THE PERSISTENCE OF THE R. A. FISHER–SEWALL WRIGHT CONTROVERSY

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ABSTRACT

This paper considers recent heated debates led by Jerry A. Coyne and Michael J. Wade on issues stemming from the 1929-1962 R. A. Fisher–Sewall Wright controversy in population genetics. William B. Provine once remarked that the Fisher–Wright controversy is central, fundamental, and very influential. Indeed, it is also *persistent*. The argumentative structure of the recent (1997-2000) debates is analyzed with the aim of eliminating a logical conflict in them, viz., that the two "sides" in the debates have different aims and that, as such, they are talking past each other. Given a philosophical analysis of the argumentative structure of the debates, suggestions supportive of Wade's work on the debate are made that are aimed, modestly, at putting the persistent Fisher–Wright controversy on the course to resolution.

KEYWORDS: Fisher, Wright, Coyne, Wade, population genetics, shifting balance theory, large population size theory

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Introduction

Between the 1920s and 1930s, J. B. S. Haldane, R. A. Fisher, and Sewall Wright ushered in the field of theoretical population genetics (Provine 1971). By the middle of the 1930s, Haldane's, Fisher's, and Wright's theories dominated the burgeoning field. Between 1929-1962 (the year of Fisher's death), Fisher and Wright were engaged in controversy concerning the main differences underlying their respective evolutionary theories (Provine 1985; 1986). Wright continued to clarify his work in the context of the debates he had with Fisher until his death in 1988. William B. Provine has called the debates between Fisher and Wright "central, fundamental, and very influential" (Provine 1985: 197, 217). Indeed, the Fisher–Wright controversy, as it is called, is not only central, fundamental, and very influential, it is also *persistent*.

Between 1997-2000, a series of scientific papers published by Jerry A. Coyne, with Nicholas Barton, and Michael Turelli (Coyne et al. 1997; 2000), and Michael J. Wade, with Charles J. Goodnight (Wade and Goodnight 1998; Goodnight and Wade 2000), have rekindled if not thoroughly reignited the Fisher–Wright controversy. The recent papers stake out, with considerable disagreement, positions on problems from the original debates between Fisher and Wright as well as on new problems. In what follows, I carefully and systematically analyze the general argumentative structure of the 1997-2000 debates led by Coyne and Wade. Based on a philosophical interpretation of the new controversy, I argue that the kind of controversy that is exemplified is in conflict with the ways in which specific theory evaluation strategies have been taken to it. And, because of the conflict in the logical structure of the controversy, Coyne and Wade are, to a significant extent, talking past each other.

In my view, the reignited Fisher–Wright controversy is what John Beatty (1995; 1997) calls a “relative significance controversy.” In such a controversy, as I will argue over the course of this article, the *explanatory adequacy* of a scientific theory is to be assessed, at least in part, according to its *scope of application* in a domain (see Shapere 1977 on the concept of a domain) and not according to its *generality of scope* in that domain. That is, rather than considering a theory explanatorily adequate because it is general, as is often done (see, e.g., Darden 1991; Newton-Smith 1981), I will argue based on ideas implicit in Beatty’s notion of a relative significance controversy that a theory is explanatorily adequate when the scope of applicability of the theory has been determined. As we will see, the latter adequacy condition is a strategy for evaluating the explanatory adequacy of scientific theories in a relative significance controversy because relative significance controversies reflect a theoretical pluralism, or the notion that the domain under scrutiny is fundamentally heterogeneous so that there is no expectation that there will be a theory with a general scope of applicability for the domain. As such, a theory is explanatorily adequate in a domain when the boundaries of its scope have been determined. Insofar as the reignited Fisher_Wright controversy is a relative significance controversy in the domain of population genetics (which I will stipulate for the purposes of the present article to be the origin and maintenance of genetic variation), the explanatory adequacy of the theories must be evaluated against the extent to which the scopes of applicability of the theories have been determined and not against the generality of their scopes.

Coyne et al. (1997; 2000) negatively assess the explanatory adequacy of Wright’s Shifting Balance Theory (SBT) by claiming via, as we will see, an appeal to parsimony, that the theory does not exemplify generality of scope. They further advocate Fisher’s, as I call it, Large Population Size Theory (LPST) on the grounds that it is explanatorily adequate because it does exemplify generality. Wade and Goodnight (1998) respond to Coyne et al. (1997) by claiming that the scopes of applicability of Wright's SBT and Fisher's LPST have not been adequately determined and, so, to dismiss or advocate one over the other is premature (at least). Indeed, for Wade and Goodnight, the domain of population genetics has plenty of room in it for both the SBT and the LPST. The response to Wade and Goodnight (1998) by Coyne et al. (2000) fails to recognize Wade and Goodnight's points and simply continues the assessments made in Coyne et al. (1997). Goodnight and Wade's (2000) response to Coyne et al. (2000) is a further attempt at more carefully making their original, i.e., 1998, point. Ultimately, little progress has been made after the 1997-1998 papers. I will attempt to assuage the logical conflict in the controversy by focusing the theory evaluation strategies so that their use is more congenial to the kind of controversy in which Coyne and Wade are engaged. My view is that unless Coyne and Wade recognize the problems with the logical structure of their debate and the ways in which the relevant evaluation strategies are to be used within it, then the reignited Fisher–Wright controversy is a long way from resolution because the disputants are essentially talking past each other. However, if my analysis is taken seriously, at least some clear, if modest, steps toward the controversy's resolution can more effectively be taken.

Fisher and Wright on Evolution

In 1930, Fisher published his fullest account of what he called his *genetical theory of natural selection* (Fisher 1930). Not coincidentally, that is the title of Fisher's 1930 book, which he revised in 1958 and which was published in a variorum edition (edited by J. H. Bennett) in 1999 (Fisher 1958; 1999). There is earlier work containing kernels of Fisher's 1930 view. These papers include Fisher's 1922 work on the dominance ratio, his 1927 work on mimicry, and his 1928 work on the evolution of dominance (Fisher 1922; 1927; 1928).

Fisher's purpose in *The Genetical Theory of Natural Selection* was to examine the theory of natural selection on its own merits (Fisher 1930: vii; cf. Gayon 1998; Provine 1971). More specifically, Fisher's aim was to formally, mathematically demonstrate how what was considered the "vague" concept of natural selection could possibly work (Fisher 1930: vii). And he does this by considering the theory of natural selection against the principles of Mendelian inheritance on an analogy with the mathematical techniques of statistical mechanics (Fisher 1930: vii-viii). The structure of *The Genetical Theory of Natural Selection* is as follows. Fisher begins in chapter 1 with a thorough critique of Darwin's blending theory and a discussion of the superiority of the Mendelian theory ("The Nature of Inheritance"). In chapter 2, Fisher sets out what he takes to be the main conditions that must be present for Darwinian mass selection, or selection acting on small differences on organismal fitnesses in large populations, to be the main mechanism acting to change allele frequencies, given Mendelian heredity ("The Fundamental Theorem of Natural Selection"). Then, to give his view indirect evidential support, Fisher applies it to the problem of the evolution of dominance in chapter 3 ("The Evolution of Dominance"). The next two chapters, 4 and 5, are more detailed discussions of the ways in which selection can maintain and refine variation ("Variation as Determined by Mutation and Selection," "Variation &tc. (continued)"). Then, Fisher discusses, in a chapter each, two special cases, the evolution of sex (with an aside on speciation) and mimicry ("Sexual Reproduction and Sexual Selection," "Mimicry"). His genetical theory set out, the rest of the book, chapters 8-12, is an attempt to use his view to ground eugenics.

There is much in the development of Fisher's view of evolution. For the purposes of the present article, a brief summary of Fisher's view of evolution as change in gene frequencies will do. It is typically understood like this: *Evolution occurs in large, randomly mating or panmictic populations and is driven primarily by natural selection, or mass selection, at low levels acting on the average effects of single allele changes (of weak effect) at single loci independent of all* *other loci*. The understanding of Fisher's view that I have just provided has remained essentially unchanged for the last 70 years (e.g., Gayon 1998; Provine 1971; 1985; 1986).

Wright's main, early published work on evolution in populations under Mendelian inheritance are his classic 1931 and 1932 papers on the topic (Wright 1931; 1932). Wright, however, produced a steady stream of papers on evolution, including his four volume *magnum opus*: *Evolution and the Genetics of Populations* (Wright 1968; 1969; 1977; 1978). Even in the last year of his life, 1988, Wright published a paper revisiting what he took his life's work to contribute to in evolutionary biology (Wright 1988). The paper was a mostly favorable reaction to Provine's biography (Provine 1986).

What Wright was looking for, at least in 1931 and 1932, were the ideal conditions for evolution to occur, given specific assumptions about the relationship between Mendelian heredity and the adaptive value of gene complexes (Wright 1931: 158; 1932: 163). Ideal conditions, for Wright, are those conditions that produce the fastest rate of evolution to the highest "adaptive peak." By the last volume of his *Evolution and the Genetics of Populations*, in 1978, Wright claimed that his Shifting Balance Theory (SBT) described the principal processes by which cumulative evolutionary change occurred in nature (Wright 1978: 1415). Wright did not carry such a strong claim through all of his work on evolution. Indeed, he vacillated throughout his career and finally backed off of the strong claim substantially in his 1988 paper, restating his problematic from the work in 1931 and 1932 of determining the ideal conditions for evolution to occur (Wright 1988: 122; cf. Provine 1986).

According to Wright, accurately representing the population genetics of the evolutionary process requires many thousands of dimensions (Wright 1932: 161-163; cf. Haldane 1931). This is because the field of possible gene combinations in the field of gene frequencies of a population is vast (approximately 10^{1000}) (Wright 1932: 161). Wright used a two dimensional graphical depiction of a metaphorical adaptive landscape as a way of intuitively conveying what can only be realistically represented in many thousands of dimensions. Wright's two main figures are reproduced in Figure 1 below.

{FIGURE 1 ABOUT HERE}

The contour lines in the diagram represent the field of gene combinations in combination with their adaptive value. The surface of the adaptive landscape is very "hilly", according to Wright, because of epistatic relations between genes the consequences for which are that genes adaptive in one combination are likely to be maladaptive in another (Wright 1931; 1932). Given Wright's view of the consequences of epistasis and the vastness of the field of gene combinations in the field of gene frequencies (10^{1000}), Wright estimates the number of adaptive "peaks" separated by adaptive "valleys" at 10^{800} (Wright 1932: 163). Peaks are represented by "+"; valleys are represented by "–."

In the explicit context of the 1932 paper, Wright used the adaptive landscape of Figure 1A to argue for his "three phase shifting balance" view of the evolutionary process (F in Figure 1B). Of the six windows in Figure 1B, Wright argued for window F. His argument was essentially a demonstration of the ways in which the conditions expressed in windows A-E solved or did not solve the problem of peak shifts. According to Wright, the ideal circumstances for a global population to reach the optimal adaptive peak requires three stages, or phases. These three phases, working in a shifting balance from one to the next, describe the ideal conditions for evolution to occur. In the first phase, random genetic drift causes gene frequencies to change and pull subpopulations semi-isolated within the global population into adaptive valleys because random fluctuations in gene frequencies are almost always maladaptive. In phase two, mass selection will then act within subpopulations and increase their fitness, dragging them from adaptive valleys to adaptive peaks. In the third phase, selection between subpopulations, which

Wright called interdemic selection, driven by differential dispersion (migration of organisms from more fit subpopulations to less fit subpopulations) would then enable the global population to be raised to its optimal peak.

Wright's SBT is summarized basically as I have described it here: Evolution proceeds via a shifting balance process through three phases:

> **Phase I:** *Random genetic drift causes subpopulations semi-isolated within the global population to lose fitness.*
>
> **Phase II:** *Mass selection on complex genetic interaction systems raises the fitness of those subpopulations.*
>
> **Phase III:** *Interdemic selection then raises the fitness of the large or global population.*

The understanding of the SBT I have just provided has, like that of Fisher's LPST, remained unchanged for the last 70 years but for Wright's change in view of the importance of random genetic drift in the evolutionary process (Provine 1971; 1985; 1986). This summary is sufficient for present purposes.

The differences underlying Fisher's LPST and Wright's SBT are manifest in the descriptions of them that I have just given. Each biologist had alternative views concerning each of the fundamental elements of population genetics theorizing. Indeed, Fisher and Wright had alternative conceptions of the main mechanisms of evolution (selection vs. drift, various modes of selection, and migration), the ecological context of evolution (large panmictic vs. small subdivided populations), the genetic basis of evolutionary change (additive vs. non-additive genetic variance), and the main mechanisms of speciation (divergent and disruptive selection vs. by-product of gene frequency changes in small populations) (see Wade and Goodnight 1998: 1538; Table 1 below). The fundamental differences between Fisher's and Wright's evolutionary theories are what drove the 1929-1962 debates between them (Provine 1985; 1986) and, as we will see, are what drive the new debates, 1997-2000.

Coyne et al. (1997): A Critique of the SBT

In the June 1997 issue of *Evolution*, Jerry A. Coyne, Nicholas H. Barton, and Michael Turelli published a comprehensive critique of Wright's SBT, "Perspective: A Critique of Sewall Wright's Shifting Balance Theory of Evolution" (Coyne et al. 1997). Their critique involves the evaluation of theoretical and empirical work from the last 70 years aimed at demonstrating the importance of Wright's proposed shifting balance process in nature. According to Coyne et al., the last 40 years of approbation of Wright's SBT is misplaced. Neither theoretical nor empirical work has gone very far toward substantiating the SBT.

Consider Coyne et al.'s explicit thesis, which they set out in their abstract (Coyne et al. 1997: 643):

> We evaluate Sewall Wright's three phase "shifting balance" theory of evolution, examining both the theoretical issues and the relevant data from nature and the laboratory. We conclude that while phases I and II of Wright's theory (the movement of populations from one "adaptive peak" to another via drift and selection) can occur under some conditions, genetic drift is often unnecessary for movement between peaks. Phase III of the shifting balance, in which adaptations spread from particular populations to the entire species, faces two major theoretical obstacles: (1) unlike adaptations favored by simple directional selection, adaptations whose fixation requires some genetic drift are often prevented from spreading by barriers to gene flow; and (2) it is difficult to assemble complex adaptations whose constituent parts arise via peak shifts in different demes. Our review of the data from nature shows that although there is some evidence for individual phases of the shifting balance process, there are few empirical observations explained better by Wright's three-phase mechanism than by simple mass selection. Similarly, artificial selection experiments fail to show that selection in subdivided populations produces greater response than does mass selection in large populations. The complexity of the shifting balance process and the difficulty of establishing that adaptive valleys have been crossed by genetic drift make it impossible to test Wright's claim that adaptations commonly originate by this process. In view of these problems, it seems unreasonable to consider the shifting balance process as an important explanation for the evolution of adaptations.

Coyne et al. (1997: 644) take themselves to be criticizing Wright's claim, and the alleged support for it, that the SBT is *the* general account of cumulative evolutionary change (Wright 1940: 181; 1978: 524, 1415). The principal thrust of Coyne et al.'s argument is their view that the SBT is not an *important explanation* in the field of population genetics, as Wright and apparently his followers claim, *because* it is not *the* general account. To be sure, there is more to Coyne et al.'s argument: Coyne et al. also argue that Wright's SBT does not account well at all even for the evolutionary data that are typically used to corroborate it. Further, there is a purely mathematical critique, in which aspects of the SBT are criticized as not being plausible on their face (see, e.g., the appendix to Coyne et al. 1997, 669-671). The present article focuses exclusively on the principal thrust of Coyne et al.'s critique, which I stated above.

As I understand Coyne et al., if the SBT is *the* general account of cumulative evolution, then it must be *explanatorily adequate* for the population genetics domain and that means that the SBT must have a *general scope of applicability* in the population genetics domain. Arguably, Wright's problematic was to propound a population genetics theory that has a general scope of applicability in the population genetics domain: Wright's aim was to account for the origin and maintenance of genetic novelty in populations (Wright 1931; 1932; cf. Wade and Goodnight 1998: 1538). And, as Wright says, the SBT, as a solution to his problematic, describes the principal process of cumulative evolution (Wright 1940: 181; 1978: 524, 1415). Coyne et al., insofar as they are explicitly criticizing Wright's claim that the SBT is *the* general theory of evolution, are criticizing the notion that, with the appropriate philosophical interpretation, the SBT has a general scope of applicability in the population genetics domain. That is, Coyne et al. are criticizing the view that Wright's SBT is explanatorily adequate.

Consider the kinds of things that Coyne et al. actually say with respect to their criticisms of Wright's SBT: Wright claims that the SBT *explains most* of evolution, that it is *the* or *a general* theory of evolutionary change, that it is *important* (Coyne et al. 1997: 643-645, 655, 664-665). Further, consider that Coyne et al.'s view is that the SBT describes a *rare* evolutionary process, that it is *limited*, that it describes a process that is too *complex* and *delicately balanced* to occur *often* in nature (Coyne et al. 1997: 646, 649, 650-651, 655, 656, 664-665). It is abundantly clear that for Coyne et al., the SBT is not explanatorily adequate for the population genetics domain; the SBT does not have the general scope of applicability that Wright and his followers apparently claim for it.

Wade and Goodnight (1998): A Synthetic Approach

In the December 1998 issue of Evolution, in "Perspective: The Theories of Fisher and Wright in the Context of Metapopulations: When Nature Does Many Small Experiments," Michael J. Wade and Charles J. Goodnight responded to Coyne et al.'s critique of the SBT (Wade and Goodnight 1998). Their response is not a point by point critique of Coyne et al. (1997). Rather, it is a review of both (hence, a "synthetic" approach as Wade and Goodnight say) the SBT and the LPST given recent (within the last 15 years) explorations into the population genetics of metapopulations. Wade and Goodnight point out that the studies they discuss in their paper were, but for one or two, omitted by Coyne et al. Wade and Goodnight claim that Coyne et al. are being premature in their dismissal of the importance of Wright's SBT and their apparently uncritical avowal of the Fisherian alternative. Wade and Goodnight's claim is grounded in what they perceive as substantive problems for both Fisher's and Wright's views (Wade and Goodnight 1998: 1537; cf. Peck et al. 1998). That is, according to Wade and Goodnight neither Fisher's LPST nor Wright's SBT is the general population genetics theory of evolution.

Wade and Goodnight consider a large amount of theoretical and empirical work on evolution in metapopulations. Wade and Goodnight begin by delineating what they take to be the fundamental differences underlying the apparently alternative theories. They present the delineation which I reconstruct in Table 1 below. The next step Wade and Goodnight take, as I interpret them, is to evaluate the LPST and the SBT against theory and evidence to determine what claims can be made about the theories' respective explanatory adequacy, scope, and generality in the domain of population genetics.

{TABLE 1 ABOUT HERE}

Painstakingly, Wade and Goodnight argue that for *each* category of difference in Table 1 population geneticists have learned different things about evolution in nature by exploring it via the different theories (Wade and Goodnight 1998: 1537, 1540). They argue the following:

(1) Explorations of evolution in nature via the LPST and the SBT demonstrate that at least elements of them are correct for various items in the population genetics domain (Wade and Goodnight 1998: 1537).

(2) There are properties of the items in the domain that Fisher and Wright did not address, e.g., the conversion of non-additive to additive variance in variously structured populations (Wade and Goodnight 1998: 1543-1546).

(3) There are specific problems for both theories in explaining the population genetics domain given recent explorations of evolution in nature under their respective rubrics (Wade and Goodnight 1998: 1549).

Taken as a response to Coyne et al. (1997) Wade and Goodnight are to be understood, in my view, as claiming the following: While Coyne et al. are correct that the SBT is not *the* general theory of the population genetics of the evolutionary process, *neither* is Fisher's LPST. Moreover, it is premature to dismiss *either* of them as unimportant in evolution given what population geneticists have learned via their exploration (Wade and Goodnight 1998: 1537, 1549).

Put in terms of the philosophical parlance of the present review, Wade and Goodnight are claiming that Coyne et al.'s finding that the SBT is *explanatorily* in*adequate* for the population genetics domain is correct. But, to claim that Fisher's alternative LPST is *explanatorily adequate* in the way that the SBT is not is incorrect. Indeed, argue Wade and Goodnight, theory and evidence show that there is plenty of room in the domain of population genetics for both the LPST and the SBT, and, moreover, that there is plenty of work left to do to determine the extent of applicability in the domain of each (Wade and Goodnight 1998: 1548-1549). Thus, in evaluating the explanatory adequacy, scope, and generality of the SBT and the LPST, the aim is not to determine which theory is the general theory of the domain. Rather, as I argue more forcefully below, the object is to evaluate the explanatory adequacy of the alternative theories for the parts of the domain for which the theories are applicable, i.e., to determine the scopes of applicability of the relevant theories and allow that such scope demonstrate the theories' explanatory adequacy within the population genetics domain.

The Coyne-Wade Debate as a Relative Significance Controversy.

The two papers by Coyne et al. (1997) and Wade and Goodnight (1998) just reconstructed comprise half of the main scientific papers in the new Fisher–Wright controversy. I discuss the other two papers, which are further responses, below (i.e., Coyne et al. 2000; Goodnight and Wade 2000). The dispute between Coyne and Wade is best understood as a relative significance controversy (Beatty 1995; 1997). Indeed, by analyzing the disagreements between Coyne and Wade as a relative significance dispute, the flaws in the debate's logical structure are made manifest. That is, analyzing the reignited Fisher_Wright controversy as a relative significance controversy demonstrates how Coyne et al. (1997; 2000) are mistaken in the way they evaluate the explanatory adequacy of Wright's SBT and how Wade and Goodnight are correct in their approach to evaluating the explanatory adequacy of Fisher's LPST and Wright's SBT.

Toward understanding the way relative significance controversies work, consider what Beatty says about the ways in which biologists argue and the nature of biological controversies (Beatty 1997: S432):

> What sorts of arguments would we expect from two scientists pursuing alternative theories or models of the same domain of phenomena? Among other things, we might expect each to argue that his or her theory is *the* correct account of the domain, and that his or her rival's theory is incorrect.
>
> And indeed, arguments in biology sometimes proceed this way. But very often they do not. Biologists pursuing alternative accounts of a domain of phenomena are often concerned instead with whether their theory provides *a* correct vs. *the* correct account of the domain. Beyond that, they are often concerned to establish the "relative significance" of their theory.

According to Beatty, “the relative significance of a theory within its domain is roughly the proportion of phenomena within the domain that the theory correctly describes” (Beatty 1997: S432). Further, “what is at issue in a relative significance dispute is the *extent of applicability* of a theory or mechanism within a domain” (Beatty 1995: 66).

According to Beatty, relative significance controversies reflect a specific kind of *theoretical pluralism* (Beatty 1995: 66): Given that relative significance disputes are about the extent of applicability of specific theories or mechanisms for some domain, what is reflected is the notion that the domain is fundamentally heterogeneous. That is, where there are relative significance controversies, the domain requires more than one, and perhaps a multitude, of *different* theories or mechanisms to explain it. Thus, for a given domain, “[t]here is no single theory or mechanism –not even a single synthetic, multi-causal theory or mechanism– that will account for every item of the domain” (Beatty 1995: 65). Moreover, the issue is not that there is insufficient evidence for some one single theory that suggests the kind of theoretical pluralism Beatty describes. Rather, the issue is that the evidence in fact *demonstrates* that the domain is heterogeneous and that multiple theories or mechanisms are required (Beatty 1995: 65).

Relative significance controversies which reflect theoretical pluralism so understood are rife in biology (Beatty 1995: 65). And Beatty enumerates several such controversies cutting across domains of biology to motivate his judgment (Beatty 1995: 65-67). An important and good example of a relative significance controversy in evolutionary biology that Beatty mentions is the ongoing debate over the extent of applicability of theories of speciation. It is commonly thought that the only important speciation mechanism is allopatry in some form or other (e.g., allopatry with pleiotropy and hitchhiking). Other mechanisms of speciation, however, have been articulated, i.e., forms of sympatric and parapatric speciation. William Rice and Ellen Hostert’s (1993) oft-cited review of 40 years of laboratory work on speciation indicates that the basic allopatry model is well supported empirically and that other models (and their forms) are less well supported. However, Rice and Hostert do not claim that the corroboration of the basic allopatry model is tantamount to claiming that it is the single correct model of speciation in the evolutionary domain. Indeed, they argue, quite strongly, that there is no good theoretical or empirical reason to think that the allopatry model is the only important one for understanding animal speciation (Rice and Hostert 1993: 1653). The thrust of the controversy over speciation, so far as I can see, is that there are multiple speciation mechanisms and that no one speciation model will account for all, or even most, speciation events (cf. Otte and Endler 1989). It is my view that the debates of the new Fisher–Wright controversy are best understood as a relative significance controversy, reflecting theoretical pluralism, of the sort Beatty describes. Beatty does not mention any aspect of the Fisher–Wright controversy in his discussions.

Figure 2 below is a diagrammatic representation of the reignited Fisher–Wright controversy that demonstrates that it exemplifies a relative significance controversy. In the diagram, the upper row of circles designates Coyne et al.'s (1997) critique of the SBT as characterized in my earlier discussion. The lower row of circles designates Wade and Goodnight's (1998) response, characterized above. The domain of population genetics is the baseline and includes all items owing to the maintenance and refinement of genetic variation (in white). The diagram requires explication. Coyne et al. (1997) argue that Wright claimed, sometimes, that his SBT explained most of the domain of population genetics at least for the evidence Wright reviewed in his *magnum opus*. If the domain is represented in Figure 2A, then Wright's claim is represented by Figure 2B. The blackened portion of the domain represents the idea that Wright's SBT explains most of the domain. Wright, as Coyne et al. say, left room for Fisher's LPST. Indeed, Wright's most explicit claim for this is in his final paper (Wright 1988): Wright summarizes four main theories of evolution, his own, Fisher's, Haldane's (1932), and

Motoo Kimura's (1968). He claims, in the last sentence of the 1988 paper, "[a]ll four are valid" (Wright 1988: 122; cf. Crow 1990; 1991). Because Wright claimed his SBT had the widest scope of applicability, in comparison to Fisher's LPST, the LPST is represented by the grey portion of Figure 2B. (Wright does not discuss what he thinks are the scopes of applicability of Haldane's or Kimura's theories and, so, I do not include them here. It is interesting to note, as Sahotra Sarkar (*forthcoming*) points out, that Haldane emphasized pluralism early on in the 1930s.)

{FIGURE 2 ABOUT HERE}

Coyne et al.'s criticism, in Figure 2C, reverses the respective scopes of the theories. The SBT, Coyne et al. have allegedly demonstrated, has much more limited scope than the LPST. However, their view is not that the SBT has *no* place in evolution; they merely think that it does not have an *important* place. Via Figures 2A-C, we see that what Coyne et al. are attempting to do is argue for the greater extent of applicability in the population genetics domain for the LPST than the SBT. This is the hallmark of a relative significance dispute. However, it is unclear whether Coyne et al. strongly support theoretical pluralism. Clearly, they leave room for both theories; only they reverse Wright's judgment so that now it is the LPST that explains most of evolution. Differently put, Coyne et al. do not think of their dispute as one which will determine *the* correct theory for the population genetics domain. They are pretty clearly interested in determining which is the most general theory; which theory explains most of the domain. And this suggests that there is some room for the theoretical pluralism so characteristic of relative significance controversies. It should be noted, however, that when Coyne et al. choose the LPST as *the* general theory, they seem to virtually jettison the SBT, casting it off as *utterly* unimportant. Indeed, we saw above that this is their explicit language. So, even though Coyne et al. support the kind of theoretical pluralism reflected by a relative significance dispute, it is strongly tempered by the fact that they do not appear to support much of a role at all for the SBT. I return to this issue, which hinges on an appeal to parsimony Coyne et al. make as a way of arguing for the generality of Fisher's LPST, below as it is crucial to understanding what I take to be the logical conflict in the new Fisher_Wright controversy.

Notice that the representation of Wade and Goodnight's (1998) response to Coyne et al. (1997) is graphically more complicated than the representation of Coyne et al.'s dispute. Figure 2D represents the population genetics domain. Wade and Goodnight support the view that the domain has plenty of room for both the LPST and the SBT. And, moreover, that neither Fisher's LPST nor Wright's SBT is best understood as *the* general theory of the domain. In Figure 2E, I represent this state of affairs by showing that both theories explain domain items, but that neither theory explains *most* of them. The scope of the LPST is represented by the diagonally-hatched ellipse. The scope of the SBT is represented by the cross-hatched ellipse. The size of the circles is arbitrary on my part, except that they are not very large. The remaining portions of the domain (in white) are yet to be explained, or, perhaps (for some parts), are satisfactorily explained by other theories.

Figure 2F represents what I take Wade and Goodnight to be doing in their synthetic evaluation of Fisher's LPST and Wright's SBT. In my view, Wade and Goodnight claim that there is some intended scope of the LPST and the SBT. Table 1 above, I take it, articulates what Wade and Goodnight believe to be the items under the intended scope of applicability of the theories. One aim for population geneticists is to determine to what extent the LPST and the SBT in fact explain the domains for their intended scope. Wright claimed that his SBT explained most of the domain of population genetics. *Neither* Coyne et al. *nor* Wade and Goodnight support Wright's view. For Wade and Goodnight, the alternatively hatched ellipses in Figure 2E are, it seems to me, representative of their assessment.

It is unclear what Fisher claimed for the intended scope of the LPST. However, as I understand the spirit of Fisher's discussion of his Fundamental Theorem Natural Selection (FTNS), the centerpiece of his evolutionary thinking, the *principal* process of evolution, contra Wright, is natural selection, or mass selection (Fisher 1930: 34-35). So, Fisher seems to have held the view that his LPST would have a wide scope of applicability. And certainly Coyne et al. (1997) hold the view that the LPST has a wide scope of applicability. Wade and Goodnight argue that the scope of the LPST is more limited. Wade and Goodnight further claim that it is important to determine the extent to which the boundaries of the intended scopes of the LPST and the SBT can be pushed. That is, they think that it is important to see what more can be learned about the population genetics domain via explorations of the alternative theories. This is represented in Figure 2F by the bulging ellipses extending beyond the assessed scopes of the LPST and the SBT. The extent to which the boundaries of the LPST and SBT can be pushed is where the severest problems for both the LPST and the SBT lie. That is, we see where the LPST and the SBT are limited in efforts to explain the domain. In part, the bulging ellipses are also where successes lie, e.g., as Wade might argue for his studies of group selection as an extension of aspects of Wright's SBT beyond what Wright claimed (e.g., Wade 1976; 1977; 1978; cf. discussions by Griesemer and Wade 1988; Lloyd 1986).

The hallmark of a relative significance controversy is aptly reflected by Wade and Goodnight's (1998) response to Coyne et al. (1997). They are attempting to determine the extent of applicability in the population genetics domain of the LPST and the SBT. Moreover, their review reflects a rather strong theoretical pluralism: Wade and Goodnight advocate *both* the LPST and the SBT as explanations of the population genetics domain. So, each has a place for explaining items in the domain of population genetics. Moreover, implicit in their discussions of the main problems for and extensions of the LPST and the SBT, they suggest that it is plausible that more theories are necessary. This attitude is not merely the spirit of Wade and Goodnight's review. It is found in explicit statements of theirs:

> [W]hen and how to apply the theories to the natural world has been and continues to be a source of controversy (Wade and Goodnight 1998: 1537).
>
> In the very large populations of Fisher's theory, considerations of genetic architecture are not relevant.... Little of consequence is lost by lumping epistatic gene interactions with the nonheritable environmental variable (Wade and Goodnight 1998: 1543).
>
> The biology of the natural world can present difficulties for one theory or the other theory and may limit the areas and questions to which each theory can be applied (Wade and Goodnight 1998: 1548).
>
> ...[F]or Fisher's theory, speciation is particularly problematic because the genetic mechanisms for reproductive isolation involve the indirect response to local adaptation. This is most unfortunate for those who would use Fisher's theory to explain all of adaptive evolution... (Wade and Goodnight 1998: 1549).

On Wade and Goodnight's view, there exist very different kinds of evolutionary systems. Some of those systems are adequately accounted for by Fisher's LPST. These are systems in which populations are large and can be understood effectively as panmictic. In such populations, random genetic drift, e.g., has little evolutionary efficacy. But, according to Wade and Goodnight, populations are not always large; there are metapopulations. And in such evolutionary systems many of Wright's considerations, such as random genetic drift, epistasis, and migration, are important. The population genetics domain is fundamentally heterogeneous. Multiple theories are required to explain it.

Summary remarks are worth making at this point. I have characterized Coyne et al. (1997) and Wade and Goodnight (1998) in philosophical parlance. I claimed that the main evaluation strategies are *explanatory adequacy*, *scope*, and *generality*. Given the discussion in the present section, it should be becoming clear that Coyne et al. and Wade and Goodnight are applying these strategies rather differently and getting different results for the relative significance controversy they are engaged in. I explore this below.

Coyne et al. (2000), Goodnight and Wade (2000): Epicycles

In the February 2000 issue of *Evolution*, Coyne et al. published a response to Wade and Goodnight (1998) (as well as Peck et al. 1998): “Is Wright’s Shifting Balance Process Important in Evolution?” (Coyne et al. 2000). Goodnight and Wade (2000) is a response, in the same journal and issue, to Coyne et al. (2000): “The Ongoing Synthesis: A Reply to Coyne, Barton, and Turelli.” What one expects from a continuation of the controversy is debate over the relevant merits and demerits of the previous works. And I think some of that is present in the latest volley between Coyne et al. and Wade and Goodnight. However, rather than the latest volley representing any kind of progress in the new Fisher–Wright controversy, ultimately what we are left with is an epicycle on the 1997-1998 exchange. That is, we are left with a series of misunderstandings of precisely what is at issue in the controversy and a set of responses that masquerade those misunderstandings as a continuing debate.

Coyne et al. (2000) respond to Wade and Goodnight’s (1998) critique of them piece by piece. I will only reiterate some of their arguments briefly here because my aim is to examine the overall structure of their responses. According to Coyne et al. (2000), they agree with Wade and Goodnight that there is evidence for such evolutionary phenomena as genetic drift, epistasis, population subdivision, differential extinction and proliferation of groups, and temporally and spatially varying fitnesses that are described and synthesized by Wright’s SBT. What they do not agree with Wade and Goodnight about is the specific mixture of these phenomena in the SBT as a description of the principal process of cumulative evolution (Coyne et al. 2000: 306). Indeed, Coyne et al.’s view is that all of the phenomena mentioned by Wade and Goodnight as problematic for Fisher are adequately captured by Fisher’s LPST as they (Coyne et al.) understand the theory.

Coyne et al.'s claim about what they do and do not agree with Wade and Goodnight (1998) about hinge on two rather specific, and in my view peculiar, claims about interpreting Fisher's LPST: The first claim concerns criticisms by Wade and Goodnight (1998) concerning Fisher's apparent ignoring of epistasis in evolution and its implications for any understanding of the LPST. According to Coyne et al., Wade and Goodnight criticize an interpretation of Fisher's LPST that Coyne et al. do not adhere to. Indeed, the interpretation, stated in my summary of Fisher's LPST above, is one that Coyne et al. (2000: 307) claim that *no one* has *ever* adhered to, *including Fisher*. Here is what Coyne et al. explicitly claim (concerning Fisher's treatment of epistasis and the broader interpretation of the LPST):

> [W]hatever Fisher's views of the evolutionary significance of epistasis, he clearly did not ignore it. For example, Fisher … explicitly discussed epistasis and made an important distinction between the biological reality of complex epistasis and the statistical importance of epistatic terms involving interactions among three or more loci. Similarly, Fisher … discussed the possible importance of two-locus epitasis for the evolution of recombination rates… [W]hile Fisher largely neglected epistatic contributions to the genetic variance…, this does not imply that he supposed the additive components of gene action to be fixed quantities, independent of the state of other genes (Coyne et al. 2000: 307).
>
> Wade and Goodnight's claim that the primary goal of Wright's SBT was "explaining the origins of adaptive novelty, whereas for Fisher it was explaining the refinement of existing adaptations" [see Table 1 above] is incorrect. As we noted …, Wright himself said that the SBT creates "the most favorable conditions for a continuing evolutionary process" … and "this shifting balance process … has been the principal basis for evolution under exclusively biparental reproduction." … In the four volumes of Wright's *Evolution and the Genetics of Natural Populations*, it is hard to find a single experiment or observation, no matter how trivial, that is not construed as supporting the SBT… (Coyne et al. 2000: 307).

I will take each comment in turn.

There has been sustained controversy over what Fisher did and did not include in his discussions of epistasis and its role in evolution. Indeed, the view of Fisher's LPST that Coyne et al. (2000) think no one has ever adhered to is, in fact, the *standard* interpretation of Fisher: *Evolution occurs in large, randomly mating panmictic populations where the (small) effects of* *selection acting on the additive (weak) effects of alleles determine organisms' evolutionary fate* (e.g., Edwards 1994; Gayon 1998; Li 1955; Lewontin 1974; Provine 1971; 1985; 1986). I think Coyne et al. are incorrect about the claims they make concerning interpretations of Fisher and so I think they are being unfair to Wade and Goodnight. Moreover, the way in which Coyne et al. are incorrect starts them down the road to misapplying the evaluation strategies of *explanatory adequacy*, *scope*, and *generality* in evaluating Fisher's and Wright's evolutionary theories. But how are Coyne et al. incorrect?

Goodnight and Wade respond to Coyne et al.'s misinterpretation charge (Goodnight and Wade 2000: 318-319). According to Goodnight and Wade, what is at issue is not that Fisher *failed* to treat epistasis, etc. Rather, what is at issue are the logical consequences for Fisher's LPST *given the way in which he, and his followers, in fact treat epistasis, etc.*:

> We agree with Coyne et al. … that Fisher was aware of the complications added by epistasis and population structure. His concept of the "average excess" was developed specifically to address complications such as assortative mating. However, in most discussions of his writings, Fisher did not deal explicitly with population genetic subdivision. In our reading of his work, … Fisher adopted the view that most species have sufficiently high levels of migration among populations to be considered effectively panmictic. Thus, although Fisher dealt with epistasis and mating structure, he effectively ignored the consequences of population genetic subdivision (Goodnight and Wade 2000: 318).
>
> We agree that Fisher was aware of epistasis and knew of the effects it could have on his statistical concepts of additive effect and average excess. Nevertheless, Fisher tended to assume a constancy of average genic effects. This is entirely reasonable if you also assume, as we believe Fisher did, that populations are typically large, and that selection is weak … In such populations, epistasis can be relegated to the environmental component of phenotypic variance, as Fisher stated. However, we believe that these features are hardly universal and, thus, that Fisher made a "value" judgment regarding the role of epistasis in evolution when he relegated it to the environmental and "nonheritable" component of variation (Goodnight and Wade 2000: 318-319).

Goodnight and Wade's claims here are quite close to my own views regarding Fisher's LPST.

Note what is especially clear here: It is not that Goodnight and Wade think that Fisher did not treat epistasis and its role in evolution. Rather, they think that Fisher *mis*treated epistasis and its role in evolution. I think that it is true, at least by 1941, that Fisher did not ignore epistasis (Fisher 1941). However, following Wade (1992), Fisher's treatment of epistasis is biologically unsound because of the averaging endemic to his (Fisher's) models: Because of the significant amount of averaging over epistatic effects, it is an artifact of the models that epistasis has little evolutionary effect on genetic variance and thus is not an important feature of the biological world as Fisher believed. Epistasis thus cannot be relegated to the environmental component of phenotypic variance by Fisher's means. Coyne et al. (2000) do not evaluate any biologist's critical treatment of Fisher's view of epistasis in a way that bolsters their view that Fisher adequately treats, or treats at all, epistasis in his models.

Let us now consider Coyne et al.'s (2000) second comment on Wade and Goodnight's (1998) interpretation of Fisher's LPST. Here, the issue is over the aims of the alternative theories. Wade and Goodnight, as is seen in my Table 1, claim that Fisher's LPST is aimed at accounting for the maintenance and refinement of existing genetic variation whereas Wright's SBT is aimed at accounting for the origin and maintenance of genetic novelty. Coyne et al. (2000) claim that this distinction is faulty. And they do so by arguing that it was Wright's aim to explain all of cumulative evolution via his SBT (Coyne et al. 2000: 306). I do not see exactly what Coyne et al. have established here. Furthermore, Goodnight and Wade (2000) do not appear to me to answer this specific claim of Coyne et al. I shall attempt to clarify the issue.

What Coyne et al. (2000) are suggesting is that Wright argued for a broader scope of applicability for his SBT than Fisher did for his LPST. That is, Coyne et al. believe that Wright thought that his SBT described the principal process of cumulative evolution, and that Fisher's did not. According to Coyne et al., then, given that Fisher and Wright differ on precisely what they take the scope of applicability of their theories to be, Fisher must not be making the same kind of claim that Wright is. However, as Coyne et al. argue, ultimately, Wright's SBT fails to do what he claims for it and where the SBT fails, Fisher's LPST succeeds. Perhaps Coyne et al. would be correct here if Fisher did not also aim to account for the principal processes of evolution. It is interesting, I think, that Fisher nowhere says explicitly what he takes the intended scope of his theory to be. However, Fisher's lack of an explicit claim is not too problematic. Given the brief discussion above concerning my understanding of Fisher's FTNS, it is clear that Fisher is attempting to construct a population genetics theory that accounts for most observed evolutionary change (Fisher 1930: 34-35; 1958). Given that the FTNS is the centerpiece of Fisher's evolutionary thinking, it seems clear that he takes the LPST to be the general theory of the population genetics of evolution.

So, if both Fisher and Wright take themselves to be accounting for all or most of cumulative evolutionary change, then to claim that somehow Wright is claiming more for his SBT than Fisher is for his is wrongheaded. What Wade and Goodnight in fact intended, it seems to me, in showing the distinction between Fisher's and Wright's intended aims for their theories is this (Wade and Goodnight 1998: 1538, 1547-1549): Even if Wright was mistaken to have claimed that the SBT describes the principal processes of cumulative evolution, Fisher's LPST is little better. After all, say Wade and Goodnight, the LPST fails to account for the *origin* of genetic novelty, something that at least Wright attempted to account for. Differently put, because Fisher's LPST has no inherent way of accounting for the genetics of speciation (because it has a seriously flawed account of epistasis) then his theory is not able to stand as *the* general theory of the population genetics of evolution any more than Wright's SBT. A main problem with Wright's theory, at least the most general problem, is that it is as yet unknown what the extent of applicability the theory has in the population genetics domain.

The criticism I raised just now against Coyne et al. (2000) brings us to precisely where it needs to bring us. And that is back to the evaluation strategies of *explanatory adequacy*, *scope*, and *generality*, and their application in relative significance controversies.

Toward Resolution (Modestly)

The relationships between theories' explanatory adequacy, scope, and generality are different for Coyne et al. (1997; 2000) and Wade and Goodnight (1998; Goodnight and Wade 2000). But because Coyne et al. and Wade and Goodnight agree that they are involved in a relative significance dispute, the strategies should have the same relationships. Because the strategies have different relationships, Coyne et al. and Wade and Goodnight are talking past each other. And, as such, the new Fisher–Wright controversy is far off the course to resolution. However, I think the two "sides" can be put on the course to resolution.

As I understand the general form of Coyne et al.'s (1997; 2000) principal argument, Wright's SBT is explanatorily inadequate for the domain of population genetics because it does not have a *general* scope of applicability. That is, Wright's SBT does not explain all or most of evolution because theory and evidence do not support such a strong claim. Notice that Coyne et al.'s claim depends upon directly connecting the explanatory adequacy of a theory with the generality of scope of the theory. As I understand Coyne et al.'s argumentative strategy, the generality is maximized by maximizing *simplicity* or *parsimony*. That is, for Coyne et al. (1997; 2000), the explanatorily adequate theory is the most general theory. And the most general theory is the one that makes reference to the smallest economy of processes and entities. That is, the most general theory will be the simplest, or most parsimonious theory. The connection between generality and simplicity that is apparent in Coyne et al.'s argument requires explication.

G. C. Williams' (1966) famous appeal to parsimony (here, synonymous with "simplicity") is often taken to ground contemporary (evolutionary) biologists' appeals to it (Sober

1984; 1990). Williams' appeal to parsimony was made in the context of the levels of selection debates (see, e.g., Brandon and Burian 1984). But it is easily generalized. Williams' view is, basically, that if the evolution of some trait can be adequately accounted for via selection acting on organisms, then there is no *need* to invoke group selection (the differential proliferation and extinction of groups of organisms) to account for the evolution of the trait (Williams 1966: 4-5, 11-13, 18-19, 123-124, 261-262; Sober 1984: 237-240; 1990: 79-84). Generalizing Williams' principle of parsimony here results in something like the following: If the evolution of populations can be explained adequately via a theory that postulates a small economy of entities and processes, then there is no need to invoke a theory with a larger economy of entities and processes. In Williams' case, group selection and groups themselves are additional evolutionary processes and entities that are not needed to explain the evolution of traits.

In the new Fisher–Wright controversy, Wright's SBT refers to processes such as random genetic drift, migration, interdemic (group) selection and entities such as demes (groups). Fisher's LPST refers only to the processes of mutation and natural selection. It seems clear on the version of parsimony just articulated that Fisher's LPST is more parsimonious than Wright's SBT. Indeed, consider what Wade and Goodnight (1998) say about Coyne et al.'s appeal to parsimony as a way of rejecting Wright's SBT:

> Coyne et al. …, echoing the early group selection literature, advocated Occam's razor … as grounds for dismissing the SBT. They argued … that "there are few empirical observations explained better by Wright's three-phase mechanism than by simple mass selection" and that "it seems unreasonable to consider the shifting balance process as an important explanation for evolution of adaptations" (Wade and Goodnight 1998: 1537).

But how does parsimony figure into generality of scope of applicability of a theory? In particular, how does parsimony figure into generality in Coyne et al.'s argument?

According to Richard Levins (1968: 7), it is not possible to maximize at the same time generality, realism, and precision of a model (or theory, as a cluster of models) during model building in population biology. For instance, generality might be sacrificed for realism and precision. In such an instance, a model builder might construct a model that includes as many of the real features of the system being modeled in a way that precisely captures the system's dynamics. A fruitful way of reading Wade and Goodnight (1998) it seems to me is by reading them as arguing that Coyne et al. are sacrificing realism for generality and, allegedly, precision. One can make such a sacrifice by simplifying the model, i.e., by constructing a model that captures the apparently essential aspects of the system under scrutiny while removing those aspects that are apparently distracting, or those that introduce only small changes to modeling results, and by introducing patently false assumptions that facilitate study (Levins 1968: 6-7).

The LPST exemplifies a fairly extreme form of the above approach to model construction in my view. Consider the following as an illustration of the point. A driving (mathematical) assumption of the LPST is that populations are infinitely large and panmictic (randomly mating). The evolutionary consequences of that assumption are important for assigning evolutionary importance to random genetic drift, migration, epistasis, etc. In other words, by assuming that populations are infinitely large, a model builder is able to treat random genetic drift, migration, epistasis, etc. as elements that introduce only small changes to the modeling results and, so, is able to treat such factors as unimportant in modeling evolution. Take random genetic drift, for instance. Random genetic drift is evolutionary efficacious in populations that are smallish (and certainly not infinitely large and panmictic). If a population is too small, drift will take it to extinction. But if the population is very large (e.g., infinite), then drift is negligible if not altogether absent. So, assuming that populations are infinitely large allows a modeler to discount the evolutionary importance of random genetic drift. Indeed, Fisher used the assumption that populations are infinitely large to great effect in *The Genetical Theory of Natural Selection*, allowing him to set aside such things as effects of drift and migration on the evolution of populations and assign considerably little importance to any evolutionary consequences of epistasis (Fisher 1930).

As I understand Coyne et al.'s critique of the SBT and advocacy of the LPST, they are claiming that the simplifying assumptions endemic to Fisher's LPST enable them to explain, in a way that preserves precision of modeling results (i.e., so that the results stay well within standards of error), a large amount of the evolutionary domain. Differently put, Fisher's simplified theory results in one with a general scope of applicability and, by virtue of that general scope of applicability, the LPST is explanatorily adequate. Notice here that an appeal to the simplification strategy I have discussed yields to an appeal to parsimony: If the evolution of populations can be explained adequately via a theory that postulates a small economy of entities and processes, then there is no need to invoke a theory with a larger economy of entities and processes. The LPST's assumption that populations are infinitely large is a key assumption that allows one to pare down its models so that what is important to understanding the evolution of adaptations are mutations of small effect and low pressures of natural selection. Yet, for Wade and Goodnight, it is the paring down of the models based on such assumptions that is a matter of debate. Consider, e.g., the following comment that Wade and Goodnight make:

> It is common place to reify additive effects and treat them as properties of genes, independent of genetic and ecological context. Perhaps the fault lies not so much with Fisher's L[P]ST as with the uncritical application of it to evolutionary problems it was not meant to solve, such as speciation, or to ecological and genetic contexts in which it does not hold, such as evolution in metapopulations. For the reasons discussed above [previously in Wade and Goodnight 1998], accepting the L[P]ST over the SBT on the grounds of parsimony … does not seem warranted to us (Wade and Goodnight 1998: 1549).

On Wade and Goodnight's view, the results of constructing explanations of the population genetics of evolution using the sorts of modeling assumptions embedded in the LPST do not result in the general explanations for which Coyne et al. (1997; 2000) argued. Indeed, there is, as Wade and Goodnight (1998) show, considerable evidence that it is not always the case that when the infinitely large population size assumption is made in a model, for example, that the results are at all precise.

In what Beatty (1995: 66) calls a controversy of the "Newtonian Ideal," Coyne et al.'s appeal to parsimony to maximize generality is appropriate. In such controversies, the aim is to determine which of a set of competing theories is *the* correct theory of the domain, or the theory that explains most or all of the domain. And this demands that the theory be demonstrably general in its scope of applicability in the domain. Beatty (1995) names the action of appealing to the Newtonian Ideal after Newton because it was Newton who propounded the criterion so thoroughly as a rule for reasoning in philosophy: "We are to admit no more causes of natural things than such as are both true and sufficient to explain their appearances" (Beatty 1995: 68). Newton's criterion is often taken as grounds for appealing to parsimony in theory construction and assessment. It is clear that the Newtonian Ideal and Williams' principle of parsimony discussed above are tantamount to each other.

However, considerable care must be taken in drawing a close connection between explanatory adequacy, generality, and parsimony because explanatory adequacy need not be so closely connected to generality. Lindley Darden (1991: 260-261) provides a discussion of explanatory adequacy and determining the scope of the domain (of a theory) that is useful for seeing that explanatory adequacy need not be so closely tied to generality. Darden suggests that the strategy of assessing the explanatory adequacy of a theory (on whatever view of explanation) is often closely tied to determining the scope of the domain of a theory. Darden's idea is that one of the aims of evaluating the explanatory adequacy of theories is determining precisely what is and what is not in the scope of the theory. In terms of relative significance disputes, the idea seems to me to be as follows. One is not looking for *generality* because one recognizes that *theoretical pluralism* is the rule. That is, one recognizes that the domain under scrutiny requires multiple theories to explain it rather than a single, general theory. So, a theory that is explanatorily adequate need not at the same time be *more* general than a competitor. And if it is not, no matter. All that matters is that we know what the theory's scope is. Differently put, what is crucial to evaluating theories in a relative significance controversy is determining the boundaries of the scope of the theory; an understanding of those boundaries is the epistemological indicator about whether a theory adequately explains. Explanatory adequacy in relative significance controversies is closely tied to determining the scope of the domain and not the generality of scope of theories. Now, Darden should not be understood as advocating the relationship between explanatory adequacy and determining the scope of applicability of a theory that I am. First, Darden is discussing the ways in which scientists (geneticists in her case) are constructing theories and the expectations about scope that go along with that process. In the 1997-2000 leg of the Fisher_Wright controversy, the theories have long since been constructed. Second, Darden does not advocate determining the boundaries of the scope of applicability of a theory as the epistemological indicator of the explanatory adequacy of a theory. Nevertheless, I think it is not problematic to take the connection between explanatory adequacy and determining the scope of applicability of a theory that Darden points out and extend it for use in the way that I suggest.

What does any of this mean for Coyne et al. (1997; 2000)? I think it means the following. Coyne et al. recognize that they are engaged in a relative significance controversy. At the same time, they are applying the evaluation strategy of explanatory adequacy as if it is solely connected to generality and simplicity. That is, Coyne et al. seem to believe that the aim of the controversy is to judge the explanatory adequacy of Fisher's and Wright's theories by determining which one accounts for more of the population genetics domain. Coyne et al. have ignored, or at least run roughshod over, the idea that the main aim of their part of the Fisher–Wright controversy is to determine the relevant scopes of Fisher's LPST and Wright's SBT. And, given that determination, to determine where, when, and how each theory is applicable.

Coyne et al. make the mistake I am claiming that they make because they are determined to demonstrate that Wright's claim that his SBT describes the principal processes of cumulative evolution is incorrect. Of course it is. As we have seen, Wright recognized this point himself almost 10 years before Coyne et al.'s critical review (Wright 1988; cf. Crow 1991). And Wade and Goodnight (1998; Goodnight and Wade 2000) are operating under the assumption that Wright's old claim from his *magnum opus* is incorrect. So either Coyne et al. are making a small and rather unoriginal point by arguing that Wright was incorrect that he has constructed *the* general population genetics theory of evolution, or they have made a more subtle error of misapplying the evaluation strategies of *explanatory adequacy*, *scope*, and *generality*.

It does not matter much which of the above state of affairs is true. But if the latter is true, then the mistake Coyne et al. make is not so bizarre. Beatty discusses this issue. According to Beatty, the Newtonian tradition has wide appeal in biology and the theoretical pluralism reflected by relative significance controversies is often only reluctantly accepted (Beatty 1995: 74). And, of course, the Newtonian tradition is commonplace in the physical sciences. Moreover, it is not necessarily a bad strategy to begin with in evaluating scientific theories. Indeed, whether parsimony is a bad scientific assessment strategy depends on the evidence (e.g., Beatty 1995: 74). My view in the case of the new Fisher–Wright controversy is that it is already fairly well established that the population genetics domain is heterogeneous (e.g., with regard to speciation). So there is no need to look for unifying population genetics theories of evolution. Or at least there is no need to determine whether Fisher's LPST or Wright's SBT is the one.

What can be said about Wade and Goodnight's (1998; Goodnight and Wade 2000) application of the evaluation strategies? I have already said that I think they are on the right track.

But how? That is, how do their evaluations of explanatory adequacy, scope, and generality of Fisher's LPST and Wright's SBT exemplify their engagement in a relative significance controversy? As I understand Wade and Goodnight (1998; Goodnight and Wade 2000), they argue that it is premature to adopt wholeheartedly either Fisher's LPST or Wright's SBT because the population genetics community has yet to determine the scopes of applicability of the two theories. That is, Wade and Goodnight agree that Wright's SBT does not account for all or most of cumulative evolution. However, continue Wade and Goodnight, there is substantial evidence that Wright's SBT accounts for some parts of the population genetics domain and that there are parts for which neither Fisher's nor Wright's theories account. Indeed, the main task of work on the new Fisher–Wright controversy, at least as far as Wade and Goodnight are concerned, is the determination of how, when, and where to apply the theories of Fisher and Wright in the population genetics domain (Wade and Goodnight 1998: 1537, 1548; Goodnight and Wade 2000: 317, 322).

For Wade and Goodnight to judge either Fisher's LPST or Wright's SBT as explanatorily adequate, there must be good evidence –e.g., some combination of fit between model and data, independent support for aspects of a model, and variety of evidence (Lloyd 1987; 1988)– that warrants a claim that the scope of applicability of the theories has been determined. According to Wade and Goodnight, there is evidence that both Fisher's LPST and Wright's SBT do in fact apply in the population genetics domain. But, it seems to me, at this point in the scientific work, Wade and Goodnight are unable to make a strong claim to the explanatory adequacy of either Fisher's or Wright's theories because of the problems that currently face them in the population genetics domain. This view is summed up, I think, nicely in Wade and Goodnight's (1998: 1549) Table 2, which I reproduce as my Table 2 below. In other words, until the scopes of the domain of Fisher's LPST and Wright's SBT are well-determined, Wade and Goodnight are unable to make any substantive claim to the explanatory adequacy of either theory.

{TABLE 2 ABOUT HERE}

In my view, Wade and Goodnight (1998; Goodnight and Wade 2000) are accurately applying the evaluation strategies of explanatory adequacy, scope, and generality in the new Fisher–Wright controversy. And, moreover, Wade and Goodnight have argued rather well for the view that the debates between Fisher and Wright, to the extent that they were over which theory, the LPST or the SBT, is *the* general theory of the population genetics of evolution, is over. The new controversy is a relative significance controversy, in which Coyne et al. are inadequately engaging. If I am right in my understanding of the status of the new Fisher–Wright controversy, then what is crucial at this stage of the controversy is a concerted effort at determining the scopes of applicability of Fisher's LPST and Wright's SBT. That is, the aim is to take the focus off trying to determine whether one or the other of Fisher's LPST and Wright's SBT are *the* general theories of evolution. Instead, the aim of work now is to determine how, when, and where Fisher and Wright were correct and then to fill in whatever gaps are left over.

Conclusion

This paper has aimed at philosophically analyzing the recent debates led by Coyne and Wade in the broader Fisher–Wright controversy in population genetics. There is no doubt that Provine (1985) was correct in his assessment, about 15 years ago, of the status of the debates between Fisher and Wright per se. They were, indeed, central, fundamental, and very influential. I take myself to have established that the debates are, because of their centrality, etc., also *persistent*. Toward the paper's aim, I have systematically reconstructed the argumentative structure of the debates over the differences underlying Fisher's LPST and Wright's SBT. I argued that the reignited Fisher–Wright controversy is best understood as a relative significance controversy and, moreover, that Coyne et al. (1997; 2000) are inappropriately engaged in it but that Wade and Goodnight (1998; Goodnight and Wade 2000) are appropriately engaged in it. I made brief remarks concerning how the two "sides" in the new Fisher–Wright controversy could redress the conflict in the logical structure of their debates. Given my philosophical analysis, what might be done, scientifically, toward resolving the new Fisher–Wright controversy?

One obvious answer to the question just asked is to engage energetically in solving the problems that Wade and Goodnight (1998) have pointed out exist for both Fisher's and Wright's theories (i.e., Table 2). A second fairly obvious answer to the question is to focus theoretical and empirical research on evolutionary phenomena which can plausibly be said to require an integration of various of Fisher's and Wright's theoretical components or which can plausibly be said to require some other, unrelated theory suggested by the further work. Such work is precisely what I think has been lacking in the new Fisher–Wright controversy, although in this vein it has been acknowledged widely that Fisher's theory of the evolution of dominance is false (e.g., Orr 1991; Mayo and Bürger 1997). It seems to me that, in spite of the disagreements between Coyne et al. and Wade and Goodnight, it has been established that neither Fisher's LPST nor Wright's SBT is the general theory of evolution. I encourage the two "sides" in the new Fisher–Wright controversy to push the limits of the theories to determine the gaps that need to be filled by other theories and what extensions of, and unifications between, Fisher's LPST and Wright's SBT can be made.

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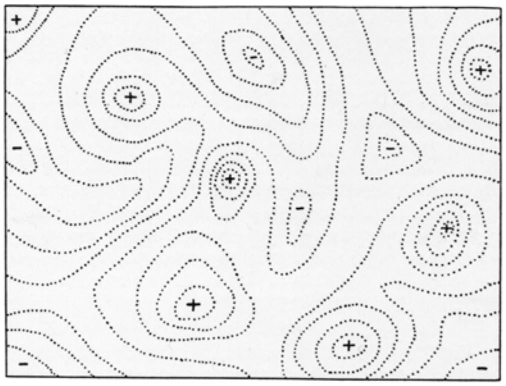
FIGURES AND TABLES



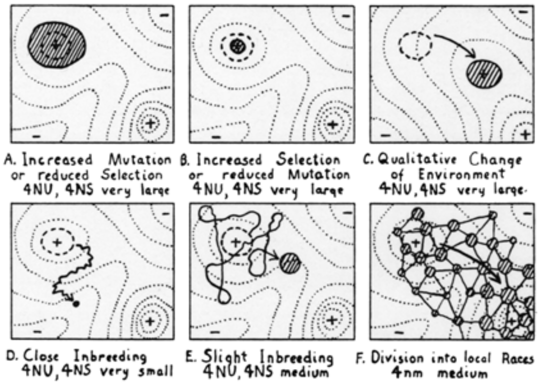


Fig. 1A

Fig. 1B

Fig. 1: Wright's two main adaptive landscape diagrams. Fig. 1A represents Wright's view of gene combinations graded for their adaptive value. Fig. 1B represents evolution on the adaptive landscape given the surface in Fig. 1A and under alternative assumptions. Windows A-E vary selection intensity (*s*) and mutation rate (*u*) in populations of varying sizes (*N*, *nm*). Window F represents Wright's view as expressed in the SBT. The figures are taken from Wright (1932: 163, 166).

	Wright	**Fisher**
Central problem of evolutionary theory	Origin of adaptation in constantly changing environments	Refinement of existing adaptations in a stable environment
Major processes of evolutionary change	Combination of local natural selection, random genetic drift, migration, and interdemic selection	Mutation and natural selection
Ecological context of evolution	Small, subdivided populations	Large, panmictic populations
Genetic basis of evolutionary change	Epistasis and pleiotropy; context dependence of allelic effects	Additive genetic effects; context independence of allelic effects
Process of speciation	Inevitable by-product of local adaptation in epistatic systems	Disruptive or locally divergent selection

Table 1: Fundamental differences in emphasis underlying Wright's SBT and Fisher's LPST. From Wade and Goodnight (1998: 1538).

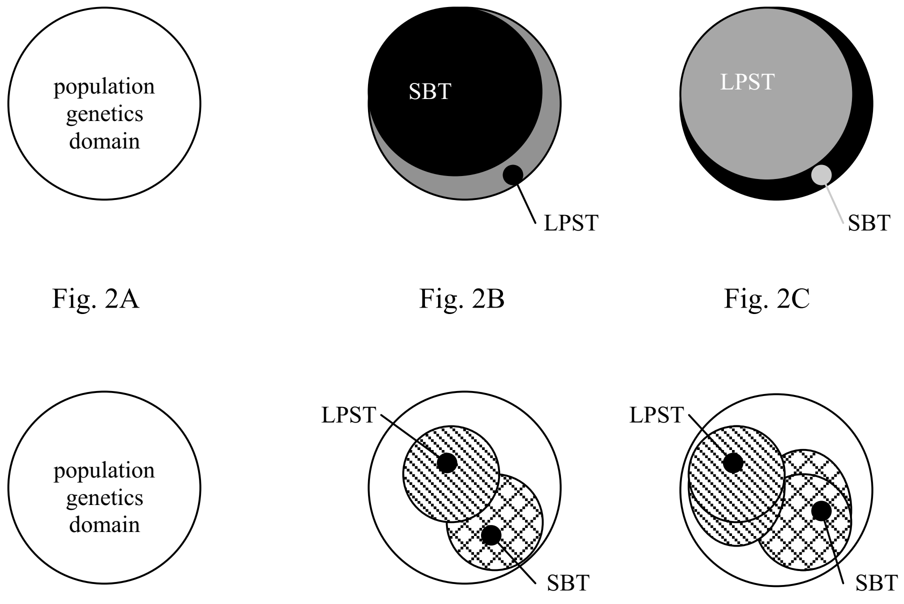


Fig. 2A Fig. 2B Fig. 2C

Fig. 2D Fig. 2E Fig. 2F

Fig. 2: Relative significance controversy diagram of the recent Fisher–Wright controversy. Fig. 2A and 2D represent the population genetics domain. The circle is the domain's boundary and the domain items are within the circle. Fig.'s 2B-2C and 2E-2F superimpose Wright's SBT and Fisher's LPST onto the domain given claims about the relative significance of each of them. Fig.'s 2B-2C represent Coyne et al.'s (1997) argument regarding the relative significance of Wright's SBT (black) vs. Fisher's LPST (grey). Fig. 2B represents Coyne et al.'s interpretation of Wright's view of the extent of applicability of his SBT vs. Fisher's LPST. Fig. 2C represents Coyne et al.'s ultimate, and exactly opposite, assessment of the relative significance of Wright's SBT vs. Fisher's LPST. Fig. 2E-2F represents Wade and Goodnight's (1998) argument regarding the relative significance of the alternative theories, with Wright's SBT in cross-hatched lines and Fisher's LPST in diagonal lines. In Fig.'s 2E-2F, both Wright's SBT and Fisher's LPST have some applicability in the population genetics domain as indicated by the circles (not to scale). Fig. 2F represents extensions in applicability of Fisher's LPST and Wright's SBT with similarly (but not equivalently) filled-in ellipses bulging beyond the relative extents of applicability from Fig. 2E. The bulging ellipses represent what biologists have learned using the LPST and SBT as points of departure in their research (e.g., Wade's work on group selection using Wright's SBT).

Natural Phenomenon	Problem
Shifting Balance Theory	
1. Genotype-by-environment interactions	Calls into question the existence of globally adaptive gene combinations
2. Population regulation	Limits interdemic selection by reducing populational heritability
3. Recombination	Lowers heritability of gene combinations and diminishes response to selection
4. Migration among demes	Limits degree of genetic divergence between demes
Large Population Size Theory	
1. Genetic subdivision of populations	Natural selection in local demes is limited by random genetic drift
2. Linkage	Interference between simultaneously selected loci increases the time necessary for adaptive fixation
3. Epistasis	Genetic effects are not properties of genes and depend upon genetic backgrounds
4. Speciation	No epistasis in main body of theory, so there is no direct connection between diversifying selection and genetic mechanisms of speciation

Table 2: Wade and Goodnight’s (1998: 1549) summary of the problems currently facing Fisher’s LPST (below) and Wright’s SBT (above). Problems are a combination of conceptual (e.g., speciation for the LPST) and empirical (e.g., evidence of genotype-by-environment interactions).