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Fisherian and Wrightian perspectives in evolutionary genetics and model-mediated imposition of theoretical assumptions

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Abstract

I investigate how theoretical assumptions, pertinent to different perspectives and operative during the modeling process, are central in determining how nature is actually taken to be. I explore two different models by Michael Turelli and Steve Frank of the evolution of parasite-mediated cytoplasmic incompatibility, guided, respectively, by Fisherian and Wrightian perspectives. Since the two models can be shown to be commensurable both with respect to mathematics and data, I argue that the differences between them in the (1) mathematical presentation of the models, (2) explanations, and (3) objectified ontologies stem neither from differences in mathematical method nor the employed data, but from differences in the theoretical assumptions, especially regarding ontology, already present in the respective perspectives. I use my "set up, mathematically manipulate, explain, and objectify" (SMEO) account of the modeling process to track the model-mediated imposition of theoretical assumptions. I conclude with a discussion of the general implications of my analysis of these models for the controversy between Fisherian and Wrightian perspectives.

Keywords: Fisher; Wright; Cytoplasmic incompatibility; Perspectives; Theories; Models; Assumptions; Evolutionary genetics; Parasite evolution

1. Context

The controversy between Fisherian and Wrightian approaches to evolution has been, and continues to be, an arduous one (historical and philosophical analyses include Provine, 1986; Lloyd, 1994, 2000; Gayon, 1998; Morrison, 2000; Skipper, 2002). A recent series of exchanges between Jerry Coyne, Nick Barton, and Michael Turelli, and Michael Wade and Charles Goodnight, in the pages of *Evolution*, highlights a number of the relevant issues. In this article, I show that, to an extent at least, these two groups of authors *share* an important set of presuppositions regarding the theory–data relation—namely, that data are independent of theory, and that theory can be straightforwardly evaluated by theory-independent data. I argue that there is another way to look at the theory–data relation that focuses on the *model-mediated imposition of theory onto data and, ultimately, onto nature* (*since nature is seen as causing data*). I do not defend my analysis as a complete picture of the theory–data relation. However, I do claim that it is necessary to consider an alternative to the usual way of thinking about this relation.

My argument consists of three parts. In the remainder of this section, I motivate the existence of model-mediated imposition of theoretical assumptions onto data and nature (or, to abbreviate, *theoretical imposition*) in the recent controversy between Fisherian and Wrightian approaches. In Section 2, I provide a general account of the modeling process, which I call the SMEO ("set up, mathematically manipulate, explain, and objectify") account, that allows for the tracking of theoretical imposition. In Section 3, I apply the SMEO account to the particular case of two models, Turelli's Fisherian model and Steve Frank's Wrightian model,[1] of the evolution of parasite-induced

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[1]It is important to note that I am considering the controversy using the *contemporary* articulations of the two perspectives. Coyne et al. observe: "There is thus a clear distinction between the Fisherian and Wrightian views of evolution: the former requires only that populations be larger than the reciprocal of the selective coefficient acting on a genotype, and the latter requires sub-divided populations, particular forms of epistasis, genetic drift that counteracts selection, and differential migration between

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cytoplasmic incompatibility (CI). As I will argue later in this section, this case of modeling is a particularly useful example of theoretical imposition. In my conclusion, I show how my examination of these two particular models of CI evolution informs the general controversy between Fisherian and Wrightian perspectives.

The two groups of authors accept that theory and its models explain, and are evaluated by, data that are both independent of, and fairly robust to, theoretical context. On the one hand, Coyne et al. "favor the view that adaptations are usually produced by Fisherian mass selection, a process that is not only more parsimonious than the SBT [Wright's Shifting Balance Theory], but has also been shown to occur widely (Endler, 1986)." (Coyne et al., 1997, p. 665). Both parsimony[2] *and* explanatory power are the two main reasons for why they "believe that most adaptations in nature can be explained by natural selection acting on intrapopulation variation." (Coyne et al., 2000, p. 306; in his analysis, Skipper (2002) focuses on parsimony). Underlying their argument is the view that Fisherian mass selection is empirically adequate and empirically sufficient to explain theory-independent data.

On the other hand, Wade and Goodnight claim that each theory is incomplete. For them, the task at hand is to characterize the respective domains of applicability (see Skipper, 2002). They write:

> We conclude that *both* [Fisher's and Wright's] theories, at least in their idealized original versions, have difficulty incorporating important features of natural populations… because of the assumptions that differ between them. We argue that this limits the application of each theory to different domains. (Goodnight and Wade, 2000, p. 317)

That is, the conditions of application depend on the relevance, precision, and realism of the theoretical assumptions intrinsic to each perspective. For example, Wade and Goodnight argue that in the domain of speciation and evolution in metapopulations, Wright's theory is more successful empirically and theoretically. Note that they discuss the existence and nature of these domains independently of any theory. Their concern with success of application is a concern with the empirical adequacy of models.

Coyne et al. as well as Wade and Goodnight (to a lesser extent[3]), thus agree on three theses: (1T) empirical adequacy is the main evaluation criterion in the process of theory choice, (2T) the data are epistemically and methodologically independent of theory and modeling, and (3T) theory choice (which here employs empirical adequacy) occurs through evaluating the degree of matching or fitting of information across two roughly independent domains: theory/model and data/nature. In contrast to (1T), I want to point to the existence of considerations besides empirical adequacy as operative in the process of theory choice, including commitment to a perspective due to its perceived simplicity or unifying power, or because it is part of a research tradition to which one belongs. In contrast to (2T) and (3T), I want to highlight the process of imposing theoretical assumptions onto data and, ultimately, nature (see Kuhn, 1970; Levins and Lewontin, 1985). An extreme commitment to theoretical imposition, which I do *not* support, would vigorously deny all three theses stated. What I will defend, for the purpose of discussing the important role of theory, models, and modeling in imposing assumptions about ontology, is a *constrained* denial of the three theses. Ultimately, such a constrained denial should be compared and intertwined with the assertion of these theses, as well as with other views regarding the theory–data relation, in order to develop as complete an understanding of this relation as possible.

Before turning to my analysis, I want to discuss two sets of phenomena which both groups of authors *explicitly* address: family level selection in chickens and CI evolution. The first example allows us to clearly see theoretical imposition on data. Although the second case is the focus of this article, I mention it here because it is important to clarify the reasons for its utility for observing and understanding theoretical imposition.

The fact that there are two differing interpretations of family level selection in chickens provides clear evidence for theoretical imposition. Briefly, Muir (1996) and Craig and Muir (1996) increased egg-laying rates in domestic chickens by selecting *cages* of full-sib sisters with high egg-laying rates, instead of selecting *individuals* with high egg-laying rates (see also the further analysis in Muir, 2005). Their selection protocol was extremely successful. Wade and Goodnight interpret this as indicating the "efficacy of intergroup selection." (Wade and Goodnight, 1998, p. 1538). Individual selection, which had been practiced

(*footnote continued*)
populations based on their genetic constitution." (Coyne et al., 1997, p. 644). Wade and Goodnight write: "Although the *mathematical details of these theories are largely in agreement*, the conceptual emphases of Wright and Fisher were so different… that where and how to apply the theories to the natural world has been and continues to be a source of controversy." (Wade and Goodnight, 1998, p. 1537, emphasis mine). I am not making exegetical claims about what Fisher or Wright themselves actually believed, since there are separate interpretative questions about this. For example, Steve Frank (pers. comm.; Frank and Slatkin, 1992) defends an interpretation of Fisher's work in which, roughly, Fisher was not a Fisherian, *sensu* contemporary debates—he defended the importance of genetic epistasis, for example. These important interpretative questions about Fisher's and Wright's work are beyond the scope of my article.

[2]As one reviewer pointed out, the argument here seems to be that the co-occurrence of the multiple evolutionary forces implied by the SBT is very improbable. Due to considerations of parsimony, the Fisherian perspective, then, is considered the more likely theory by these authors (on the complex connections among parsimony, probability, and the likelihood of a hypothesis, see Sober, 2003).

[3]Wade (pers. comm.) also accepts the alternative interpretation of the theory–data relation I defend in that he endorses a position, adopted by Neyman et al. (1956), that articulates the complex interaction among theory, experiment, statistics, and data.