How to understand casual relations in natural selection: Reply to Rosenberg and Bouchard

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Introduction

In "Two Ways of Thinking About Fitness and Natural Selection" (Matthen and Ariew [2002]; henceforth "Two Ways"), we asked how one should think of the relationship between the various factors invoked to explain evolutionary change – selection, drift, genetic constraints, and so on. We suggested that these factors are not related to one another as "forces" are in classical mechanics. We think it incoherent, for instance, to think of natural selection and drift as separate and opposed "forces" in evolutionary change – that it makes sense to say, for instance, that selection contributed 80% to the actual evolutionary history of the human eye, and drift only 20%. We proposed instead a statistical view of the Theory of Evolution, a view in which fitness is not a cause of evolution, but rather a measure of growth. We also argued for a "hierarchical realization model" for thinking about the relationship between evolutionary factors such as those mentioned above, and suggested that in a "fully specified model", as we call it below, there is no distinction between natural selection and evolution.

In "Matthen and Ariew's Obituary for Fitness: Reports of Its Death Have Been Greatly Exaggerated" ("Obituary"), Alex Rosenberg and Frederic Bouchard ("R&B") contest these conclusions. They allege, in particular, that the statistical view of evolution is not "fundamental", defend the separability of natural selection and drift, and recommend a notion of "ecological fitness" which is supposed to meet our doubts concerning the causal role of fitness.

Below, we examine and rebut their arguments.

I.

We begin by dealing with a misinterpretation of our motives for trying to undermine the causal role of fitness. That R&B misinterpret us is of little interest in itself, except to our spouses and children, and if truth be told, not even to them. However, the misunderstanding is diagnostic of our differences with our interlocutors, and it is worth examining for this reason. As we shall see, the tautology problem is a problem for *them*, a problem which (as it turns out) we do not have to face up to.

This is what R&B say:

> The apparent problem is obvious. Define fitness as some biologists implicitly do, in terms of actual survival and reproduction, and the principle of natural selection turns into an empty tautology: those organisms which survive and reproduce in larger numbers, survive and reproduce in larger numbers. . . . Mohan Matthen and André Ariew ['s] . . . way of dealing with this problem is to expunge altogether the concept of fitness from the theory of natural selection. No fitness, no fitness problem. ("Obituary", p. xxx.)

The so-called "tautology problem" alluded to above was not in fact an important part of our motivation. (See, however, Matthen and Ariew 2002: 69, n. 19.) We think that it is no more a problem for the theory of natural selection (i.e., the Darwinian theory of evolution) that it has at its heart a "tautology" – more accurately, a (non-empirical) truth of mathematics – than it is for physics that it relies on such mathematical truths as "$2 + 2 = 4$".

We claimed that the fundamental proposition of the theory of natural selection is some such abstract characterization of selection as the following:

> *C. C. Li's Theorem* In a subdivided population the rate of change in the overall growth-rate is proportional to the variance in growth-rates.

The proof of Li's Theorem consists just in showing that if one subdivision of a population grows fast, and the others slowly, the fast-growing subdivision will eventually come to dominate the whole, and the whole will thus converge upon the growth-rate of this fast-growing subdivision. (Li's Theorem assumes constant growth-rates.)

Li's Theorem is mathematically true, but it does not exhaust the theory of natural selection. For Li's Theorem does not imply that evolution will occur. To get evolution out of Li's theorem, you need to add a number of additional propositions. Minimally, you need to posit that *there is* (or rather once was) a non-zero variance in growth rates. This posit is not mathematically true; there does not need to have been any variance of fitness, and so there does not need to have been evolution. Further, to derive any truths about the subpopulations

themselves, and about the actual course of evolution, you need a great deal of information on mechanisms of heredity, estimates of growth rate, the nature of the historical environment, the adaptive value of various parts of animals, and so on. Li's Theorem, therefore, has the same status as other mathematical theorems that play a central role in evolutionary biology, including the Hardy-Weinberg Law. The Hardy-Weinberg Law is a mathematical result; however, it is an empirical issue whether the alleles at a particular locus exemplify the conditions required for a population to enter into Hardy-Weinberg equilibrium. In short, the fact that a mathematical proposition such as Li's Theorem plays a central role in a theory does not imply that the theory is non-empirical. There is no tautology problem.

This being said, we must now note that the role played by non-empirical abstract principles marks out the theory of natural selection as a special kind of science. For it is a striking fact that Li's Theorem and other abstract characterizations of selection yield predictions of overall growth-rate not only in the biological realm, but also in *any other* domain that can be subdivided into sub-domains with varying growth rates. There are populations divided by growth rates in operant conditioning, the immune reaction, cultural growth, the economy, and a thousand other realms. In all of these, Li's theorem holds good. What is more: in all of these realms, there exist phenomena strictly analogous to natural selection in the biological realm, and *Li's theorem plays exactly the same role in explaining these non-biological phenomena as it does explaining natural selection.*

Now, the italicized clause immediately preceding might strike many evolutionary biologists and philosophers of biology as truistic (cf. Hull et al. 2001). However, it is actually quite an unusual feature of the theory of natural selection that it has such a principle at its heart. In this respect, it strictly parallels the case of statistical mechanics. Lawrence Sklar (1999) remarks of the latter that it "has universal applicability across all of the domains of physics", and thus has no place in the "usual hierarchy of constitutive or dynamical theories." What Sklar means is this. A law like "$F = ma$" applies only to things that have mass and acceleration. A mathematically similar principle like Charles' Law "$V = kT$") is not thought of as simply another application of Newton's Second Law, in virtue of the fact that both are expressed by first-order linear equations with two variables. Similarly, Coulomb's Law ("$F = C\ (e_1.e_2/e4^2)$") holds only of electric charges: the fact that it is an inverse square law similar in form to the Law of Gravitation ("$F = G\ (m_1.m_2/r^2)$") is not taken to imply that both of these are special cases of some overarching law. These laws are grounded not in mathematical structure but in the identity and nature of the entities and quantities that figure in them. Newton's Second Law is, in Sklar's terminology, a "dynamical" theory, which

depends on the identity of the physical quantities it designates; Coulomb's Law is a constitutive theory, which depends on the kind of entity it describes.

Li's theorem, by contrast, like the second law of thermodynamics, applies to *all* domains – it has "universal applicability", as Sklar says – and it can be used to predict outcomes in *any* domain that satisfies its antecedent.

This is the basic motivation for the hierarchical realization model we proposed in "Two Ways". R&B fasten on to what, in this context, seems like an irrelevant aspect of our analogy between population genetics and statistical mechanics. They argue that statistical mechanics is not reducible to classical mechanics: we don't agree with them, but it is incidental to our purpose to argue the point here. The point of our analogy is that abstract formulae of selection, such as Li's Theorem, are *universally applicable*, and not limited to the biological realm: this universal applicability shows, we contend, that they are about mathematical structures at the ensemble-level, not causal relations at the individual-level.

II.

R&B (in effect) *deny* that it is permissible to have a mathematical principle at the heart of a theory. This is why they think that the "tautology problem" is a problem; this is why they seek to replace abstract principles of selection with "causal principles" which are supposed to possess empirical content. Unfortunately, their attempt to do this side-swipes the universal applicability of natural selection: it ends up denying that the explanation of the other phenomena mentioned earlier – immune response, operant conditioning, etc. – appeal to the same principle as that of natural selection in the biological realm.

What is the alternative that R&B envisage? Apparently, a "law" like:

PNS (x) (y) (E) [If x and y are competing populations and x is fitter than y in E at generation n, then probably (x's size is larger than y in E at some generation n' later than n)]

PNS is used in the proof of Li's theorem. Interpret "fitter" as "has a higher growth rate". (On this interpretation, PNS is a mathematical truth.) Then, the antecedent of PNS postulates a subdivision of the entire population $(x + y)$, into two groups, one of which has a higher growth rate. This is the antecedent of Li's Theorem. Because of its higher growth rate, x will come to represent a higher and higher proportion of the whole. Thus, the growth rate of $(x + y)$ will approach that of x.

R&B intimate that PNS is a *causal* law. This implies that fitness is not just a measure of growth-rate, but some sort of causally potent quantity. What

quantity? "Ecological fitness", they say, but they do not tell us what this is. Perhaps they intend something PNS to become something like Brandon's Principle of Adaptation, which states roughly that if population x is better adapted to environment E than y, then x will probably be larger than y in later generations. Perhaps "ecological fitness" is "adaptation" by another name. On this interpretation of fitness, PNS is *not* a universally applicable principle. We said in the last section that the theory of natural selection applied equally to domains like the immune response (where certain antibody clones reproduce faster than others). On R&B's interpretation, however, PNS does not apply to the immune response, just as Brandon's Principle of Adaptation does not: ecological fitness is not a quantity that operates in the immune response. The transfer to a different domain can only take place when you interpret "fitter" as "has a faster growth rate". This is the interpretation they want to reject. So they are in fact interpreting PNS as a "constitutive or dynamic" theory.

The problem is that, if you take this line, the vacuity of PNS is going to come back to haunt you. Look at Brandon's principle. Or look at R&B's version of PNS, in which 'fit' means 'ecologically fit'. How do you define this quantity? How do you cope with the fact that what makes a leopard ecologically fit is very different from what makes a violet so? It is hard to resist the impression that "adaptedness" and "ecologically fit" must be defined by growth rate. For there is nothing that unites the fit leopard and the fit violet except their aptness for having more descendants than their competitors. Thus, 'well-adapted' might mean something like 'is physically so constituted as to possess the propensity to reproduce a lot, and to live long enough to do so'. (This is the so-called "propensity" interpretation of fitness.)

On this interpretation, PNS comes to the following:

(x) (y) (E) [If x and y are competing populations and members of x and y are physically so constituted at generation n that members of x possesses a greater propensity to reproduce a lot in E than members of y, and to live long enough to do so, then probably (x's size is larger than y in E at some generation n' later than n)].

By seeking causally potent quantities to instantiate the terms of principles such as the above, R&B invest such principles with non-universal causal status. In other words, they think that there is a quantity specific to biology, ecological fitness, as they call it, that is causally active in accordance with the above principle. The problem is that the above principle has no empirical content. If you treat non-empirical principles as domain-specific causal laws, you flounder on the tautology principle.

Another problem is that this kind of law gives us no mathematical grasp on the phenomena of selection. In "Two Ways", we allowed that in some sort of

vague way, it was alright to say that organisms with a competitive advantage will prosper at the expense of others, especially if you are willing to specify what physical qualities contribute to such a competitive advantage. This is the conception of fitness we called "vernacular fitness". (By the way, we did not "expunge" fitness in "Two Ways": we talked about two conceptions of fitness, one acceptable in comparative, but non-quantified talk, the other apt for mathematicization.)

Such a conception of fitness does, however, not lend itself to quantification: it is *merely* comparative. Perhaps we might be forgiven if, this one time only, we block-quoted ourselves.

> Vernacular fitness is specified in comparative terms and in restricted contexts. For example, you might learn that the optimal reproductive strategy with respect to sex- determination is to produce male offspring when there are fewer males in the population, and females when there are fewer females. But this only tells you about the relative merits of strategies within a circumscribed set, with other factors held constant. The analysis does not tell you whether producing offspring of the minority sex is more or less advantageous than other fitness-relevant things you can do; there is, generally speaking, no way of combining the effects of a good strategy in this game, with good or bad strategies in other games. For example, we have no way of calculating whether a given sex-selection strategy interacts with a given parental care strategy, and how the fitness produced by variants of these strategies combine. This inability to add the "forces" of fitness is even more pronounced when the source laws are in unrelated domains. Suppose a certain species undertakes parental care, is resistant to malaria, and is somewhat weak but very quick. How do these fitness factors add up? We have no idea at all. (67)

The above passage would, we suspect, be equally valid if "ecological fitness" were substituted for "vernacular fitness". R&B simply assume (without argument) that comparative differences in ecological fitness can be "arithmetically aggregated", as they say. But how? There is no problem aggregating if fitness is understood as a growth-rate. But, as we have seen, this is the very interpretation of fitness that they want to avoid. Perhaps it is possible to mathematicize ecological fitness without reference to growth-rates, but we are sceptical.

III.

Suppose that Li's Theorem and PNS are, as we are claiming, non-empirical, universally applicable principles. What is the correct way to apply them to

explaining an empirical proposition E – for instance, the proposition that the human eye is thus-and-so? The situation here is no different from that of applying any other non-empirical mathematical proposition to empirically determined facts. We need to say how E answers to the antecedent of the universal principle. In the case of Li's Theorem, for example, we need to say how the population subdivides, and why the growth-rates of the subdivisions are different. Then we will not only predict the change in the population, but also understand the sources of this change. So, if you want to understand the evolution of the human eye, you want to say what its various historical antecedents were, and how some of these contribute to a greater growth-rate than its alternatives. This endeavour takes you into studies of the historical environment, optimality studies, heredity, etc.

This was the reasoning that motivated our adoption of the so-called hierarchical realization model. This model consists of a specification of all the growth-rate factors relevant to a case like the evolution of the human eye. How large is the population? How much advantage does this design have over others? What is the mechanism of inheritance? Etc. Our main contention was that the complete explanation of the evolution of the human eye consisted in the correct specification of all growth-rate relevant factors. This would provide a *correct completely specified* natural selection formula for the case at hand. Alternative specifications of growth-rate factors result in *possible completely specified* natural selection formulae. Ignorance of the value of some of these factors will result in not specifying them, i.e., in an *incomplete natural selection formula*. A formula which specified the optical optimality of the eye, but did not specify the cost of producing it as compared to other alternatives would be such an incomplete natural selection formula.

Now consider a fully specified formula. It tells you exactly what the growth-rates are for variant subpopulations, and why these subpopulations have such growth-rates. But it tells you this in a probabilistic way. That is, it tells you what level of confidence to assign to each possible outcome. It does not tell you that the human eye had to be such-and-so, but what the probabililty of its turning out that way is. An analogy is this. Applied to a sequence of four coin-tosses, the theory of probability tells you what level of confidence you should attach to each possible outcome. That is all the theory can tell you. Thus, in the case of the coin-tosses, there is nothing in the setup that is available to tell you why four heads came up, rather than two heads and two tails. It does tell you that the former is a less likely outcome, but not why one or the other actually came to pass.

Similarly in the case of evolution, a fully specified natural selection formula will tell you what confidence to place in each possible outcome. An omniscient person would be able to assign probabilities in such a knowing

way as to be able to discern when actual outcomes were *not* the most likely (as with the four-head outcome). In principle, an evolutionary analysis of the human eye ought to tell you that it was unlikely to have turned out the way it did. In practice, this simply does not happen. Evolutionary theorists usually assume that the actual outcome must have been the most likely analysis, and they infer the historical state of other factors based on this assumption. Bracketing this, we can see how the different explanatory factors interact in this formula. If you want to know how sexual reproduction contributes to the evolution of the human eye, you compare the probabilities in the fully specified formula *with* sexual reproduction with those in a fully specified formula that specifies asexual reproduction, and with the incomplete one that neither specifies sexual nor specifies asexual reproduction. The assignment of probabilities is, as it were, holistic in each such formula.

Why holistic? Because it makes no sense to try to analyse the influence of each factor taken separately. Biologists and philosophers of biology sometimes talk as if genetic constraint, for example, *opposes* selection. In the much discussed case of sickle-cell anaemia, for example, they claim that selection is "trying" to eliminate the fatal condition, but is "thwarted" by sexual reproduction, which preserves the occurrence of the fatal allele in the gene pool. This is a conceptually confused way of thinking. For inheritance is as much a part of natural selection as is the uneven survival rates of certain specimens. It is true that under asexual reproduction, the fatal allele *would* be eliminated. But to parse this as sexual reproduction *thwarting* and asexual reproduction *helping* selection is a misleading, and indeed incoherent, way of speaking. Selection has no goal taken on its own; mechanisms of reproduction do not have goals either. So this is not a case of the two factors acting in their own directions. The various factors are not interacting with one another as forces do (see "Two Ways"); taken altogether, they determine a probability distribution. The correct mathematical operation for combining such factors is, we would argue, logical conjunction, not vector addition. The mathematics of 'and' is very different from that of vector addition.

Now think of how natural selection operates subject to a particular specification of relevant factors. Populations are subject to various gene-frequency changing events: births, deaths, matings, mutations. Call these events i-level selection events. In the long run, i-level selection events will cumulatively distribute themselves in agreement with the probability distribution predicted by the correct fully specified formula. That is, the *frequencies* of the various possible outcomes will, in the long run, align themselves with the *probabilities* assigned to these outcomes by this formula. Now, one might ask: What is the cause of a particular one of these selection events? Some biologists and philosophers of biology are inclined to answer the question in

light of its prior probability: A selection event that brings about an improbable event is caused by drift; one that brings about a likely event is caused by selection. (R&B don't quite say this, but they do say something close, namely that drift is an event with deviant initial conditions.) This, we would contend, is a mistake. Selection results both in improbable events and in expected ones: in the long run, both will occur, though the improbable ones will occur less frequently than expected ones. Notice that selection has an inclusive sense in this exposition: it is just the unfolding of events in frequencies that correspond to predicted probabilities. Since Darwinian evolution is just the outcome predicted by a correct fully specified natural selection formula, it makes little sense to *contrast* evolution and natural selection in this way of "thinking about fitness and natural selection".

This leads to the question why probabilistic theories are invoked, given that they are causally not fundamental.

Probabilistic theories are invoked in two kinds of situations. The first is when you lack knowledge of all the factors. Coin-tosses are an example. We don't know about the initial conditions of every single coin-toss, and we don't have the means to calculate the outcome from them in any case. So we calculate from what we know. Some of the things we know turn out to be irrelevant. For instance, we know, of a given coin-toss, whether it occurs in the morning or evening, whether the wind is blowing east or west, whether the coin is warm or cold, and so on. It turns out that none of these factors changes the probabilities: the probability of a coin coming up heads with no conditions specified is the same as that of it coming up heads given that the wind is blowing from the east. The elimination of irrelevant factors leaves just a few accessible factors that need to be specified. The probabilities are specified in terms of these. We do not have access to, and therefore do not invoke, Newtonian conditions.

The second kind of situation in which probabilistic theories are invoked is where you want to concentrate on some rather than other factors. This is a case of abstraction, not ignorance: some factors are deliberately ignored, they are not simply beyond our reach. In the Darwinian case, the aim is understand why organisms of some sorts are present in the world, and others not. In particular, the interest is in inheritable characters. So we consider only those factors that surround inheritable characters. We want to know, for instance, why eyes of a certain sort are the norm among humans, and not eyes of another sort. So we consider the causes and effects of eyes of that and other sorts, but not circumstances incidental to that. Joe has bad eyes, and dies by being pushed off a cliff by Mary. His relationship with Mary had nothing to do with his eyes; it is not inheritable, in any case: we ignore it. Joe's death advances the cause of human eyes, but we take his death to be

a part of the probabilistic indeterminacy of eye-survival, not part and parcel of it. The theory of natural selection abstracts away from certain causes and effects in the world.

From this kind of abstraction certain patterns in variegated events emerge. A complete causal description of the events that led to the evolution of leopards would be entirely distinct from the causal description of the events that led to the evolution of violets. These causal descriptions would not invoke fitness at all, let alone any probabilistic concepts. Yet, the causal explanation then lacks generality, it applies only to the particular event, being that of the lions or that of the violets. Hence, the deterministic description does not serve to identify what lions and violets have in common with each other and many other evolving populations (including non organic one). That is, the deterministic desciption fails to indicate that these populations have undergone similar sorts of histories. That is the point of assigning probabilistic terms such as fitness

R&B do not, we would contend, fully appreciate the implications (a) of universally applicable non-empirical theories, and (b) of probabilistic reasoning, or at least their attachment to the Newtonian paradigm of deterministic constitutive theories prevents them from appreciating theories with these characteristics. Their approach to the theory of natural selection is informed by their attitude. This prevents them from an appreciation of why this theory is superior in a certain respect to a Laplacian specification of the positions and momenta of all particles in the universe. Given Newtonian determinism, such a specification would meet their demands of complete explanation, and repair the alleged gaps in the knowledge offered us by Darwin. On the other hand, Darwin gives us a kind of understanding that Laplace does not.

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