern than either by itself."
>
> Sewall Wright, an unpublished manuscript on *Linanthus parryae* (1960) (Sewall Wright Papers, American Philosophical Society, Series IIa, Folder 29)

1. Introduction

Stephen Jay Gould (1980, 1982, 1983, 2002) has famously argued that the modern synthesis in evolutionary biology hardened over time. In the 1930s, evolutionary biologists were pluralistic in the sense that they accepted both adaptive and nonadaptive evolutionary processes as important in nature, but in the next three decades, they moved toward the hard-line selectionist view that natural selection is the most important (and prevalent) process in evolution.[1] One of Gould's prime cases of the hardening is the development of Sewall Wright's shifting balance theory of evolution.[2]

Following Gould, William Provine argues that Wright's theory hardened (Provine, 1983; 1986, pp. 287–291, 361–362, 420–435). According to Provine, in the 1930s Wright claimed that taxonomic differences above the species level were largely nonadaptive, thereby making genetic drift not only important at the level of a small local population but also at the levels of species and genera (e.g., Wright, 1932, pp. 363–364). In saying this Wright was following the systematists' view that taxonomic differences are nonadaptive. By the 1950s, however, systematists argued that supposedly nonadaptive taxonomic differences turned out to be adaptive. Wright thus held that only local differences within a species were nonadaptive, suggesting that drift plays an important role *only* at the level of subpopulations of a species (e.g., Wright,

[1] For a review and analysis of the debates over the relative importance of drift and selection, see Beatty (1984).

[2] Gould's other cases are the works of Theodosius Dobzhansky, Julian Huxley, Ernst Mayr, and G. G. Simpson, and Gould's thesis has been analyzed by other scholars (e.g., Beatty, 1987; Provine, 1983, 1986; Smocovitis, 1999; Turner, 1987).

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1948). Gould and Provine interprets this change in Wright's view as indicating that natural selection became more important in Wright's theory.

Gould's and Provine's interpretation of Wright may sound counterintuitive, for Wright always maintained that subdivision of a population into small, partially isolated demes provides the balance between random genetic drift and natural selection that is most favorable for rapid adaptive evolution. On this view, drift and selection act together in adaptive evolution: drift provides a continuous supply of intraspecific variations on which natural selection may act. In fact, Provine acknowledges this point:

> In one sense, Wright's theory has never changed substantially since he first conceived it in 1925. He has always argued that a certain "balance" among the various factors affecting the evolutionary process exists and that generally all the factors are acting in the balance. Thus, to say that natural selection or random drift is the primary determinant of the evolutionary process, makes no sense in Wright's scheme. Both are working, and it is the balance of their interaction that (along with all the other factors, of course) determines the course of evolution. Wright has never veered from emphasizing the "balance" of his shifting balance theory (Provine, 1986, pp. 361–362).

Nonetheless, Provine argues that Wright's theory hardened because Wright came to restrict the role of drift to the subpopulation level. For Provine, the "balance" of Wright's theory tilted toward selection.[3]

Even if we grant that Wright changed his view about the nonadaptive taxonomic differences, Gould's and Provine's hardening interpretation of the development of Wright's evolutionary theory is misleading in two ways. First, Wright's theory did not fit nicely with what Gould describes as pluralism in the 1930s. For Gould, an evolutionary theory would be pluralistic if it simply recognized drift and selection as important, alternative processes in evolution, and his pluralism does not require that evolutionary phenomena be explained by appeal to the balance between drift and selection. In Wright's theory, however, drift and selection are cooperating rather than alternative factors, and his theory appeals to the balance of factors (Wright, 1931, 1932). Thus, to say that Wright's theory was pluralistic in Gould's sense does not capture the nature of the relationship between drift and selection in Wright's theory. Second, Wright's theory was opposed to hard-line selectionism. As Provine noted, Wright always emphasized the interaction of different evolutionary factors, that is, the balance of the shifting balance theory. In this theory, no single factor can be given preeminent importance. Wright appealed to this point to distinguish his view from hard-line selectionism of Fisher and Ford (Fisher & Ford, 1947, 1950; Wright, 1948, 1951).[4]

Thus, although the hardening story seems to represent an influential trend in evolutionary theory between the 1940s and the 1960s, it fails to do justice to Wright's shifting balance theory. My aim in this paper is to provide a more adequate account of the development of Wright's theory during the hardening of the modern synthesis. My account has two parts, both of which occur in the context of Wright's work on the geographical distribution of flower color dimorphism in *Linanthus parryae*, a population of desert plants that Wright regarded as an example of his shifting balance theory.[5] The first part concerns Wright's criticism of the selectionist explanation of dimorphism in *Linanthus* and his analysis of the balance of factors in the *Linanthus* population (Sections 2 and 3). This part shows that even in the heyday of the hardened synthesis, the balance or interaction of factors occupied pride of place in Wright's theory, a fact obscured by the hardening story. The second part concerns the development of Wright's theory of isolation by distance and his application of it to *Linanthus* (Sections 4 and 5). Wright used the theory of isolation by distance to quantitatively describe how drift, selection, and migration interact with each other in the *Linanthus* population, and it underpinned his criticism of the selectionist explanation of dimorphism in *Linanthus*. This was Wright's major theoretical and empirical work in the 1940s and 50s, which is neglected in the hardening story. Taken together, my account shows that while the community of evolutionary biologists hardened, Wright not only criticized hard-line selectionism but also provided an increasingly sophisticated, quantitative analysis of the balance of drift and selection in a subdivided population. Furthermore, my account suggests ways in which the development of Wright's shifting balance theory is relevant to broader issues in evolutionary biology and philosophy of biology (Section 6).

2. Balance of factors in *Linanthus parryae*

Linanthus parryae is a diminutive desert annual in the Mojave Desert in California. It has blue and white flower color morphs, the former being dominant to the latter (Epling, Lewis, & Ball, 1960, p. 238). It is pollinated exclusively by a species of soft-winged flower beetles, whose flight distance is one to ten feet, and seeds are dispersed passively (Epling et al., 1960, p. 240, p. 243; Schemske & Bierzychudek, 2001, p. 1270). The life cycle of *Linanthus* shows two patterns. In wet years, when there is enough rainfall in winter, seed germination occurs, and plants flower in early to late April, shedding seeds in late May to early June. In dry years, no seed germination occurs, although seeds can remain dormant in the soil for seven years or longer (Epling et al., 1960, p. 240, p. 250; Schemske & Bierzychudek, 2001, p. 1270). In a favorable wet year, thousands of plants bloom and cover the desert as if snow has fallen: hence the common name "desert snow" (Epling & Dobzhansky, 1942, p. 318).

In April 1941, a population of 10–100 billion blooming *Linanthus* plants covered an 840-square-mile region of the Mojave Desert (Epling & Dobzhansky, 1942, pp. 329–330; Wright, 1943a, p. 141). The distribution of flower color exhibited interesting patterns. Overall, white flowers were most abundant, and in some areas there were only white flowers. But in three separate areas—referred to as the "variable areas" (Epling & Dobzhansky, 1942, p. 323, p. 323)—blue and white flowers coexisted (Fig. 1). There were no obvious geographical barriers that might have been responsible for these patterns. This striking dimorphism caught the attention of the UCLA botanist Carl Epling, and after he told Theodosius Dobzhansky about the *Linanthus* population, Dobzhansky saw that its conspicuous dimorphism seemed to facilitate a study of population structure, which he had been working on. At Dobzhansky's urging,

[3] Wright does not seem to think that his view has hardened (Wright, 1988, p. 121).

[4] Provine (1986, pp. 429, 435) acknowledges this point too but argues that Wright's view became more selectionist.

[5] Wright's work on *Linanthus* is relevant to contemporary biology, as the empirical test of Wright's shifting balance theory is an ongoing problem (Coyne, Barton, & Turelli, 2000, 1997; Goodnight & Wade, 2000; Peck, Ellner, & Gould, 1998; Plutynski, 2005; Skipper, 2002; Wade & Goodnight, 1998) and the recent studies of the *Linanthus* population challenge his work (Schemske & Bierzychudek, 2001, 2007; Turelli, Schemske, & Bierzychudek, 2001).