

Why a convincing argument for causalism cannot entirely eschew population-level properties: discussion of Otsuka

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Abstract Causalism is the thesis that natural selection can cause evolution. A standard argument for causalism involves showing that a hypothetical intervention on some population-level property that is identified with natural selection (e.g., variation in fitness) will result in evolution. In a pair of articles, one of which recently appeared in the pages of this journal, Jun Otsuka has put forward a quite different argument for causalism. Otsuka attempts to show that natural selection can cause evolution by considering a hypothetical intervention on an individual-level property. Specifically, Otsuka identifies natural selection with the causal relationship between a trait and fitness, claims an intervention on the strength of this relationship can cause evolution, then concludes that natural selection can cause evolution. Below I describe why Otsuka's argument for causalism is unconvincing. Central to my criticism is that Otsuka's argument works only if one adopts an indefensible account of natural selection, according to which natural selection can occur in the absence of trait or fitness variation. I go on to explain why any attempt to demonstrate the truth of causalism via a hypothetical intervention on an individual-level property would appear to require one to adopt an account of natural selection that is inadequate for the same reason. This in turn means the plausibility of causalism does indeed depend on the plausibility of the claim that population-level properties, which supervene on the properties of the individuals in the population, can be causally efficacious.

Keywords Causalism · Statisticalism · Jun Otsuka · Natural selection · Trait and fitness variation · Individual-level and population-level properties · Supervenience and causation · Theoretical terms

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Introduction

There is currently a debate in philosophy of biology between *causalists* and *statisticalists*. They disagree about much. Central to the dispute, however, is whether natural selection can cause evolution. Causalists, as the name implies, maintain that it can (Reisman and Forber 2005; Millstein 2006; Forber and Reisman 2007; Shapiro and Sober 2007; Sober 2011, 2013; Otsuka 2016a, b). Statisticalists deny this (Walsh 2000, 2007; Matthen and Ariew 2002, 2009; Walsh et al. 2002, 2017).

Typically, causalists argue that natural selection can cause evolution by demonstrating that an intervention on a population-level property that is taken to represent natural selection (e.g., variation in fitness) will result in evolution (Reisman and Forber 2005; Millstein 2006; Forber and Reisman 2007; Shapiro and Sober 2007; Sober 2011, 2013). These arguments often also include an explicit defense of the idea that population-level properties can be causally efficacious despite that they supervene on the properties of the individuals in a population (Reisman and Forber 2005, pp. 119–122; Millstein 2006, *passim*; Forber and Reisman 2007, pp. 621–622; Shapiro and Sober 2007, *passim*). This causalist defense of the efficacy of supervenient properties is made largely in response to statisticalists, for statisticalists appear to claim that supervenient properties are causally inert (Walsh et al. 2002).

In the pages of this journal and elsewhere, Jun Otsuka has put forward a quite different argument for the thesis that natural selection can cause evolution (Otsuka 2016a, b). Otsuka claims that an advantage of his argument is that it does not require one to maintain that population-level properties can be causally efficacious (Otsuka 2016b, pp. 477–478). Otsuka's argument is based around a causal model with exclusively individual-level variables: a trait variable (Z) has a causal influence on an individual's fitness (W), where the strength of this causal influence is represented by a causal parameter (β).¹ Otsuka claims intervening on β will result in a change to the population's mean value of Z ($\bar{Z}$). He takes this to show that natural selection can cause evolution.

While I do believe natural selection can cause evolution, I do not believe Otsuka's argument for that thesis succeeds. Central to my criticism is that Otsuka's argument works only if one adopts an indefensible account of natural selection. As mentioned, Otsuka identifies natural selection with the causal relationship between a trait and fitness. This account entails that natural selection can occur in the absence of trait or fitness variation, and even that natural selection can occur in a population with a single member. If for these reasons we reject Otsuka's claim that natural selection can be identified with the causal relationship between a trait and fitness, then the

¹ One could attach subscripts to β to indicate that it represents the causal influence of Z on W . Since I do not use β for any other purpose in this paper, I will leave these subscripts out.

result of an intervention on the causal relationship between a trait and fitness will of course not tell us whether natural selection can cause evolution.

After expounding on the above, I go on to explain why the failure of Otsuka's argument for causalism is symptomatic of the broader argumentative strategy he employs. By using exclusively individual-level properties to attempt to demonstrate that natural selection is causal, Otsuka does indeed avoid having to endorse the claim that population-level properties can be causally efficacious. But the cost of this argumentative strategy is that Otsuka is forced to re-describe what natural selection is: Otsuka is unable, given the constraints he imposes on himself, to say that trait or fitness *variation*, which is a population-level property, is a necessary condition for natural selection.

Indeed, for reasons I will describe, any causalist argument that entirely eschews reference to population-level properties would appear to face similar obstacles. If this is so, then we have support for a claim that has been suggested elsewhere (Millstein 2006; Shapiro and Sober 2007; Sober 2013) and which Otsuka had hoped he could disprove: Namely, causalism is plausible only if population-level properties can be causally efficacious.

Otsuka's argument for causalism

Otsuka's argument for the claim that natural selection can cause evolution goes as follows.

First, Otsuka assumes that the *interventionist* (or *manipulability*) account of causation is an appropriate framework to use to determine whether natural selection can cause evolution (Otsuka 2016a, pp. 248, 251–253, *passim*; 2016b, p. 475, *passim*). Eliding some subtleties, the interventionist account holds that, relative to some model with variables X and Y , the variable X is a cause of Y if there is some manipulation of X (from $X=x$ to $do(X=x')$, where $x \neq x'$) that, while holding fixed the variables off the path(s) from X to Y , would change the probability that Y will take a particular value (Spirtes et al. 2000; Woodward 2003; Pearl 2009). This " $do(\circ)$ " operator is from Pearl's work and indicates that we are *intervening* to set the value of X to x , not merely conditioning on $X=x$ (Pearl 2009).²

Second, Otsuka claims natural selection *is* or at least *occurs whenever* there is a causal influence of some trait on fitness, sometimes also requiring a causal influence of environmental factors on fitness. This description of natural selection is couched in the language of a causal model in which there is an edge from a trait variable Z to a fitness variable W ($Z \rightarrow W$), where β represents the strength of the causal relationship between Z and W , and there is also an edge from fitness affecting environmental factors (E_W) to W ($E_W \rightarrow W$). (See, for instance, Otsuka 2016a, Figs. 3 and 4 and

² Since I, along with the majority of other participants in the debate over causalism and statisticalism, endorse roughly this account of causation, I will not provide a more in depth description or defense of it. The unfamiliar reader should consult Woodward (2003) and Pearl (2009) for particularly illuminating exegeses.

Otsuka 2016b, Fig. 1). Otsuka writes: "...selection must be understood as a causal process (a trait affecting fitness)" (2016a, p. 248); "We say that trait Z is selected if and only if it, along with an environmental factor denoted by E_w , causally affects fitness W " and, therefore, "Selection can thus be represented" by " $Z \rightarrow W$ and $E_w \rightarrow W$ " (Ibid., pp. 255–256); "Selection...is a causal influence of the trait on fitness, whose linear magnitude is measured by coefficient β " (Ibid., p. 265).³

So far as I can tell, there is only one place in which Otsuka suggests that natural selection involves trait or fitness variation. He writes, "Selection is the process in which parental phenotypes lead to *differential* reproductive success" (Ibid., p. 255, my emphasis). Variation in reproductive success appears to imply variation in parental phenotypes. But this claim is inconsistent with the sentence that immediately follows it, in which Otsuka provides necessary and sufficient conditions for selection (Ibid., pp. 255–256), which I quoted in the previous paragraph. Moreover, it makes sense that Otsuka would describe natural selection without requiring the phenomenon to involve trait or fitness variation: variation in this context is a population-level property, and Otsuka explicitly says he can show that natural selection can cause evolution while *only* referencing properties that belong to individuals (Otsuka 2016b, p. 477).

Third, Otsuka claims an intervention on the strength of the causal relationship between a trait and fitness, where β represents the strength of this relationship, will result in evolution.⁴ Let ΔZ refer to the change to the mean value of Z between a parent and offspring generation, and let $\mathbb{P}(\alpha|\gamma)$ refer to the probability of α , conditional on γ . Otsuka explains, "In general, we have $\mathbb{P}(\Delta Z|do(\beta)) \neq \mathbb{P}(\Delta Z|do(\beta'))$ for any $\beta \neq \beta'$ " (2016a, p. 265).

Fourth and finally, Otsuka claims that, because he has shown that an intervention on the strength of the causal relationship between a trait and fitness—i.e., an intervention on β —can result in a change to the mean value of Z , he has thereby shown that natural selection can cause evolution. After stating the inequality presented in the previous paragraph, in the next sentence Otsuka puts forward the causalist conclusion of his argument: "It thus follows that selection does cause evolution" (Ibid., p. 265).

A critical assessment of Otsuka's argument for causalism

What is problematic with Otsuka's argument is his claim that natural selection is or at least occurs whenever there is a causal relationship between a trait and fitness. This account of natural selection entails that there can be natural selection even when there is no trait or fitness variation in a population or even when a population has but one member. If for this reason we reject Otsuka's account of natural

³ Otsuka's description of natural selection may remind some readers of descriptions of "selection for." But the similarities only go so far; "selection for" is typically understood to occur only when there is trait and fitness variation (Sober 1984a). See also Lewens (2010) for discussion of these issues.

⁴ One potential objection to Otsuka's discussion of an intervention on β is that interventions are typically understood to be carried out on variables, not parameters. I will not consider that objection here.

selection, then we cannot treat an intervention on the causal influence of a trait on fitness as tantamount to an intervention on natural selection. Demonstrating that an intervention on the causal influence of a trait on fitness can result in evolution does not establish that *natural selection* can cause evolution.

If trait or fitness variation is necessary for natural selection, then the following example should make clear why one cannot identify natural selection with the causal influence of a trait on fitness. (I will defend the antecedent of this conditional in Sect. 4.) Imagine a population of individuals in a homogenous environment and that each individual has precisely the same phenotype and fitness—that is, there is no trait variation and no fitness variation. These clones will of course possess some trait (Z) that causally affects fitness (W)—for instance, their (identical) hearts. So it is true of this population that $Z \rightarrow W$ and, thus, that β is nonzero. In fact, there will still be a causal relationship between Z and W even if there is but one individual in this population. According to the standard account, there is no natural selection in this example, since there is no trait or fitness variation in the population. According to Otsuka's account, there *is* natural selection, since we have a trait that causally affects fitness (that is, $Z \rightarrow W$), where the strength of this relationship has a nonzero value represented by β .

Why, in the above example, will β be nonzero even in the absence of variation in Z or W ? According to the interventionist account, a causal relationship between Z and W means that, *were one* to manipulate Z , then, at least in some circumstances, the value of W would change. And the value of β quantifies how much W would change were such an intervention on Z to take place. But whether there is *in fact* variation in either Z or W is a separable matter; the causal relationship between Z and W will be there either way.⁵

Now, if one wants to use regression to generate a defined, nonzero *estimate* for the strength of the causal relationship between Z and W , then Z and W do need to vary. Regressing W on Z requires calculating $\text{cov}(W, Z)/\text{var}(Z)$, whose value will be undefined or nonzero if there is no variance in W or Z . While a causal relationship between two variables exists in the absence of variation in the values of variables, estimating the strength of these causal relationships is not possible, at least if one uses regression, if these variables do not vary.⁶

Thus, Otsuka's account of natural selection entails that there can be natural selection in the absence of trait or fitness variation or even in a population with one member. This seems odd. To be sure, different authors do indeed adopt different descriptions of natural selection. Sober claims fitness variation is both necessary and sufficient for natural selection to occur (Sober 1984a, 2013). Mills and Beatty (1979), along with Brandon (1990), claim fitness variation is necessary but not sufficient for natural selection to occur; there must also be an ordinal correspondence between individuals' realized and predicted fitness values. Lennox and Wilson (1994) claim natural selection requires fitness variation in addition to a "struggle for existence," a view

⁵ See McLoone (2015) for a discussion of how this issue relates to the definition of "group selection" articulated by some proponents of the "contextual approach" to multilevel selection.

⁶ See Sober (1984b) for a related discussion, though his is focused on the difference between type- and token-level causal claims.

one can find in the *Origin* (Darwin 1859). Sometimes natural selection is described as occurring only when trait variation results in differences in fitness variation (Endler 1986), while sometimes an explicit reference to trait variation is left out because one assumes a homogenous reference environment, within which fitness variation is necessarily the result of trait variation (Brandon 1990; Sober 2013).

Despite the differences, what these and the overwhelming majority of other descriptions of natural selection have in common is that they treat trait or fitness variation as at least a *necessary* condition for natural selection. Trait or fitness variation is similarly treated as a necessary condition in what are generally understood to be the leading descriptions of evolution by natural selection (Lewontin 1970; Godfrey-Smith 2007, 2009).

If one rejects Otsuka's account of natural selection because it entails that there can be natural selection in the absence of trait or fitness variation, then this is not good news for the rest of Otsuka's argument. For Otsuka wants to claim that natural selection can cause evolution by demonstrating that an intervention on the strength of the causal relationship between a trait and fitness will result in evolution. If we reject the notion natural selection is the strength of the causal relationship between a trait and fitness, then one cannot legitimately use an intervention on the latter to justify claims about the causal efficacy of the former.

Before moving on, I should make a few additional comments. I have criticized Otsuka's argument for the claim that natural selection causes evolution. This does *not* mean that Otsuka's derivations of standard equations in evolutionary biology from causal models in his (2016a) are flawed. The derivations of these equations do not rely on an account of natural selection at all, set aside whether the account is good or bad. The derivations show that, given a causal model of the relationship between a phenotype variable, an environment variable, and a fitness variable, if one were to assume that there was variation in certain of the model's variables, then certain other variables in the model would covary in a specifiable way, given by the trek rule. The derivations go through regardless of how (or whether) one defines "natural selection." They are an interesting and important contribution to the literature on how population genetics and causal models are related.

Likewise, one might wonder whether any of the mathematical terms in the equations from evolutionary biology that Otsuka derives from his causal models could serve as plausible representations of natural selection. After all, I claim we should not identify natural selection with a parameter, β , whose value represents the strength of a causal relationship between a trait and fitness ($Z \rightarrow W$). But if Otsuka derives standard equations from evolutionary biology—e.g., the Price equation and the breeder's equation—from a model in which Z is a cause of W , then how could any term that appears in those equations be legitimately used to represent natural selection if the causal model itself does not legitimately represent natural selection? Indeed, perhaps this would be a *reductio* of my argument, since some of the terms in these equations—e.g., a positive covariance between a trait and fitness in the Price equation, or a positive value of the selection differential in the breeder's equation—are quite often used as formal representations of natural selection.

This worry, which was voiced by a reviewer of this article, is unfounded. A positive value for the covariance between a trait and fitness and a positive value for the

selection differential both require there to be trait and fitness variation in a population. That is why they are plausible formal representations of natural selection. The strength of the causal relationship between a trait and fitness can have a nonzero value even when there is no variation in either traits or fitnesses. That is why it is an inadequate formal representation of natural selection if we accept the requirement that trait or fitness variation is necessary for natural selection.

Can an account of natural selection justifiably leave out trait or fitness variation?

Above, I rejected Otsuka's account of natural selection because it entails there can be natural selection in the absence of trait or fitness variation, which differs markedly from how natural selection is generally understood. But I did not provide much in the way of a defense of why lack of fit with standard usage is an appropriate basis to reject an account of natural selection. Is it legitimate to appeal to standard accounts of natural selection in order to reject a novel description of the phenomenon? Why can't we let Otsuka re-describe natural selection as he pleases?

There are, in fact, a few reasons an appeal to standard accounts of natural selection seems warranted in the present context.

First, the component of the debate between causalists and statisticalists that I am concerned with in this paper concerns whether natural selection in fact has the causal efficacy that evolutionary biologists and philosophers of biology have typically assumed that it does. Implicit in the debate, then, is that we are concerned with the causal efficacy of natural selection *as the phenomenon is typically understood*. It is basically irrelevant to the debate to claim that natural selection is (or is not) causal while adopting an extremely rare, perhaps unique account of the phenomenon.

Second, Otsuka rejects a statisticalist description of natural selection because of its lack of fit with standard usage. If Otsuka is justified in doing so—and I believe he is—then Otsuka's own account of natural selection cannot be shielded from the same form of criticism. Those who are familiar with the contours of the debate between causalists and statisticalists will recall that statisticalists sometimes claim that natural selection logically or mathematically entails evolution, for they assume "natural selection is evolution due to heritable variation in fitness" (Matthen and Ariew 2009, p. 204). This is a non-standard account of natural selection.⁷ These

⁷ Matthen and Ariew write that they "assume Sober's fairly orthodox treatment" of natural selection, namely, "natural selection is evolution due to heritable variation in fitness" (Matthen and Ariew 2009, p. 204). In fact, this is not Sober's account of natural selection. The part of Sober's book that Matthen and Ariew explicitly reference says this: "If the organisms in a population differ in their ability to survive and reproduce, and if the characteristics that affect these abilities are transmitted from parents to offspring, then the population will evolve" (1984a, b pp. 21–22). This is different than saying, "natural selection is evolution due to heritable variation in fitness," which is the interpretation Matthen and Ariew ascribe to the passage. Later in that same chapter, Sober also provides a case that he explicitly and plausibly describes as one in which there is selection but not evolution (Ibid., pp. 40–41). Sober writes later in that book, "selection doesn't imply evolution...Selection implies evolution only when no other evolutionary force counteracts it *and the trait being selected is heritable*" (Ibid., p. 151, emphasis in original).

statisticalists then claim that natural selection cannot *cause* evolution since the two relata are instead in a non-causal dependency relationship. Commenting on this argumentative move, Otsuka writes (2016b, p. 475),

...concluding the causal inertness of selection on this ground is just moving the goalposts. In fact, their ‘definition’ of natural selection is a far cry from its common usage and contradicted by the very opening sentence of Fisher (1930): ‘Natural selection is not evolution’.

Otsuka takes lack of fit with the relevant literature to legitimately ground a rejection of a description of natural selection, particularly within the context of a debate about whether natural selection can cause evolution. This is the same methodology I employ.

Third, Otsuka provides no compelling reason as to why we should adopt his description of natural selection. It is certainly justifiable to modify the intension of a theoretical term, or its presumed extension, if one can adduce a good reason such modification is called for. In fact our accounts of natural selection have changed since Darwin (Gayon 1998). For instance, Darwin often (e.g., 1859, pp. 126–127, 489–490) though not always (e.g., Ibid., pp. 62–63) took natural selection to involve competition for limited resources. But there is a case to be made that the underlying logic of the theory does not require this (Lewontin 1970), and contemporary accounts of natural selection therefore typically leave out reference to resource competition (see Godfrey-Smith 2007, 2009, chapter 2). As another example, Darwin at times appears to combine what many would now distinguish as natural selection and evolution *by* natural selection (1859, p. 61, pp. 126–127). That natural selection can occur without evolution is plausible given the relative ease with which one can imagine apparent cases of natural selection (variation in fitness or even heritable variation in fitness) in the absence of evolution (Sober 1984a, pp. 40–41; Godfrey-Smith 2009, chapter 2). (It is for this reason, incidentally, that Matthen and Ariew’s (2009) account of natural selection, in which natural selection is claimed to entail evolution, strikes both me and Otsuka as indefensible.)

In contrast, Otsuka provides little or no reason as to why his novel account of natural selection should be adopted. The closest Otsuka comes to offering a defense of his account occurs when he claims causal models are the most rigorous framework to understand why and how a population will evolve and that “the meaning and nature of the concepts like fitness, selection, and drift are determined unequivocally within these causal models” (2016b, p. 480). But one can consistently maintain that causal models should be used to predict and explain evolution and also maintain that trait or fitness variation is a necessary condition for natural selection—see, for instance, Glymour (2006). This is because the meaning of a concept like natural selection is *not* determined unequivocally by the causal models Otsuka references. The models Otsuka references relate certain trait, environmental, and fitness variables via edges and causal parameters. It is a decision to interpret one or a few of the variables, edges, and parameters in the model as a representation of natural selection; the model itself says precisely nothing about the matter. Even if we grant that one must first have an underlying causal model to develop a legitimate account of natural selection, it does not follow from this that natural selection must be identified

with the causal relationship between a phenotype and fitness or that trait or fitness variation is not necessary for natural selection.

Thus, given that Otsuka does not provide a compelling reason to adopt his account of natural selection, and given its lack of coherence with accepted usage, we have no reason to accept Otsuka's account and we have a few reasons to reject it. If, moreover, we do reject Otsuka's account of natural selection, then his argument for the claim that natural selection can cause evolution does not succeed.

The population-level character of natural selection

A general lesson that can be gleaned from the above discussion is that, if trait or fitness variation is a necessary condition for natural selection, then any attempt to describe natural selection by referencing exclusively the properties of individuals will fail. This is because trait or fitness variation is a population-level property. Variation is like frequency in this regard. The frequency of red marbles in a set of marbles is a property of the set, not a property of any particular marble. This is why it makes no sense to speak of "the frequency of red marbles of that red marble." Likewise, we can speak of "trait or fitness variation in a population," but not "the trait or fitness variation of individual i in the population," unless, of course, we mean by that something entirely different. If an account of natural selection requires reference to either trait or fitness variation, then a description of natural selection that references individual properties taken separately will always be inadequate. To integrate a property like variation into the description, one must also reference properties of the ensemble of individuals.

How do the above points relate to the debate between causalists and statisticalists over whether natural selection can cause evolution? A population-level property like trait or fitness variation supervenes on the properties of the population's individual members. If trait or fitness variation is a necessary component of natural selection, then natural selection itself supervenes on the properties of the individuals in a population. Recall, statisticalists appear to claim that, because natural selection is supervenient in this way, natural selection is itself causally inert (Walsh et al. 2002). There are two standard causalist responses to this argument. First, causalists claim supervenient properties can be causally efficacious according to the interventionist account of causation, the account of causation that statisticalists also adopt (Millstein 2006; Forber and Reisman 2007; Shapiro and Sober 2007). Second, causalists claim that, if one adopts the view that only a supervenience base can be causally efficacious, then it is unclear how one could consistently maintain *any* properties above those of microphysical particles could be causally efficacious (Reisman and Forber 2005; Shapiro and Sober 2007). This second point is taken both to be a *reductio* of the statisticalist position and to show that the statisticalist position is self-undermining: statisticalists wish to claim individual-level properties are causally efficacious, but individual-level properties of course have a supervenience base as well.

In his own work on causalism, in contrast, Otsuka explicitly says he wants to avoid this debate over whether a population-level, supervenient property can be

causally efficacious (2016b, pp. 477–478). Otsuka does not wish to show that natural selection can be causally efficacious *despite that* natural selection is a population-level property. Rather, Otsuka hopes to sidestep the debate by attempting to show that “the causes of evolutionary changes,” of which he takes natural selection to be an example, “all belong to *the level of individuals*, in the sense that these variables, including environmental factors, denote properties of individuals” (2016b, p. 477, emphasis in original).

As we saw, however, because Otsuka attempts to formulate an argument for causalism using exclusively individual-level properties, Otsuka is forced to adopt an account of natural selection in which reference to trait or fitness variation is necessarily absent, since trait and fitness variation are population-level properties. The result of this strategy is that we no longer seem to be talking about the causal power of *natural selection*, at least as the phenomenon is generally understood. We are instead simply recognizing that individual-level properties, such as an individual’s phenotype, can have a causal influence on an individual’s fitness. If fitness is treated as a realized value, as Otsuka insists it should be (2016b), then that claim is not remotely controversial. In any case, the claim is only obliquely related to the dispute over causalism.

This raises another important point, with which I will close. Otsuka derives standard equations from evolutionary biology through an application of the trek rule to an underlying causal model (2016a, pp. 258–259). Briefly, the trek rule allows one to calculate the covariance of two variables, X and Y , in a causal model by looking at the variance of other variables in the causal model and the values of the path coefficients between variables (see Ibid., pp. 252–253 for lucid exegesis). The trek rule has nothing to say about a causal model when the variables in the model, X and Y included, do not vary. Thus, for Otsuka to go from his causal models to an equation that has (co)variance terms, such as the Price equation, Otsuka employs the following procedure: *If* we assume the variables in the causal model have nonzero variance, *then* the trek rules tells us how the variables would covary, and from this we can derive standard equations from evolutionary biology, such as the Price equation.

But here is the rub: In this context, variance is a property of a population of individuals. While a trait Z and its fitness W denote properties of an individual, the variance of Z or W is a property of a population of individuals—e.g., the variance of Z describes the extent to which the values of Z in a population deviate from the mean of these values; the same is true, *mutatis mutandis*, for the variance of W . Thus, while it is true that Otsuka’s underlying causal models relate exclusively individual-level properties, it is not true that he uses only individual-level properties to derive standard equations from evolutionary biology.

Conclusion

Otsuka has put forward a different sort of argument for the claim that natural selection can cause evolution, an argument that, Otsuka claims, avoids a commitment to the view that population-level properties can be causally efficacious. But it is precisely because Otsuka eschews reference to population-level properties that the

argument fails: With only individual-level properties at his disposal, Otsuka cannot formulate an adequate account of natural selection, and so he cannot develop a compelling argument that natural selection can cause evolution.

To be sure, some many well find Otsuka's argumentative gambit, in which one adopts an atypical account of natural selection and thereby avoids a commitment about the causal efficacy of population-level properties, appealing. As a causalist, it concerns me little that the fate of causalism depends on the claim that population-level, supervenient properties can be causally efficacious. But I would be concerned indeed if the fate of causalism depends on the plausibility of the claim that there can be natural selection in the absence of trait or fitness variation.

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