Sarkar on Frank

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In a recent paper, Sahotra Sarkar compares the Standard Dynamical interpretation of natural selection with the Information-Theoretic interpretation from Steven A. Frank. I address Sarkar's three arguments against Frank's interpretation. I show that Sarkar's major argument that a key component of Frank's account "does not have any natural biological interpretation" is premised on a contradiction stemming from a mathematical error. Consequently, Sarkar's major argument is unsound. I also address Sarkar's claim that a central equation in Frank's interpretation is dynamically insufficient and his claim that Frank's interpretation uses nonintuitive parameters to simply rewrite familiar results.

1. Introduction. In a recent paper, Sarkar (2014) compares what he calls the Standard Dynamical interpretation of natural selection with what he calls the Information-Theoretic interpretation, from Frank (2012b). In this discussion note, I address Sarkar's three arguments, one major and two minor, against Frank's interpretation. I show that Sarkar's major argument that a key component of Frank's account "does not have any natural biological interpretation" (2014, 28) is premised on a contradiction stemming from a mathematical error. Consequently, Sarkar's major argument is unsound. Next, I address Sarkar's claim that a central equation in Frank's interpretation is dynamically insufficient. I argue that this claim commits a category error and that dynamic sufficiency is appropriately evaluated not for an equation but for the model on which both the Standard Dynamical and the Information-Theoretic interpretations are based. Finally, I address Sarkar's criticism that Frank's interpretation uses nonintuitive parameters to do little more than rewrite results from the Standard Dynamical interpreta-

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tion. I argue that Sarkar fails to consider that Frank's project has the heuristic goal of providing a formal connection between Information-Theoretic measures and the statistical measures typically used to interpret classic equations.

2. Simple Haploid Model. Sarkar uses what I call the Simple Haploid Model to compare the Standard Dynamical and Information-Theoretic interpretations (cf. Frank 2012b, 2379). The model treats a population of allele tokens with the following properties: (a) population size is infinite, (b) there is a single locus with n alleles i, (c) the set of n alleles is fixed, (d) generations are discrete, (e) the fitness w_i of allele i is fixed, and (f) inheritance is simple so that descendants of a token of allele i are themselves tokens of allele i. Changes in population allele frequencies are given by equation (1): the frequency p_i' of allele i in the next generation is the product of allele i's relative fitness $w_i/\bar{w}$ and its frequency p_i in the present generation,

$$p_i' = \left(\frac{w_i}{\bar{w}}\right)p_i, \tag{1}$$

where $\bar{w} = (1/n)\sum_{i=1}^{n} w_i p_i$. (Analogous forms of the model can be stated in terms of types other than alleles.)[1]

2.1. Standard Dynamical Approach. The Standard Dynamical approach treats the change in population average fitness $\Delta\bar{w}$ from generation to generation using population variance in fitness V_w. The central result is that the change in population average fitness $\Delta\bar{w}$ equals the population variance in fitness divided by the population average fitness $\bar{w}$ (on this well-known result, see Okasha [2006]):

$$\Delta\bar{w} = \frac{V_w}{\bar{w}}.$$

Sarkar notes that this is "perhaps the simplest version of the FTNS [Fundamental Theorem of Natural Selection]" (2014, 26). Like the approach behind the FTNS, the Standard Dynamical approach ignores causes of evolutionary change other than natural selection (Price 1972; Sarkar 2014, 22–23).

2.2. Information-Theoretic Approach. The Information-Theoretic approach expresses the change in the population average Malthusian parameter (log fitness or growth rate) $\bar{m}$ from generation to generation, where $m_i = \ln w_i$, using the Jeffreys divergence measure $\mathcal{J}$. The central result is that the change in the population average Malthusian parameter equals the Jeffreys divergence,

1. Equation numbers are from Frank (2012b).

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$$\Delta\bar{m} = \mathcal{J}(p', p),$$

and thus that $\bar{m}$, which is typically expressed with statistical measures like (co)variance, can be expressed with an Information-Theoretic measure. (Frank adds a subscript, giving $\Delta_s\bar{m}$, to make explicit the distinction between "changes by selection" [Δ_s] and "total evolutionary change" [Δ]; Frank 2012b, 2380–81.)

3. Misunderstanding m_i. Sarkar's first criticism of Frank's Information-Theoretic approach concerns Frank's $\Delta\bar{m}$ parameter. This concern vanishes once we see that it is based on a mathematical error in Sarkar's account. Sarkar's troubles begin with his introduction of Frank's system. Sarkar writes: "To obtain the IT [Information-Theoretic] interpretation, we begin from equation (2). First, define the Malthusian parameter, $m_i = \ln w_i$. Then $m_i = \ln \bar{w} + \ln(p_i'/p_i)$ (6). Note that, even though the w_i are constant, the m_i are not constant from generation to generation because $\bar{w}$ changes" (2014, 26). From the facts that $m_i = \ln w_i$ and that w_i is constant, $\ln w_i$ is constant. Thus, by definition and contrary to Sarkar's claim, the m_i are constant.

Sarkar's mathematical error not only leads to a contradiction, but it makes unsound his four derivative critiques of "the definition of $\Delta\bar{m}$ as given by equation (8),"

$$\Delta\bar{m} = \sum_{i=1}^{n} \Delta p_i m_i, \tag{8}$$

that it "is not the change in mean log fitness," that it requires holding $\bar{w}$ constant and thus "requir[es] natural selection not to increase mean fitness (in any generation)," that its derivation by Frank is suspect because the derivation requires the constraint from the Simple Haploid Model that the m_i are constant and this constraint contradicts (6), and that given these problems it "does not have any natural biological interpretation" (2014, 27–28).

Why does Sarkar claim that "the m_i are not constant from generation to generation"? Were this true, it would conflict with Sarkar's starting definition of m_i. Sarkar's answer is that $\bar{w}$ changes, or, at least, it changes in cases of interest, those where natural selection occurs. Although given the model and differences in w_i for different alleles i we expect $\bar{w}$ to change, this does not change m_i. It is possible that this mathematical error resulted from the particular formulation of m_i considered. From the Information-Theoretic definition of m_i,

$$m_i = \ln w_i,$$

and the Simple Haploid Model's rule (1), we can derive (6),

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$$m_i = \ln \bar{w} + \ln\left(\frac{p_i'}{p_i}\right). \tag{6}$$

Looking at m_i in this form (6), it is not obvious that both right-hand-side (RHS) terms are functions of $\bar{w}$. However, Sarkar points out that (1) can be rewritten as (2),

$$w_i = \bar{w}\left(\frac{p_i'}{p_i}\right), \tag{2}$$

which can also be rewritten as

$$\frac{w_i}{\bar{w}} = \frac{p_i'}{p_i}.$$

If we follow this last form of (1) and substitute its left-hand side (LHS) for the second RHS ln argument in (6), we can express the second RHS term of (6) in terms of fitness values, not frequencies:

$$m_i = \ln \bar{w} + \ln\left(\frac{w_i}{\bar{w}}\right).$$

As expected, the $\bar{w}$ values in these terms cancel each other out to give our starting definition of m_i:

$$\begin{aligned} m_i &= \ln \bar{w} + \ln\left(\frac{w_i}{\bar{w}}\right) \\ &= \ln\left(\frac{\bar{w}w_i}{\bar{w}}\right) \\ &= \ln w_i. \end{aligned}$$

4. Sarkar's Second Criticism. Sarkar's second criticism addresses Frank's use of the Jeffreys divergence measure. Sarkar writes:

> Even if equation (8) can be rehabilitated, a final interpretive worry will persist. Because $\mathcal{J}$ refers to both the present (0th) and the next generations, equation (8) violates a minimal condition of dynamical sufficiency (*sensu* Lewontin 1974): it does not allow the prediction of the future based entirely on parameter estimates available at the present generation. I am not suggesting that the model being analyzed is itself dynamically insufficient: it obviously is not, as its analysis using standard dynamics (sec. 3) showed. Rather, the problem is with the IT interpretation, and this feature of $\mathcal{J}$ should be taken as providing an additional reason to prefer the SD interpretation over the IT interpretation of the model. (2014, 28)

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Lewontin writes that for a given evolving system, a state description, composed of state variables, is dynamically sufficient if it can be used along with model parameters ("values that are not themselves a function of time or the state of the system"; 1974, 7) to construct and evaluate a transformation law for that system (6–8). A transformation law enables one to predict the state of the system at some time using the state of the system at some other time. Thus, a transformation law is recursive (Frank 1995, 377–78). The minimal predictive power necessary for dynamical sufficiency depends on a domain's accepted "tolerance limits," which establish how specific a state description must be for practical purposes (Lewontin 1974, 8–9).

When it comes to the Standard Dynamical and Information-Theoretic interpretations, equations like (8) or (13) are not proper subjects of the predicate *dynamically* (*in*)*sufficient* since they are not state descriptions. (These equations are not transformation laws either—they are derived from the transformation law [1] in the Simple Haploid Model and are not recursive themselves.) Additionally, since the equations of the Standard Dynamical and the Information-Theoretic interpretations are derived from equations in the (shared) Simple Haploid Model, it is the state description in the Simple Haploid Model we should examine for dynamic sufficiency. Thus, Sarkar is wrong to suggest that either of these interpretations can be dynamically (in)sufficient and that an analysis of dynamic sufficiency, whatever the subject, can favor one interpretation over the other.

Is the state description in the Simple Haploid Model dynamically sufficient?[2] Although this question is conceptually clear, asking it of the Simple Haploid Model in this context is a red herring. Sarkar and Frank consciously employ a simplified, incomplete model (see sec. 2, above). Even if we ignore things like environmental change, population size change, mutation, migration, frequency- or density-dependent selection, multilevel selection, and inheritance, the Simple Haploid Model ignores basic constraints on possible populations: real populations are finite (and frequencies do not exist in infinite populations anyhow), in finite populations actual fitness may not equal w_i due to rounding errors, and dynamics in finite populations are stochastic (cf. Brandon [2006] on drift and Hardy-Weinberg models). The Simple Haploid Model is unsuitable for work with many (any?) real systems given a plausible set of "tolerance limits."

5. Sarkar's Third Criticism. Sarkar's third criticism is less technical and is more of a worry than a cut-and-dried objection. Sarkar writes: "Suppose that the problems addressed in [Sarkar's] section 5 can be successfully addressed. There still remains the question whether the information-theoretic reformulation of the results of [Sarkar's] section 3 is any more than rewriting fa-

2. Thanks to an anonymous referee for suggesting I pursue this point.

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miliar results in new notation" (2014, 28). Analysis of the structure of the Information-Theoretic interpretation's equation (13) compared with that of the Standard Dynamical interpretation's equation (5) shows that Frank's project involves more than "rewriting familiar results in new notation"—(5) and (13) have different structures because they are meant to play different roles. The Standard Dynamical model derives a statistical result (5),

$$\Delta\bar{w} = \frac{V_w}{\bar{w}}, \tag{5}$$

from the Simple Haploid Model's transformation law (1), $p_i' = (w_i/\bar{w})p_i$. Equations (1) and (5) are similar in that they have a future-generation variable on the LHS and no future-generation variable, just present-generation variables, on the RHS. These equations allow one to predict future values from present values.

The Information-Theoretic interpretation does something different. Equation (13),

$$\Delta\bar{m} = \mathcal{J}, \tag{13}$$

has on the LHS a term of interest easily connected to the LHS of (5), since $m_i = \ln w_i$, and on the RHS an equivalent term involving an Information-Theoretic measure. Equation (13) is an identity. Both sides of (13) employ present- and future-generation variables, as Sarkar pointed out in his second criticism: "$\mathcal{J}$ refers to both the present (0th) and the next generations" (2014, 28). But this difference between the structures of (5) and (13) is not a problem. If they had the same structure, then the Information-Theoretic interpretation might be just a "rewriting [of] familiar results in new notation" (28).

It is critical for Frank's exposition that (13) is an identity—his goal is to connect "classic" statistical equations, like (5), derived from models like the Simple Haploid Model, to Information-Theoretic expressions (Frank 2012b, 2379). Frank's project on information theory and natural selection is an effort to explore the possible heuristic benefits of studying natural selection in what he thinks (contra Sarkar) are more intuitive terms (Frank 2012b, 2377; Sarkar 2014, 28). The value of a "mathematical or statistical equivalence" like (13) or the Price equation (Frank 1995) is not predictive but heuristic—it depends "on enhanced analytical power that eases further derivations and calculations and on the ways in which previously hidden relations are revealed" (Frank 2012a, 1004). Just as the Price equation's decomposition of one central term into two has facilitated theorizing about between- versus within-group selection and about selection versus transmission (Frank 1995, 375–79; Okasha 2006), so Frank thinks his inter-

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pretation's connection of statistical measures with Information-Theoretic measures via equation (13) will facilitate advances in natural selection theory. Frank is not announcing an "information-theoretic unification of the sciences" (Sarkar 2014, 29). Frank is developing a formal interpretation of natural selection, the use of which does not obviate and need not exclude the use of other interpretations.

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