

**Proceedings of the Pittsburgh Workshop in History and Philosophy  
of Biology, Center for Philosophy of Science, University of  
Pittsburgh, March 23-24 2001**

**Session 3: Natural Selection as a Causal Theory**

- **John Hodge (University of Leeds) Natural Selection: A Causal Theory**
- **Robert Olby (Pittsburgh) Commentary**
- **Megan Delehanty (Pittsburgh) Commentary**
- **Workshop Participants**

# Natural Selection: A Causal Theory<sup>1</sup>

Jon Hodge

## 1. The position and the argument

The principal thesis defended here is that natural selection is best viewed as a causal theory. The main argument will be a normative, historical one: the theory was originally constructed as a causal theory, and nothing done to it since has made it less so. I shall argue that we can best assess various current suggestions - such as that fitnesses are supervenient on physical properties; that fitnesses are propensities (probabilistic dispositions), and how natural selection is distinguishable from random drift - by asking persistently about the causal relationships (and hence causal-explanatory relationships) in question.

## 2. The main challenge

The leading modifications to the understanding of natural selection since Darwin can be put under four headings: Mendelism, molecular biology, multilevel selectionism, and mathematics. The first three are broadly empirical and causal and, it will be argued, introduce no radical transformation to the structure of causal inquiry and explanation, only complementary extensions. Mathematics, as such, I take to be not causal and so without causal-explanatory import. Among all the diverse philosophies of mathematics, none, it seems, requires us to credit mathematics with adding extra causal-explanatory content to any theory when it is brought into its formulations. In understanding the transformations of the theory of natural selection since Darwin, one should make, then, a sharp distinction between its causal-explanatory enhancement by Mendelism, molecular biology, and multilevel selectionism, and its representational and derivational reformulations through novel mathematics; for these reformulations have not and could not have constituted, in themselves, causal-explanatory innovations.

## 3. The way forward

By making causality the prime focus, various unhelpful legacies from logical positivism and from some more recent philosophies can be circumvented. Because causality is not (*pace* Carnap and others), explicable as predictability, one needs to distinguish throughout between the causal import of natural selection theory and the predictive import, and so between the ontic and the epistemic, as Wesley Salmon would put it. The concept of fitness belongs on the epistemic side of this great divide, once fitnesses are construed, as they should be, as reproductive expectancies analogous to life expectancies and as having, like them, no causal efficacy nor, therefore, any causal-explanatory import. Within the mathematics of fitness differences, where there is no gap between expectancies and their fulfilments, and so within the derivations of the predictive consequences of these expectancies, there is no ground for reifying the formal abstractions into general causes conforming to universal laws. The theory of natural selection is explanatory because it is causal, not because it is nomic. Its causes and its causal processes are not usefully likened to forces in classical - nor, I suspect, in quantum physics - for forces are most plausibly construed (as by Ellis), not as causes, but as causal relationships; and in any case, there are no very edifying analogs in evolutionary theory to force laws or to force/mass relationships. Mechanics-envy, like positivism (which often suffered from that condition), misleads us concerning the structure and function of natural selection theory.

When - in a forthcoming paper with two other coauthors - Dennis Walsh counters his one-time mentor Elliott Sober's claim that evolutionary theory is a theory of forces by saying that no, it is not a dynamic theory, but a statistical theory about population structure, one should gently insist that they have both erred and that there is a preferable third view: not forces, nor statistics, but causal processes.

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<sup>1</sup> This is an abstract of a presentation based on my paper in volume two of K. Gigerenzer et al (eds.), *The Probabilistic Revolution*, MIT Press, 1987. For a recent piece in the same causalist vein, see Roberta Millstein's 2002 paper 'Are random drift and natural selection conceptually distinct?' *Biology and Philosophy* 17 (1): 1-31.

#### **4. Natural Selection and the theory of theories**

Whether any post-positivist theory of theories – the semantic view, for instance – is much better at illuminating natural selection theory remains, despite several valuable analyses, an open question. For the question has not yet been properly posed, I would respectfully submit. To frame it appropriately, one would have to ask how far some theory of theories illumines natural selection not as a mathematically formulable theory, not as a nomically unifying theory, not as an axiomatisable – or otherwise – theory, but as a causal theory descending, with no discontinuous modifications in the structure of its causal –explanatory inquiries, from the version first offered by Darwin.

## Comments on Jon Hodge's paper

Robert Olby

It is a special pleasure and a privilege to comment on the 2002 abstract and the 1987 paper of my former Leeds colleague Jon Hodge. Jon is one of the foremost Darwinian scholars and he has brought to the great Darwin industry his formidable knowledge of nineteenth century biology and philosophy and his fruitful commingling of historiographical and philosophical enquiry, a feature dear to the Pittsburgh department.

In his abstract he asks:

‘... how far some theory of theories – the semantic view, for instance – illumines natural selection not as a mathematically-formulable theory, not as a nomicallly-unifying theory, not as an axiomatizable or otherwise-theory, but as a causal theory descending, with no discontinuous modifications in the structure of its causal-explanatory inquiries, from the version first offered by Darwin.’

Clearly there are a number of approaches to a philosophical analysis of the status of Darwinian theory that he does not like. Instead he favors causal theories, but not those involving causal relationships as in Newtonian theory, and he chooses causal processes rather than causal events - following here the lead of Wes Salmon. But what does he mean by ‘the structure of its causal-explanatory inquiries’? Here he could be referring to the *vera causa* principle advocated by Newton, extended by Thomas Reid and used by Charles Lyell - namely causes that can be called real because of their *existence*, their *competence* to account for the phenomenon in question, and their observed *responsibility* for that phenomenon. But I suspect he has in mind something else – namely the *form or structure* of the theory rather than any empirical and nomic content that might be claimed for it. This places us in the semantic theory-of-theories world of Patrick Suppes and van Fraassen, and more specifically it reminds us of John Beatty's paper: ‘What's Wrong with the Received View of Evolutionary Theory?’ (1980) Beatty explained that the Hardy-Weinberg equation and the Mendelian laws upon which it is based are dependent upon meiosis which is subject to many exceptions, a process that has been evolved and could be altered, we might suggest, in the future course of evolution. Therefore he favored viewing the theory of natural selection in the light of the semantic approach as stating the kind of system into which the empirical data fit.

Since Jon has referred us to his '87 paper ‘Natural Selection as a Causal, Empirical, and Probabilistic Theory’, I will use that where possible to expand on his abstract. This paper was written for a conference series held in the years 1982/83 on *The Probabilistic Revolution* where one of the issues discussed was the ‘distinction between *epistemic* and *ontic* interpretations of probability.’ The editors of the volume pointed out that the increasing use of statistics was not necessarily associated with a trend to an ontic interpretation of probability. Indeed besides probabilistic revolutions in the sciences ‘there were counter-probabilistic revolutions’. Hodge by no means denies Natural Selection a place in the sun of the probabilistic revolution, but he regrets that empiricism in its more positivistic forms ‘has construed the main questions about evidence and explanation in science as questions about universal statements of law rather than existential claims for causation.’ Having by then witnessed two decades of criticism of the positivist tradition he saw the eighties as ‘an appropriate time to develop further the *original* interpretation of natural selection, i.e., Darwin's, as a causal and empirical theory.’ In the abstract for this workshop he adds that evolutionary theory is neither a matter of forces, nor of statistics but of *causal processes*. So we are all enjoined to cast aside ‘mechanics-envy’, stop being mesmerized by sophisticated mathematical representations of the evolutionary process, and to mark and inwardly digest the ‘deep divide’ that exists between the predictive import of natural selection and its causal import, between the epistemic and the ontic. As for axiomatizing Natural Selection – away with it! Down with nomicallly-unifying it. Get back to Darwin and we will get it right – the password is ‘cause’.

I say ‘Amen’ to that, and to Darwin's judgment that natural selection is the chief but not the only cause of evolutionary change: but let's not go too far. I do have some reservations about Darwin worship, especially if it comes from the Darwin industry.

From the point of view of the philosopher this turn of affairs does represent some carnage. Those who want to express natural selection in mathematical equations – play the *fundamental theorem* game, might be disappointed, even affronted. Can't we effect a rescue operation somehow? For instance, couldn't we save axiomatization? I turned to Alexander Rosenberg's *The Structure of Biological Science* (1985) and studied his account of Mary Williams' axiomatization (1970). It has five axioms, and as Rosenberg remarks its 'Achilles' heel is that the term 'fitness' is a primitive. As far as I can see Chevalier Lamarck would have been happy with all five of Williams' axioms (except perhaps the possibility of extinctions)! The axiomatization has to be so expansive in its claims – its terms, Rosenberg tells us, do not restrict it to any place or time in the universe! Indeed some renditions of Mendelian genetics that I have encountered in reading about axiomatization look as if they refer to life on another planet, not this one. Hence it pleases me that Jon Hodge appears not to like axiomatization any more than I do.

Perhaps post-positivism has resources for the restoration of sanity? Does the semantic approach offer greater scope for the diversity of the phenomena in the evolutionary process and is it comfortable with the absence from evolutionary biology of any exceptionless laws? Yes, and this has been well argued by Beatty, although he did not make clear just how diverse are the phenomena of organic evolution. Consider, for instance the prokaryotes (bacteria): they constitute a major part of the life on this earth. In every gram of soil there are on average not a million but a billion bacteria. They clean our water, breakdown organic refuse, nitrify the soil, they have exploited every conceivable environment from hot geysers to frozen soils, deep ocean rifts with pressures of one thousand atmospheres, salt pans, sulfur and iron deposits. You name it, they live in it or feed from it – even petroleum and kerosene are food for some bacteria. What a remarkable story of evolutionary divergence the bacteria present, and how crucial are their activities for all other forms of life. Yet Mendelian segregation and recombination through sexual reproduction involving meiosis and whole genome transfer? – not in bacteria: some of them practice conjugation (which is not fertilization) but you cannot do Mendelian-breeding experiments with bacteria. What, then, has a theory of natural selection couched in terms of the population genetics of Hardy/Weinberg, itself based upon Mendelian genetics to offer them? As Beatty has emphasized, evolution had first to give rise to meiosis, hence a general theory of natural selection has to rely on no specific form of gene transfer but should embrace in its generality bacterial conjugation (plasmid transfer), transduction (viral transfer) and transformation (DNA transfer). What the bacteria and higher forms of life share is an hereditary material – DNA – and the processes of its replication, recombination and mutation. These processes are not just molecular events. For in one way or another they involve virtually the whole cell.

Hodges distinguishes two aspects of natural selection:

1. Its *predictive import*, expressed in terms of *fitness* as *reproductive expectancies* analogous to life expectancies (an apt analogy due to Hodge) and having no causal efficacy, its formal abstractions undeserving of reification.
2. Its *causal import*, adaptation (often referred to also as fitness – a bad habit, but rife in the literature), this is of course relative to the physical and biotic environment.

Why is it so important to distinguish these two imports of natural selection? Hodge claims that with the causal import we can avoid the criticism of natural selection that it is a tautology, and we should be able to distinguish what has been due to drift from what has been caused by selection (Megan Delehanty will be discussing this point). One might add that *adaptation* includes the means a species has used for preserving its favorable genetic constitution – i.e., *speciation*.

Now Natural Selection is not evolution. Granted the distinctive character of the Darwinian theory of evolution rest principally upon natural selection, but the Darwinian theory is more like a cluster of theories. Not all elements of the cluster are necessarily involved at any one time. This brings me to Jon's remark that Mendelism, molecular biology, and multilevel selectionism have *enhanced* the theory of Natural Selection. Can we be sure that none of these will revise it? The revelations of developmental genetics have caused some to raise again the question whether macroevolution is microevolution writ large or something else? Hodge's emphasis on causal processes rather than wide-ranging axioms is surely the choice to make if we want an answer. I suggest, however, there is a difficulty about separating the ontic from the epistemic so sharply. We need the latter to establish the

status of the former, i.e., to show that mutation and selection are adequate to account for evolutionary change we analyze the empirical data with the aid of the mathematics of population genetics, we also simulate the process therewith. Just how distinct, then, are the ontic and the epistemic in practice?

## Comments on Jon Hodge's paper

Megan Delehanty

I will focus on Hodge's primary claim that natural selection is best viewed as a causal theory rather than a dynamic (as represented by Sober<sup>2</sup>) or statistical theory (as claimed by Walsh *et al.*<sup>3</sup>, and less exclusively by Brandon). In particular, I want to look at how we should understand the notion of cause or causal process in the context of fitness.

In his abstract and his 1987 paper<sup>4</sup>, Hodge makes two points that are important in relating his position to others', and particularly to those we will hear more about tomorrow. First, he says that he takes mathematics, as such, to be "not causal and so without causal-explanatory import" (Hodge abstract, section 2). Yet, proponents of statistical interpretations of selection and drift clearly intend that this account *is* explanatory – where does the disagreement come in? Second, he clearly states (again in his 1987 paper) that he takes selection to be a process. Since this is a matter of dispute in Brandon and Millstein's papers<sup>5</sup>, I suggest we look at whether Hodge's position on this point actually is identical to Millstein's and where the disagreement with Brandon occurs.

With regard to the first point, Hodge points out that in addition to the standard conditions required for selection to occur (variation, heritability of variation, and differential reproduction of heritable variation), there must be specified some further criterion which can distinguish selection from drift. On this much, there is no disagreement. Hodge's next step is to claim that specification of this further criterion must "take into account both the judgments which are already being made as to which real or imaginary processes count or would count as natural selection" (as well as being guided by the questions motivating the historical development of the theory). Doing so, he says, brings us to "an explicit definitional insistence on causation itself, on, that is, its physical ingredients *rather than mathematical representations* or teleological interpretations" (1987, p. 251). Selection is to be distinguished from drift because the physical property differences which constitute the hereditary variation that is being differentially reproduced are not merely *correlated* with differences in reproduction – they are *causally relevant* to them. But cannot a statistical interpretation of selection and drift also make this distinction? In order to make such a determination of causal relevance and so distinguish selection from drift, we must be able to tell expected fitness (reproductive success) from actual fitness (reproductive success). This is clearly an essential part of the statistical interpretation. And it is here, I think, that we see causal processes entering into this interpretation. In order to provide a fitness estimate for an organism in a particular context, we have to do just as Hodge states and make judgments about which sorts of causal processes count as selection in this interaction. In effect, causal processes are hidden in fitness estimates. This is clear, for example, in Brandon's discussion of the case of the moths where he points out the importance of relativizing the fitness estimate to the context and determining whether the selective environment is homogeneous or heterogeneous. In effect, what this does it to extend or restrict the set of causal processes that will be considered selection in a given context and to embed them in the assigned fitness value. In this way, the statistical interpretation does have causal-explanatory content - there is not actually any disagreement over the importance of causal processes in producing differences in fitness.

Up to this point, Hodge's and the statistical interpretation can be reconciled, but what happens when we turn to the second point, that selection should be taken as a process? Here the dispute is over how to explain what actually happened - how fitness differences generate differences in actual reproductive

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<sup>2</sup> Sober, E. (1984). *The Nature of Selection*. MIT Press: Cambridge, MA.

<sup>3</sup> Walsh, D.M., Lewens, T., and Ariew, A. The Trials of Life: Natural Selection and Random Drift. *Philosophy of Science* (in press).

<sup>4</sup> Hodge, M.J.S. (1987). Natural Selection as a Causal, Empirical, and Probabilistic Theory. In L. Kruger (ed.), *The Probabilistic Revolution*. MIT Press: Cambridge, MA, pp. 233-270.

<sup>5</sup> Millstein, R.L. (2002). Are Random Drift and Natural Selection Conceptually Distinct? *Biology and Philosophy* 17:33-53.

Brandon, R. (2002). The Difference Between Drift and Natural Selection: A Reply to Millstein. These proceedings, Session 4.

success. Hodge and Millstein claim that we need to distinguish discriminate from indiscriminate sampling. In order to count as selection, the *process(es)* by which the actual reproductive success was achieved, have to be those that were antecedently identified as causally relevant properties of the system in estimating fitness values. Causal processes act to realize certain levels of reproductive success and fitness differences (propensities) cannot constitute causes here. Brandon and Walsh, on the other hand, claim that there is only one process, sampling, and that it is the outcome that allows us to distinguish between selection and drift. Walsh and co-authors claim (p. 15) that “though there are causal processes, even forces, which change trait frequencies, these cannot be identified with natural selection because these forces also cause drift”. Yes, but in any particular context, might we not be able to (at least in theory) say whether a particular process is related to a physical property which varies between individuals? Fitness may be a supervenient property, but there is some physical basis for it and some subset of physical properties will, in interaction with the environment, be causally related to an organism’s reproductive success. Despite his insistence on outcomes, Brandon seems to hint that he too may take process into account. Consider his statement in his conclusion that “Drift is any deviation from the expected levels of reproduction *due to* sampling error. Selection is differential reproduction that is *due to (and in accord with)* expected differences in reproductive success.” Could we not take this to suggest that causal processes which act after the establishment of the physical differences underlying fitness do make a difference to whether something is selection or drift? Otherwise, why make this distinction between “due to” and simply “in accord with”? Perhaps this disagreement with Millstein is not that the process does not matter at all, but that *both* outcome and process need to be considered.

So far I have considered a view of selection as a causal process and the view of it as a statistical theory about population structures. The third alternative Hodge argues against is selection as a dynamical theory. Note that Walsh and co-authors also distinguish between force and causal processes in the quote I just read. So what is the difference and how does it make a difference whether we talk of forces or of causal processes? My understanding of Hodge’s paper is that he identifies two problems with the concept of force as applied to selection (and perhaps to biological systems in general). The first is the non-additivity of various contributions to the net effect observed on trait or gene frequencies. Especially relevant to the case of selection is the change in causal structure that may accompany a change in the population structure. The second problem seems to be the inability to formulate physics-style laws applying to selection. Because natural selection *consists of the processes of interaction* of organisms and their environment, and we cannot distinguish any agency or force from these objects and their interactions. Because of the spatiotemporal specificity of these processes, there can be no general statement of law but only potentially well-confirmed generalizations about the workings of selection in specific conditions and referring to organisms possessing specified properties. If all we are talking about here is making a distinction between forces as (perhaps) being capable of a law-like description while causal processes are more compatible with a more localized description, it may be that the dynamical theory of selection is also reconcilable with the causal view.

### **Workshop Participants**

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