How is Biological Explanation Possible?
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ABSTRACT

That biology provides explanations is not open to doubt. But how it does so must be a vexed question for those who deny that biology embodies laws or other generalizations with the sort of explanatory force that the philosophy of science recognizes. The most common response to this problem has involved redefining law so that those grammatically general statements which biologists invoke in explanations can be counted as laws. But this terminological innovation cannot identify the source of biology's explanatory power. I argue that because biological science is historical, the problem of biological explanation can be assimilated to the parallel problem in the philosophy of history, and that the problem was solved by Carl Hempel. All we need to do is recognize that the only laws that biology—in all its compartments from the molecular onward—has or needs are the laws of natural selection.

My topic is the nature of explanation in biology, more specifically perplexity which philosophers of biology should feel about how it works. But to set the stage, let us recall some ancient history in the analysis of explanation: the controversy surrounding the nature of historical explanations.

1 Preamble: the philosophy of history

From earliest papers on the subject onwards, Hempel ([1942]) responded to the lack of any laws adduced in historical narratives by advancing two claims: first, laws about rational action are implicit in the appeal to causal relations between explanans and explanandum; second, historical explanations, like many explanations in science, are explanation sketches, which either presuppose information available to interlocutors or give promissory notes

to deliver further details hereafter that will complete the explanation. Few working in the philosophy of history were satisfied with these two ways of defending the covering law model of explanation. Instead, a variety of alternative accounts of explanation in history were offered that did not require general laws, either explicit or implicit. Most of these alternatives focused on the notion of 'narrative' as the vehicle for historical explanation, and provided accounts of the non-nomological links that hold a narrative's components together and make it explanatory. None of these accounts of how narratives explain was satisfactory. Some of them linked events cited in a narrative by appeal to a principle of rationality, which was claimed to be a necessary truth. But given the conviction that factual explanations be ampliative, unlike logical proofs, this proposal could not work. On the other hand, to treat a principle of rational action as a contingent generalization simply generates the covering law model that these writers rejected. Others claimed that narratives work by redescribing the event to be explained. This approach trades on the intentional character of action explanations—the fact that we cannot individuate intentions, beliefs and desires—except via their content, and that content will include the actions intended. Thus, explaining an action is a matter of redescribing it in the terms under which it was intended. The trouble with this tactic is, again, that even if redescriptions are apt, their causal relevance to the event to be explained can only be vouchsafed by a contingent generalization, which is what the covering law model demands. Otherwise, events under re-descriptions become self-explanatory. Accordingly, opponents of the applicability of the cover-law model in history increasingly embraced the view that historical explanation, and in particular narrative explanation, was non-causal, or the wider philosophical thesis that causation is non-nomological. The trouble with these two approaches is that neither move solves the problem of how narratives explain. By contrast, the covering law model's 'implicit law' and 'explanation sketch' approach did provide for the explanatory force of narratives, though not simply by assimilating them to causal explanation or committing itself to a Humean theory of causation. The covering law model made narratives explanatory by showing how the explanans is contingently connected to the explanandum—the implicit law is contingently true, and by showing how the explanatory relevance of the explanans to the explanandum can be empirically tested—by formulating the implicit law and testing it. Similarly, if narratives provide non-nomological explanations, the connections they establish must be contingent and testable. If not testable we cannot tell the difference between real explanation and pseudo-explanation; if not contingent we must admit that historical narratives provide synthetic *a priori* knowledge or else that some historical events can explain themselves (say, by redescription). In short, if historical narratives explain, and don't do it

via implicit laws (about, say, rational action), it is a mystery how they do explain.

Make no mistake. The issue is not whether the deductive nomological model provides necessary and sufficient conditions for historical explanation. The issue is how narratives explain. We could restate the problem in 'modern dress' by adducing Kitcher's ([1989]) account of explanation as unification. On this view, explanation is deductive unification which balances the desiderata of a small number of assumptions, a large number of consequences, and factual stringency in the derivation of 'objective dependencies'. What we want to know is whether the events related in a narrative reflect objective dependencies. Laws or empirical generalizations that approximate to laws provide such dependencies. It is hard to see what else might.[1]

2 The nomological vacuum of biology

So much for the preamble. Let us turn now to the nature of explanation in biology. It is widely agreed that there are no biological laws. The agreement that there are no such laws in biology is manifest in the valiant attempt of philosophers to redefine the concept of law so as to be able to dub descriptions of widespread historical patterns as laws, or necessary truths as laws (see for example, Sober [1993], and Lange [1995]). Of this more hereafter, but first we need to see why there can be few if any strict laws in biology and then why there are no non-strict laws.

It is the nature of any mechanism which selects for effects that it cannot discriminate between differing structures with identical effects. And functional equivalence combined with structural difference will always increase as physical combinations become larger and more physically differentiated from one another. Moreover, perfect functional *equivalence* isn't necessary. Mere functional similarity will do. Since selection for function is blind to differences in structure, there will be no laws in any science which, like biology, individuates kinds by naturally selected effects, that is by functions. A law in functional biology will have to link a functional kind either with another functional kind, for example, 'all amphibians reproduce sexually', or link the functional kind with a structural kind, for example, 'all genes are composed of DNA'. But neither of these statements can be a strict

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[1] In a subsequent work, Kitcher ([1993]) identifies deductive patterns of explanatory unification characteristic of various disciplines, and in particular of evolutionary biology. However, to answer the question of what the 'objective dependencies' on which explanation depends consist in, it will not suffice to identify the 'patterns of explanation' characteristic of history, or, as we shall see, of biology either. Our question is what makes patterns of explanation explanatory, to what 'objective dependencies' do they advert? See Section 5 below for further discussion of Kitcher's account of biological and particularly evolutionary explanation.

law, because of the blindness of natural selection (which forms structurally heterogeneous functional kinds) to structure (which will heterogeneously realize functional kinds). Natural selection makes for the supervenience of the functional on the physical and the consequent absence of strict laws. The details of this argument are relegated to a footnote.[2]

Any science in which kinds are individuated by causal role will have few if any strict laws. But, of course, it has been widely held that biological explanation does not require strict laws. Non-strict, *ceteris paribus* laws will suffice. A defense of the nomological status and explanatory power of exception-ridden generalization may even be extended, as Nancy Cartwright has argued, to the claim that many generalizations of the physical sciences are themselves bedecked with *ceteris paribus* clauses; accordingly, the ubiquity of such generalizations in biology has no special implications for the nature of its explanations. Whether or not there are non-strict laws in physics and chemistry, there is a good argument for thinking that the exception-riven generalizations—the 'non-strict laws' of biology—will not be laws at all.

The reason is that what makes for the allegedly *ceteris paribus* claims of physics does not obtain in biology. In physics, Cartwright ([1998]) notes rightly, there are a finite (indeed small) number of forces—mechanical, electromagnetic, thermodynamic—which all work together to produce actual outcomes which we seek to explain. To the extent that a text-book generalization of mechanics such as $F = gm_1m_2/d^2$ is silent on these other forces, it is not a completely true description of physical processes, but rather a *ceteris paribus* law. Cartwright admits of course that there are what she calls

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2   To see why there can be no strict laws in biology, consider the form of a generalization about all *F*s, where *F* is a functional term, like gene, or wing, or belief, or clock, or prison, or money, or subsistence farming. The generalization will take the form $(x)[Fx \rightarrow Gx]$, a law about *F*s and *G*s. *Gx* will itself be either a structural predicate or a functional one. Either it will pick out *G*s by some physical attribute common to them, or *Gx* will pick out *G*s by descriptions of one of the causes or effects that everything in the extension of *Gx* possesses. But there is no physical feature common to all items in the extension of *Fx*:*Fx* is a physically heterogeneous class since its members have been selected for their effects. So *G* cannot be a structural predicate. Of course some structural feature may be shared by all of the members of *F*, but it will not be a biologically interesting one. Rather it will be a property shared with many other things—like mass, or electrical resistance. These properties will have little or no explanatory role with respect to the behavior of members of the extension of *Fx*. For example, the generalization that 'all mammals are composed of confined quarks' does relate a structural property (quark confinement) to a functional one (mammality), and is exceptionlessly true. But it is not a law of biological interest. The existence of a functional property different from *F* that all items in the extension of the functional predicate *Fx* share is highly improbable. If *Fx* is a functional kind, then owing to the blindness of selection to structure, the members of the extension of *Fx* are physically diverse. As such, any two *F*s have non-identical (and usually quite different) sets of effects. Without a further effect common to all *F*s, selection for effects cannot produce another selected effect; it cannot uniformly select all members of *F* for some further adaptation. Thus, there is no further function kind which all *F*s share in common. Whether functional or structural, there will be no predicate *Gx* that is linked in a strict law to *Fx*. A recent discussion of how functional individuation together with multiple realizability obstructs the possibility of strict laws in biology and the so-called 'special sciences' is Shapiro ([2000]). Shapiro's treatment rehearses a well-known literature which begins with Fodor ([1981]).

'super-laws', which include the finite number of forces actually operative in nature. These, in effect, will be strict laws. And they underwrite the nomological character of her alleged *ceteris paribus* laws by specifying exactly what forces interfere to prevent other things from being equal, and thus excuse the predictive failures and explanatory imprecision of the non-strict *ceteris paribus* laws.

But in biology the role of natural selection does not limit the number of interfering forces that would turn a *ceteris paribus* law into a 'super' or strict law. The reason is to be found in the role of the environment in setting adaptational or design problems for evolving lineages to solve. At a relatively early stage in evolution, these design problems take on the reflexive character of what Dawkins and others have called 'arms races': dynamic strategic competitions in which every move generates a counter-move so that conditions are never constant and *ceteris* are never *paribus*.

Ever since Darwin's focus on artificial selection, it has been recognized that in the evolution of some species, other species constitute the selective force channeling their genetic changes. The interaction of predator and prey manifest the same relationship. Since the importance of frequency-dependent selection became apparent, it has been recognized that an interbreeding population can be an environmental force influencing its own evolutionary course. At least since the work of Waters,[3] philosophers have recognized that among the environmental features that filter genetic variations and allow comparatively more adaptive ones to pass through, are other genes, both within a gene's own cellular milieu, and beyond it in competing as well as cooperating organisms. Competition for limited resources is endemic to the biosphere. Any variation in a gene, individual, line of descent, or species which enhances fitness in such a relentlessly competitive environment will be selected for. Any response to such a variation within the genetic repertoire of the competitor gene, individual, lineage, or species, will in turn be selected for by the spread of the first variation, and so on. One system's new solution to a design problem is another system's new design problem. If the 'space' of adaptational 'moves' and counter-moves is very large, and the time available for trying out these stratagems is long enough, we will be able to add to the 'so on' of the penultimate sentence, the words '*ad infinitum*'.

What this means of course is that any functional generalization in biology will be a *ceteris paribus* generalization in which, over evolutionary time scales, the number of exceptions will mount until its subject becomes extinct. Take a simple example, such as 'Zebras have black and white vertical stripes.' The explanation for why they do is that lions are color-blind and the stripes tend

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[3] This point was first made by Waters ([1991]). See also Philip Kitcher, and Kim Sterelny ([1988]), who expanded on Water's argument.

to provide camouflage both because individual zebras will be hard to detect in high grasses and because when grazing together it will be hard to tell where one zebra ends and another begins. This strategy for survival can be expected in the long run to put a premium on the development of ocular adaptations among lions—say color vision—that foil this stratagem for zebra survival. This in turn will lead either to the extinction of zebras or the development of still another adaptation to reduce lion predation—say, green stripes instead of black and white ones. And in turn this stratagem will lead to a counter-stroke by the lion lineage. The fantastic variety of adaptational stratagems uncovered by biologists suggests that there is a vast space of available adaptive strategies among competing species, and that large regions of it are already occupied. The upshot is that, to the extent that general laws must be timeless truths to which empirical generalizations approximate as we fill in their *ceteris paribus* clauses, no such laws are attainable in biology because we can never fill in these clauses.[4]

One nice set of examples of this state of affairs is to be found at the basement level of molecular biology where it was once assumed that we had exceptionless strict general laws. Consider the generalizations that all enzymes are proteins, that hereditary information is carried only by nucleic acids, or the so-called central dogma of molecular genetics: DNA is transcribed to RNA, and RNA is translated to protein. Each of these apparently exceptionless generalizations has been discovered in recent years to be subject to exceptions. It turns out that RNA catalyzes its own self-splicing, that prions (proteins responsible for, for example, BSE) carry hereditary information, and that retroviruses carry their own hereditary material in RNA and transcribe it to DNA. In each case the full story of how these exceptions to the relevant generalizations emerged is a story that reflects the operation of natural selection finding strategies in adaptational space that advantage one or another unit of selection in the face of stratagems employed by others.

Over the long run, the number of exceptions to any functional general-ization will increase, and increase in ways we cannot predict. If laws are timeless truths, then there will be no laws in biology, or at least none to which our generalizations will visibly approach in approximation. For if the *ceteris paribus* clause of a biological statement is subject to a huge number of qualifications, from which some drop out and others are added as a result of the vagaries of local environmental changes, the traditional defect of *ceteris*

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[4] This analysis of why there are no biological laws must be distinguished from an apparently similar one due to John Beatty. On Beatty's 'evolutionary contingency thesis', there are no laws in biology because the indeterministic character of actual evolutionary pathways precludes the identical initial conditions from resulting in the same outcome. This argument requires that evolutionary processes be indeterministic, a tendentious assumption, and does not turn on the strategic character of biological interactions. See Beatty ([1995]).

paribus laws becomes manifest, namely their comparatively greater unreliability for prediction and the difficulty of establishing the putative explanations they purport to provide. The comparison to alleged *ceteris paribus* laws of physics is not apt.

Thus the nomological vacuum of functional biology is complete. No strict laws, and no non-strict ones either. The apparent generalizations of biology are disguised statements about evolutionary etiologies of particular properties of biological systems on this planet. This is where we came in, so to speak. For if the apparent generalizations of functional biology are not real ones, do not support counterfactuals in the way laws do,[5] are often predictively weak[6] and have the prospect of becoming weaker over time, how do they explain? The question is not rhetorical. That these apparent generalizations are accepted among biologists as explanatory, and should be so accepted, is not under challenge. It is the philosopher's account of what makes them explanatory and how they explain that needs elucidation.

Of course biology could circumvent one of the limits on the discovery of laws governing the processes it treats, if it were to forego functional individuation. By adopting structural identifications of the kinds about which we theorize and predict, it could avoid the multiple realization problem bequeathed by the conjunction of functional individuation and natural selection. It is not clear that this would enable biology to circumvent the strategic interaction problem that natural selection generates, but in any case the suggestion is a non-starter. For the suggestion that biology forego functional individuation constitutes methodological advice no one is likely to follow in biology or elsewhere beyond physical science. The reason is that foregoing functional individuation is too high a price to pay for laws: the laws about structural kinds that creatures like us might uncover will be of little use in real-time prediction or intelligible explanation of phenomena under descriptions of interest to us.

What would it mean to give up functional individuation? If you think about it, most nouns in ordinary language are functional; in part, this preponderance is revealed by the fact that you can verb almost any noun these days. And for reasons already canvassed, most terms that refer to unobservables are functional as well, or at least pick out their referents by their observable effects. What is more to the point, the preponderance of functional vocabulary reflects a very heavy dose of anthropomorphism, or at

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[5] For a cogent summary of the problem of counterfactual support for biological *ceteris paribus* clauses, see Lange ([1995]), pp. 436–7.

[6] Where we can predictively rely on *ceteris paribus* generalizations of biology, occasionally in ecology, more so in genetics, even more in anatomy, and much more so in physiology, and in cellular and certain parts of molecular biology, it is because nature is acting on a time-scale slow enough for us safely to neglect the chance of 'arms race' changes in biological processes local to us. See the discussion of Lange ([1995]) below, in Section 3.

least human interests. It's not just effects, or even selected effects, which our vocabulary reflects but selected effects important to us because we can detect them unaided and/or because we can make use of them to aid our survival. We cannot forego functional language and still do much biology about phenomena above the level of the gene and protein. 'Plants', 'animal', 'heart', 'valve', 'cell', 'membrane', 'vacuole'—these are all functional notions. Indeed, 'gene' is a functional notion. To surrender functional individuation is to surrender biology altogether in favor of organic chemistry.

3 Searching for substitutes for real laws

Oddly enough, the one area in which most philosophers of biology have declined to argue that there are true nomological generalizations is within the theory of natural selection itself.[7] Perhaps one reason is that biologists do not identify a small number of general statements as providing the content of this theory the way that physicists identify the three laws of Newtonian mechanics (Sober [1984], p. 74). Another reason is that when biologists do attempt so to formulate the theory, they often express its leading idea—that the fittest survive and reproduce—as a disguised tautology, because they define fitness in terms of differential reproduction (see Rosenberg [1985], Chapter four, and Brandon [1990], pp. 134ff).

The alternative definition most fashionable among philosophers makes fitness into a probabilistic disposition to reproduce. This definition has the virtue of making the slogan 'the fittest survive' into a contingent truth and the vice that it turns the theory into a falsehood.[8] In consequence, some philosophers have followed Popper and argued that the 'Principle of Natural Selection' [PNS] is not a law or set of laws. Brandon ([1990], p. 142), writes:

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[7] Kitcher ([1993]), p. 121, writes: 'success in achieving exceptionless generalizations is by no means a sine qua non for good science [. . .]. Darwinian evolutionary theory has served us as an example.' According to Sober ([1984]), p. 51, '*general* source laws are hard to come by in evolutionary theory' [italics in original].

[8] As first recognized by Beatty and Finsen ([1989]). See also John Beatty ([1992]). In brief, what Beatty and Finsen showed is that any definition of fitness in terms of reproductive rates—either expected or actual—fails to reflect important distinctions between quality and quantity of off-spring. Moreover, it is blind to multigenerational (expected or actual) reproductive differences that reflect fitness differences. In many environments, the fitter organism leaves (or is probabilistically expected to leave) a smaller number of higher-quality off-spring while the less fit organism leaves a larger number of lower-quality off-spring. Leaving a smaller number of high quality off-spring in generation n which results in a higher number of descendants in generation $n + 1$ reflects higher fitness than leaving a larger number of off-spring in generation n which results in a lower number in generation $n + 1$. Beatty's and Beatty and Finsen's treatment of the problems of the propensity interpretation rely on a series of papers by J. H. Gillespie, culminating in Gillespie ([1977]). If fitness is to be defined in terms of a probabilistic propensity, it will be a more generic one, which allows for a disjunction of different (and indeed changing) probabilistic descendant-expectations depending on the environment in which organisms find themselves. This interpretation will allow it to do the work required of fitness in the version of Darwinian theory outlined below.

> If, as I have argued, the world is such that a general testable and
> empirically correct version of the PNS is impossible, then our best option
> is to adopt the general, but untestable schematic PNS as a unifying
> principle [. . .] as untestable PNS is at the core of the theory.

So, philosophers of biology have accepted that generalizations in biology are
not laws of the sort we are familiar with from physical science. But instead of
going on to rethink the nature of biological explanation, this conclusion has
led them to try to redefine the concept of scientific law to accommodate the
sort of non-nomological statements that biological explanations do in fact
appeal to.

Between them, Elliot Sober and Marc Lange represent the two extremes
among philosophers who have sought to redefine the meaning of scientific
law to accommodate the explanatory devices of biology. Lange argues for

> a conception of natural law according to which 'The robin's egg is
> greenish-blue' states a natural law despite the natural variation in the
> colors of robin's eggs, despite the fact that it is an 'accident of evolution'
> that the robins egg is greenish blue, and despite that fact that 'robin'
> refers to an individual object (Lange [1995], p. 430).[9]

Lange provides a clear and careful discussion of such species-restricted
generalizations, which shows that they implicitly mention particular places,
times and objects, and that they do not support counterfactuals, owing in
part to the fact that they contain implicit *ceteris paribus* clauses.

According to Lange, laws about particular species take the form, 'The S is
a T', for example, 'The robin's egg is greenish-blue' or 'The crow is a black
bird'. He writes,

> My view is that in biological practice, 'The S is T' (Ss are
> characteristically/typically Ts) specifies a kind of default assumption
> about Ss: if you believe (with justification) that something is an S then
> you are entitled to believe it T in the absence of information suggesting
> that it is not. In other words, 'The S is T' means that when we have
> certain purposes (which are left unstated, but are understood by those
> who understand 'The S is T'), we ought to take as our default assumption
> that any given S is T, though we should not necessarily believe a given S
> to be T if we have sufficient evidence to the contrary or if our purposes
> are outside of those for which this default is useful. Whether 'The S is T'
> is sufficiently reliable to be true depends on how reliable it is—for
> example, on how readily available 'information to the contrary' is when
> an S is not a T—and on how tolerant of error we can afford to be when
> we have the relevant purposes. So, for example, we are more willing to
> say 'The lion is tawny', while knowing that white lions occur
> occasionally, than to say 'The Witch's Hat mushroom is nonpoisonous',

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[9] Lange ([1995]), p. 430. Note that the individuality of 'robin' is a reflection of Lange's
acceptance of the Gheselin/Hull thesis that species names name extended spatio-temporal
particulars.

while knowing that poisonous Witch's Hats occur occasionally, because
our tolerance for eating poisonous mushrooms is lower than our
tolerance for making inaccurate predictions of a lion's color (Lange
[1995], p 440).

This passage is not without interpretational problems. Foremost among them
is that of how to understand the suggestion that a sufficiently reliable 'The S
is T'-statement is therefore a true statement. If reliability is jointly a matter of
the availability of information, and a matter of our ability to survive
inaccuracy, then truth is assimilated to warrant, and not just warrant for any
rational creature, but warrant for creatures of our informational limitations
and our human needs and interests. This frankly instrumentalist interpreta-
tion of biological claims requires a broader instrumentalism about scientific
explanation itself.

Lange's conclusion is that 'whether a claim is *regarded by scientists* as
stating a natural law should be judged by whether that claim functions in
scientific practice as a law statement' (Lange [1995], p. 442, emphasis added).
This is an unexceptional claim, as is the report Lange makes of biological
practice. But the issue here is not whether biologists offer explanations and
invoke statements of the form 'The S is a T' when their purposes are
explanatory, but do not invoke such statements when their purposes involve
predictions that require a high degree of reliability (owing to their falsity or as
Lange puts it, because of our [in]tolerance of error). The question is how such
statements as 'The S is T' explain, in virtue of what do they have explanatory
power or nomological force, given Lange's admissions about the character of
these statements and the impact of natural selection on generalizations over
time.[10] Recall the equivalent problem in the philosophy of history. If we are
to accept Lange's conclusions, we could solve all the problems about the
explanatory character of historical narratives by the same stratagem:
whatever historians do is explanatory, therefore whatever general statements
we can extract from their explanations must be laws.

There is an interpretation of Lange's conclusion which makes it an
illuminating claim about how and why biology differs from physical science.
Lange tells us that 'what counts as a natural law [. . .] varies with the
scientific discipline' (Lange [1995], p. 444). What this turns out to mean, in
Lange's view, is that what we humans, with our current cognitive and
computational capacities, and our current interests, treat as general laws will

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[10] These problems vex a similar view advanced in Woodward ([2000]). Woodward argues that
generalizations are employed to explain in the special sciences if they are robust, stable, or
invariant under a relevant class of changes, usually ones beyond the power of human
interveners. Thus a generalization can be invariant even if it has exceptions or holds only over a
limited spatio-temporal interval, provided that falsifying it is beyond our powers or interests.
The question for Woodward, as for Lange, remains one of why invariance under human
intervention makes a generalization explanatory.

depend on what will be reliable in our inductive strategies for meeting these interests with this conceptual/computational equipment. Elsewhere (Rosenberg [1994]), I have argued that biology is best construed as an instrumental science, whose explanatory strategy and comparative predictive weakness reflect limits on what we can rely on in making real-time predictions and explanations intelligible to us. I held further that this is a difference between biology and physical science largely consequent to the operation of natural selection in conferring biological systems here on earth with a complexity beyond our powers fully to assimilate. But of course my conclusion was that in most biological theorizing, we make do without scientific laws, whereas Lange's conclusion is that scientific laws are whatever it is we make do with in biological theorizing.

Just because we use statements of the form 'The S is T' in biology in default of general laws is by itself no reason to dub these 'The S is T'-statements laws, and it cannot solve the problem of illuminating how biological explanation proceeds. A similar conclusion faces Elliot Sober's argument that a quite different set of general statements in biology are its laws of nature. Sober writes:

> Are there general laws in biology? Although some philosophers have said no, I want to point out that there are many interesting if/then generalizations afoot in evolutionary theory.
>   Biologists don't usually call them laws; models is the preferred term. When biologists specify a model of a given kind of process, they describe the rules by which a system of a given kind changes. Models have the characteristic if/then format we associate with scientific laws [. . .] they do not say when or where or how often those conditions are satisfied (Sober [1993], p. 15).

Sober provides an example:

> R. A. Fisher described a set of assumptions that entail that the sex ratio in a population should evolve to 1:1 and stay there [. . .]. Fisher's elegant model is mathematically correct. If there is life in distant galaxies that satisfies his starting assumptions, then a 1:1 sex ratio must evolve. Like Newton's universal law of gravitation, Fisher's model is not limited in its application to any particular place or time (Sober [1993], p. 16).

True enough, but unlike Newton's inverse square law, Fisher's model is a mathematical truth, as Sober himself recognizes:

> Are these statements [the general if/then statements] that models of evolutionary processes provide empirical? In physics, general laws such as Newton's law of gravitation, and the Special Theory of Relativity are empirical. In contrast, many of the general laws in evolutionary biology (the if/then statements provided by mathematical models) seem to be nonempirical. That is, *once an evolutionary model is stated carefully, it often turns out to be a (non-empirical) mathematical truth.* I argued this point with respect to Fisher's sex ratio argument in sec. 1.5 (Sober [1993], p. 71).

If the generalizations of biology are limited to mathematical truths, then there are indeed few laws in this science. Sober recognizes this fact:

> If we use the word tautology loosely (so that it encompasses mathematical truths), then many of the generalizations in evolutionary theory are tautologies. What is more we have found a difference between biology and physics. Physical laws are often empirical, but general models in evolutionary theory typically are not (Sober [1993], p. 72).

In fact it is not clear how the models which Sober denominates the laws of biology could do what he says they are designed to do: 'they describe the rules by which a system of a given kind changes.' A necessary truth is like a rule of chess: at most it can describe the constitutive rules to which a system of a given kind must adhere if it is to remain a system of the given kind. As such, models cannot actually explain exactly how a system changes while remaining of the same kind, or for that matter why it changes kinds. This is for the same reason that the rules of chess cannot limit a person's actual moves to just those permitted by the rules. The real work in explaining the moves players actually make at a chess board is done by empirical hypotheses about their intentions to employ the rules, their desires to win the game, their beliefs about what the rules are, and generalizations linking these causes to their effects in action—moves in the game or beyond it. The rules are relevant only to the degree they are represented in the causes. *Mutatis mutandis*, necessarily true mathematical models will have a role in explanation only to the degree that they are reflected in generalizations that describe actual causal processes, unless of course biological explanations are not empirical.[11]

Why in fact does Sober label as 'laws' the mathematically true models which characterize many theoretical biology laws? The reason cannot be the same as that which leads us to say that models in physical science—like the ideal gas law, or the Bohr atom—are approximations to, or simplifications of, laws, and derive their explanatory power from these nomological generalizations. Models in biology cannot effect explanation in the same way models in physical science do, because as philosophers of biology have recognized, these models are fundamentally different from those of physical science. This difference is reflected in the almost universal allegiance among philosophers

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[11] It is perhaps worth making clear at this point that if, as Armstrong ([1983]) and others hold, laws of nature effected necessary connections between universals, then there might after all be ampliative necessary truths known *a posteriori* which could explain objective dependencies. And if biological truths are to be found among them, then objective dependencies might be explainable by necessary truths. But this sort of necessary truth is not at issue in the present context, for such truths will be synthetic, and here we are considering only analytic truths. No one thinks that the Armstrong theory of laws can ground the claim that there are laws in biology or illuminate biological explanation.

of biology to the semantic approach to theories, which treats theories as nothing more than sets of models of the very sort Sober ([1993], p. 15) has described. Most exponents of this approach to the nature of biological theorizing admit openly that on this conception, the biologist is not out to uncover laws of nature. Thus, Beatty writes, 'On the semantic view, a theory is not comprised of laws of nature. Rather a theory is just the specification of a kind of system—more a definition than an empirical claim' (Beatty [1981], p. 410). Models do not state empirical regularities, do not describe the behavior of phenomena; rather they define a system. Here Beatty follows Richard Lewontin ([1980]): in biology, 'theory should not be an attempt to say how the world is. Rather, it is an attempt to construct the logical relations that arise from various assumptions about the world. It is an 'as if' set of conditional statements.'

In the physical sciences models are way-stations towards general laws about the way the world works. The sequence of equations of state for a gas moves from the ideal gas model towards successively greater predictive accuracy and explanatory unification. Any such equivalent expectation in biology is ruled out by the absence of nomological generalizations of the familiar sort we know and love in physics and chemistry. Consider the set of models that characterize population biology—models which begin with a simple two-locus model that reflects Mendel's 'laws' of independent assortment and segregation. After the first disconfirming complication was discovered—gene linkage—geneticists added a *ceteris paribus* clause to Mendel's laws. Then genetic crossing-over was discovered. After a certain point, geneticists ceased adding qualifications to Mendel's laws, and began to treat them as the historically earliest and simplest in a sequence of models that have been continually complicated as research has uncovered the multitude of different ways in which natural selection has explored adaptational space. Because there are so many survival/reproduction strategies available to nucleic acids, Mendel's two original laws have been so riddled with exceptions that it isn't worth revising them to accommodate exceptions. Biologists ceased adding qualifications to them, and instead began to construct other models, which introduce more and more loci, probabilities, recombination rates, mutation rates, population size, etc. But they have done so without elaborating a single population-genetic theory that could underlie and systematize them the way that physical theory underwrites its models.

For what could the theory which underlies and systematizes these Mendelian models be like? Since the models' predicates are all functional, the theory systematizing them will be expressed in functional terms as well. But we know already that any theory so expressed will itself not provide the kind of exceptionless generalizations that a systematization of the models

requires, that is, a set of laws that will explain when they obtain and when they do not obtain.[12]

In the absence of nomological generalizations of the sort to be found in physical science, there are two alternative ways to treat biological models: either we treat them as unimproveable, exception-riven, historically contingent reports about some characteristics of a spatio-temporally limited range of biological systems, or we treat them as a set of implicit definitions, or necessary truths, more or less applicable to biological processes which, however, never exemplify them perfectly. The temptation to treat necessarily true mathematical models in biology as laws is now pretty clear. Faced with the choice of treating apparently disconfirmed hypotheses as false or as *ceteris paribus* statements, biologists and philosophers will choose the latter. Faced with treating *ceteris paribus* statements as vacuous tautologies masquerading as laws or as definitions and necessarily true models, biologists and philosophers will choose the latter when they can. But the question of how such non-nomological generalizations and models explain remains unanswered. Or at any rate the most obvious answers to the question are ruled out. Biological explanation cannot be a matter of identifying and unifying 'objective dependencies' because necessary truths can not reveal such dependencies.

4 Biology as history

Students of the philosophy of history should by now be having a strong *déjà vu* experience. Recall the suggestion that historical narratives explain by redescription, or by linking the explanans to the explanandum through the operation of implicit necessary truths—albeit analytic truths—about rational action. For example, Caesar's crossing of the Rubicon is explained by redescription as Caesar's provocation of the Roman Senate, and this redescription works because it trades on intentional states of Caesar and of the members of the Senate, which are linked to actions by allegedly analytic truths about the connections among beliefs, desires and actions. Here too a model, which we know not to be grounded in (reducible to) more fundamental generalizations (because we cannot reduce the intentional, the mental, to the extensional, the physical), explains, and does so non-causally.

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[12] Could a theory expressed in non-functional vocabulary systematize these models, explain when they work and when they don't? Among contemporary philosophers of biology and biologists, the answer to this question is no, no such theory is possible. And the reason is two fold: a) biological kinds are not reducible owing to their multiple realizability, their supervenience on the physical, and b) the autonomous explanatory adequacy of biological explanations with regard to their own domain. See for example Kitcher ([1984]), and Sober ([1993]), Chapter two. The first of these reasons is cogent; the second raises the question here at issue: how does biology explain?

Historical explanation is alleged to be autonomous and distinctively different from scientific explanation. To what extent is this approach to historical explanation repeated in biological explanation? Perhaps 'repetition' isn't the right word. Perhaps biological explanation is a species of historical explanation, so that there are not two distinct problems, that of the nature of historical explanation and that of the nature of biological explanation, but just one problem.

The attempt to assimilate evolutionary theory and explanation to history and historical explanation has a pedigree in the philosophy of biology that goes back at least to T. A. Goudge's *Ascent of Life*. There Goudge argued that the explanations evolutionary biology provides are typically 'narratives', which consist

> not in deducing the event [to be explained] from a law or set of laws, but in proposing an intelligible sequence of occurrences such that the event to be explained 'falls into place' as the terminal phase of it. The event ceases to be isolated and is connected in an orderly way with states of affairs which led up to it. [. . .] The explanatory force of the resulting pattern of statements resides not in any general laws which it involves, but rather in the extent to which it establishes an intelligible, broadly continuous series of occurrences which leads up to the event in question (Goudge [1961], pp. 72–7).

Recall the interpretive stratagem of philosophers who follow Popper and argue that evolutionary theory provides an untestable schematic unifying principle. As such the 'principle of natural selection' as Brandon calls it will have the same status with respect to evolutionary narratives as the principle of rational action has to narratives of human history. That is, it will be the responsibility of biologists and historians to explain by showing that the event to be explained was the result of a sequence of occurrences intelligible by the lights of their respective necessary truths. The fact that such explanations lack empirical content, have no predictive power, cannot be tested, etc. was never very disquieting among philosophers of history who defended them. If biological explanation is narrative as well, and narrative explanations require no laws, then the problem of biological explanation is solved, or at least assimilated to the problem of historical explanation.

This may be part of Sober's strategy in labeling necessary truths as laws. For following Goudge, Sober too insists that Darwin's theory is not a body of general laws but a claim about events on and in the vicinity of the Earth:

> The two main propositions in Darwin's theory of evolution are both *historical hypotheses* [. . .]. The ideas that all life is related and that natural selection is the principle cause of life's diversity are claims about a particular object (terrestrial life) and about how it came to exhibit its present characteristics (Sober [1993], p. 7).

Moreover, Sober is (rightly) committed to the insight, originally advanced by Dobzhansky ([1973]), that 'nothing in biology makes sense except in the light of evolution.' These two commitments generate a thoroughly historical conception of all of biology:

> Evolutionary theory is related to the rest of biology in the way the study of history is related to much of the social sciences. Economists and sociologists are interested in describing how a given society currently works. For example, they might study the post World War II United States. Social scientists will show how causes and effects are related within the society. But certain facts about that society—for instance its configuration right after World War II—will be taken as given. The historian focuses on these elements and traces them further into the past:
>
> Different social sciences often describe their objects on different scales. Individual psychology connects causes and effects that exist within an organism's own life span. Sociology and economics encompass longer reaches of time. And history often works in an even larger time frame. This intellectual division of labor is not entirely dissimilar to that found among physiology, ecology, and evolutionary theory (Sober [*op. cit.*], p. 7).

Sober's view is echoed by Kitcher ([1993], p. 21) as well: 'The main claim of the *Origin of Species* is that we can understand numerous biological phenomena in terms of Darwinian histories of the organism involved.'

So, evolutionary theory is to the rest of biology as history is to the social sciences. History is required for complete understanding in biology because biological theories can only provide an account of processes within time periods of varying lengths, and not across several or all time periods. Let us leave aside the claim, controversial among functionalist social scientists, economists, game theorists and other rational choice inspired political scientists, that Sober has the relation between history and the social sciences exactly backwards (history being, for these social scientists, the arena in which their pure, timelessly true, general theory is applied and tested).

The trouble with the historical assimilation of evolutionary theory is that it still leaves unanswered the question of what biological explanation consists in. Learning that evolutionary theory is a historical science, and that all compartments of biology are contingent on history, doesn't get us very far in understanding biological explanation. All it does is redouble the need for an account of how narratives explain, whether in human history or natural history. Kitcher illustrates the problem in his own exposition of how evolutionary explanations proceed:

> One of [the projects of evolutionary biology] consists in explaining the prevalent traits among groups of organisms (or more generally accounting for distributions of traits). In completing this explanatory enterprise we do not appeal to any 'principle of natural selection.' Instead

we instantiate some selectionist pattern (NEO-DARWINIAN SELECTION . . .). And a critical part of the explanation is an analysis of the ecological conditions that *ground differences* in expected reproductive success [. . .]. [B]iologists who aim to explain the prevalence of particular traits do not just count descendants and conclude that the bearers of the prevalent traits left more off-spring than their rivals. They supply analysis of the relationships between variant traits and the environment that show, at least in some qualitative way, *why this was to be expected* (Kitcher [1993], p. 48, n. 68, emphasis added).

Recall Hempel's general condition of adequacy of scientific explanation, a condition Kitcher rightly honors here: 'any rationally acceptable answer to the question ''Why did event X occur?'' must offer information which shows that X was to be expected—if not definitely [. . .] at least with reasonable probability' (Hempel [1965], p. 368). Given Kitcher's explicit repudiation of laws in evolutionary biology (see footnote 11 above), it becomes mysterious how on his model of biological explanation ecological conditions can ground differences, or how we could rationally be led to expect one outcome rather than another.

Kitcher's model of explanation in evolutionary biology involves a schematic pattern for the deduction or derivation from ecological conditions to reproductive outcomes via premises of the schematic form:

(2) Analysis of the ecological conditions and the physiological effects on the bearers of P, P_1, . . ., P_n [traits whose distribution in any generation is to be explained; Kitcher, *op. cit.*, p. 28].

Analysis involving reasoning from causes to effects requires either a set of substantive inference rules or a major premise embodying a generalization, either of which must be capable of satisfying some version of Hempel's dictum as Kitcher honors it. But as has been well known at least since Nagel's treatment of the notion of ampliative inference rules (Nagel [1961], pp. 66–7), the difference between such rules and substantive general laws is largely notational. If evolutionary explanations really do not appeal implicitly or otherwise to an ampliative 'principle of natural selection', the explanatory force of Kitcher's selectionist explanatory pattern remains ungrounded. There is only a narrative, and what Kitcher calls 'objective dependencies' continue to elude us.

5 Hempelian historical explanation in biology

By now we have canvassed enough blind alleys in the philosophy of biology to reconsider and give an answer to the question of what biological explanation consists in, which has not been very popular over the last

generation or so in the philosophy of biology. Recall that Hempel's strategy for dealing with the nature of historical explanation invokes the notion of explanation sketch and implicit law. Can we apply this strategy more successfully to the nature of biological explanations? Let us try.

We could begin by adopting the view that the principles of the theory of natural selection are nomological generalizations of the sort we are familiar with in physical science. A good deal of the mechanism of natural selection which Darwin expounded in *On The Origin of Species* may be expressed in the following generalizations:

(1) Biological systems not on the verge of extinction or fixity reproduce with heritable variations.
(2) If heritable variation obtains among biological systems, then there will be fitness differences among the biological systems.
(3) In the long run, the more fit variants will leave a higher proportion of descendants than the less fit variants.

Among the conclusions Darwin derives from these principles of his theory is the following:

(4) Until fixity or extinction is attained, there will be descent with modification, i.e. evolution.[13]

This presentation of the theory of natural selection is not the only one nor perhaps the most perspicuous or economical one. Some contemporary versions will substitute 'replicators' and 'interactors or vehicles' for 'biological systems' in order, for example, more explicitly to accommodate selection at different levels of biological organization. Nevertheless, let us consider whether these principles and the generalization derivable from them can be accepted as laws—strict or non-strict.

Do they run afoul of the arguments of section 2 of this paper, owing to the functional individuation of their kind-terms, the blindness of natural selection to structure, and the strategic character of selection? They do not seem to do so. In particular, none of them is subject to qualifications or *ceteris paribus* clauses in virtue of the operation of selective forces on the earth. After all, these principles constitute the mechanism of natural selection itself; there is no scope for natural selection to qualify, limit or shape its own operation.

But, are there positive grounds for the truth and the nomological force of these principles? We already have a good deal of terrestrial biological evidence in their favor, and no serious terrestrial evidence against them. But

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[13] Versions of these generalizations are to be found in the *Origin of Species*, Chapters 1–3. I have argued at length for the nomological character of an alternative equivalent formulation of the theory due to Mary B. Williams in Rosenberg ([1985]), Chapter six.

this evidence is insufficient to ground a claim of universality and nomological necessity. Indeed, an imaginative philosopher of biology can envision circumstances that would falsify them, and so require their emendation with *ceteris paribus* clauses. For example, there could be heritable variations among biological systems and yet all the variants be equal in fitness, thus falsifying (2) above. Thus, we require not only positive evidence for the universality and nomological necessity of these principles, but also evidence that will allow us to treat such apparently possible scenarios in the same way we treat apparent counter-examples to physical law.

Evidence that these principles begin to be instantiated in chemical processes well before the appearance of anything properly called biological could provide grounds for their universality and nomological necessity. After all, we have good reason to believe that the laws of chemical synthesis obtain universally and have nomological status. It is not difficult to provide this evidence of the instantiation of principles 1–3 in molecular systems, and evidence of the consequent evolution of these molecular systems.

Consider (1) above, which requires that items—whether biological or molecular—reproduce with heritable variation. Chemical theory suggests that even at very low levels of molecular organization, molecules can begin to make copies of themselves by catalysis and template-matching. Evidence in synthetic chemistry establishes that several types of molecules self-replicate by autocatalysis and by template synthesis. (See Winter [1996] for an example.) Replication is greater in those cases where the molecules are stable for more than one cycle of template-copying or catalysis. When each of their successor molecules is itself stable, rates of replication will increase so long as substrate-molecules continue to be available. In fact, in the replicating molecules that chemists have synthesized, autocatalysis and template-copying are produced by the same molecules. How replicating molecules give rise to more complex self-replicating systems is a matter for discussion below.

Thermodynamics and conservation consideration in physics suggest that finite regions of space contain only limited quantities of energy. Even the core of a star produces only finite amounts of energy. Any system which persists and reproduces faces limits to its size and/or number of its copies that reflect this energetic constraint. Thus, there will be competition among replicating molecules as they interact chemically with finite quantities of substrates for which they serve as templates and on which they can act catalytically. Those molecules with lower reaction-barriers to templating, and higher catalytic coefficients will make more copies than others. These differences in template-synthesis and catalysis rates are of course the fitness differences that principles (2) and (3) require.

But where do the molecular variations come from that make for competitive advantages, once autocatalytic template synthesis begins,

cookie-cutter-like, to produce perfect copies of the original molecules? All three principles requires hereditary variation in lineages of replicating molecules. Again, chemical theory leads to the expectation that differences in the molecular milieu, temperature and pressure, the availability of substrates, amounts of ultraviolet light, and of course indeterministic radiation events, will all affect the outcomes and rates of chemical synthesis. In effect, they produce variation by mutation. These in-principle expectations about how variations in replicating molecules come about have also been substantiated by recent work in synthetic chemistry (Hong, Feng, Rotello, Rebek [1992]). And the long run to which principle (3) adverts is the same long run to which the phenomenological second law of thermodynamics appeals, and which is ultimately cashed in probabilistically by the statistical version of the second law. This 'long-run' qualification is implicit in principle (2) as well. In the case of principle (2), the long-run probabilities are also the results of quantum indeterminism in radiation and other processes. These probabilities along with long-run thermodynamic considerations allow for the imaginative philosopher's counter-example to principle (2) as a temporary exception. But they assure that the impact of probabilistic processes will be sufficient to provide variations among molecules and aggregations of them large enough to make for fitness differences over the long run. Thus, the *ceteris paribus* clause which (2) might require is the one familiar to us from physical theory, and is not generated by arms races of natural selection.

Selection of those molecular variants more efficient at replication will result in the emergence of rudimentary 'phenotypes'. A replicating molecule will have effects on other (non-reproducing) molecules in its surroundings: it may foster their synthesis and/or bind to such molecules, or it may inhibit their synthesis and/or repel them. These effects on other molecules feed back to accelerate or retard the rate of replication of the self-reproducing molecule. Thus a replicating molecule's effects on other non-self-replicating molecules will be selected for or against. The resultant further variation among molecules increases the scope for natural selection when it results in growth in complexity and size of competing chemical systems (replicating molecules plus bound non-replicating 'phenotypic' molecules).

At some point or other these molecular lineages begin to have the characteristics of asexual reproduction with mutational variation. How the environmental constraints and the random variations in lineages of macromolecules eventuate in sexually-reproducing, genetically-recombining organisms is a matter on which biologists have been speculating for a generation. (See, for instance, Margulis and Sagan [1986], and Hamilton, Axelrod and Tanese [1990].)

Recall, the task here is to show evidence that principles (1)–(3) are universal and nomologically necessary. It would be too much to demand of

the physical grounding of the basic principles of *On the Origin of Species* that it shed light on exactly how molecules evolve into organisms, still less sexually reproducing ones. After all, natural selection does not guarantee that reproduction must become sexual. All we need to show is that the principles of the theory of natural selection can obtain simply as a result of the interaction of molecules at relatively low levels of complexity. Physicalism assures us that natural selection among molecules will result in functional biological systems. That all biological systems we are acquainted with behave in accordance with these three principles we already have a good deal of evidence for.

Thus, evolutionary theory describes a mechanism—blind variation and natural selection—that can operate everywhere and always throughout the universe. Evolution obtains whenever tokens of matter have become complex enough to foster their own replication and variation so that selection for effects can take hold.

Adopting the view that the theory of natural selection comports real laws, it would be reasonable to hold that explanations in biology are always explanation sketches involving these principles as implicit laws. This makes biological explanation no more mysterious in principle than physical explanation (which is also often explanation-sketch). Beyond the theory of natural selection, the rest of biology is a set of subdisciplines historically conditioned by the operation of natural selection on local conditions (the Earth). To begin with, biology is a historical science, since all functional individuation reflects the vagaries and vicissitudes of natural selection; almost all biological kinds are the result of selection over variation in order to solve design problems. Second, solutions to the same problem are multiple and one biological system's solution sets another biological system's next design problem. Thus, each system's environment varies over time in a way that makes all putative biological generalizations historically limited (with the important exception of the laws of the theory of natural selection itself). Any subdiscipline of biology—from paleontology to developmental biology to population biology to physiology or molecular biology—can uncover at best historical patterns, owing to the fact that a) its kind vocabulary picks out items generated by a historical process, and b) its generalizations will always be overtaken by evolutionary events. Each of the historically limited 'generalizations' of the 'The S is a T' form in these disciplines is itself to be explained by appeal to the operation of the principles of natural selection on local conditions—some of these 'The S is a T' statements will describe long-established and widespread historical facts, such as the ubiquity of nucleic acid as the hereditary material; others will be local and transitory, such as the description of the primary sequence of the latest AZT-resistant mutation of the AIDS virus.

In most cases, the explanations of why these 'generalizations' obtain will be at most explanation sketches of course: sketches, which cannot be completed because the completing details will be too numerous and long ago effaced in the course of evolution. In order to complete an 'ultimate' or adaptational explanation of any particular 'The S is T' statement, it would be necessary to show why Ss having a T, rather than an R or a W etc., came to be the actual solution to the design problem set by S's environment. This would require an identification of the in-principle alternative solutions to the problem T solves, an account of which of them were available to S, details which show why T solved the problem better than the other available solutions, and an account of the subsequent environment of S which shows why T is maintained even after local environmental conditions (and their adaptational problems) have changed. Since such auxiliary information is neither available nor otherwise worth securing, adaptational explanations would perforce be explanation-sketches with assumptions not open to direct and obvious test. But at least their explanans and explananda would be linked (in 'objective dependencies') to their explanans by nomological generalizations in the way required for scientific explanations, were we to accept the components of the theory of natural selection as laws. Though biology cannot fill in the details, it can be confident that the nomological generalizations involved are known and have been since 1859.

'Proximate' explanations of events, states, or processes in molecular or cell biology will almost always be explanation-sketches as well, for several reasons. For example, consider the explanation of how genes are copied that appeals to semiconservative chemical synthesis in the 5′ to 3′ direction of a double-stranded DNA molecule, initiated by the action of an RNA primer, a set of proteins that untwist the molecule, and completed by DNA polymerases which stitch the nucleotides together. To begin with, it is natural selection which makes the process described by organic chemistry causally/explanatorily relevant to gene-copying. It is in virtue of natural selection that this macromolecular process eventuates in gene-copying. Second, the available description of the chemical process of how genes are copied turns out to have known and unknown exceptions. For example, the genes in RNA viruses are not double-stranded DNA molecules to begin with. Of course, we can accommodate this exception quite easily (and RNA genes actually require the DNA replication process as a component of their copying). More important, the unknown exceptions that already exist or that will exist in the future are due to the operation of natural selection continually searching adaptational space. Third, many of the items which a macromolecular explanation adverts to—e.g. gene, primer, polymerase—are functional kinds, produced by natural selection, though its role is unmentioned in the explanation-sketch. Because they are naturally selected

kinds, they will be structurally heterogeneous, and pending the discovery of all the structurally diverse ways macromolecules can realize these kinds, the biochemical explanation of gene-duplication will be a sketch. Finally, even in molecular biology, proximate explanation turns out to be implicitly evolutionary. Here is a particularly nice example of how proximate explanation in molecular biology invokes connections effected by the theory of natural selection to answer an (italicized) question about a process:

> A striking feature of [the process of replication] is the intricate interplay of many proteins. Genetic analysis suggests that at least fifteen proteins directly participate in DNA replication. Why is DNA replication so complex? *In particular why does DNA synthesis start with an RNA primer that is subsequently erased?* An RNA primer would be unnecessary if DNA polymerases could start de novo. However, such a property would be incompatible with the very high fidelity of DNA polymerases [. . .]. DNA polymerases test the correctness of the preceding base pair before forming a new [. . .] bond. This editing function markedly decreases the error frequency. In contrast, RNA polymerase can start chains de novo because they do not examine the preceding base pair. Consequently, their error rates are orders of magnitude higher than those of DNA polymerase. The ingenious solution [. . .] is to start DNA synthesis with a low fidelity stretch of polynucleotide but mark it 'temporary' by placing [. . .] [short RNA primer] sequences in it. These short RNA primer sequences are then excised by DNA polymerase I and replaced with a high fidelity DNA sequence [. . .]. [M]uch of the complexity of DNA replication is imposed by the need for very high accuracy (Stryer [1983], p. 587, emphasis added).

The principles of natural selection haunt this entire discussion, if only because it is natural selection that imposes the demand for very high fidelity in information storage by genes, and relaxes the demand in information-transmission and protein synthesis by RNA. In this and in other proximate explanations in biology, the connection between the explanandum and the explanans is effected by the principles of natural selection so clearly that, like principles of rational action in history, they need not even be mentioned to eke out the explanation.

Within the philosophy of biology, the claim that there are laws of natural selection has much to recommend it. A good deal of the tortuous character of contemporary philosophy of biology is both illuminated and avoided by the claim that Darwinian theory constitutes the one and only set of laws in biology. The tortuousness in question is illustrated in the package of moves forced upon philosophers of biology by the alleged nomological vacuum of biology. Unable to find a non-circular interpretation of the principle of the survival of the fittest, some philosophers have resigned themselves to treating evolutionary theory as a methodological prescription or a research program, or a law-free narrative of events on the Earth, or a set of explanatory schema

extracted from biologists' practice instead of biological processes. Others, unpersuaded by the claim (Rosenberg [1983]) that (like mass in Newtonian mechanics) 'fitness' is a primitive term undefined in the theory, have adopted a propensity-definition of fitness that fates the theory of natural selection to falsity. (See footnote 8 above.) Attempting to reconcile the practice of biologists to an explanatory strategy that looks something like that of the rest of science's appeal to laws, other philosophers have embraced necessary truths or claims about historical patterns among spatio-temporally distributed particular objects as biology's version of 'laws'. These moves just make biological explanation even harder to understand. But if the only laws in biology are those Darwin discovered, then recognition of this fact shows both what is the matter with these tortuous expedients and why they are unnecessary.

Biology is indeed a historical discipline. But the main principles of Darwin's theory are not historical narratives—not even world-historical ones. They are the only (*ceteris paribus*) laws of biology. And it is the application of these laws to initial conditions that generates the functional kinds which make *the rest* of biology implicitly historical: in our little corner of the universe, the universally ubiquitous process of selection for effects presumably began with the precursors of hydro-carbons, nucleic and amino acids. That local fact and its adaptational consequences explain the character of the sub-disciplines of terrestrial biology. Their explanations are 'historically' limited by the initial distribution of matter on the earth, and the levels of organization into which it has assembled itself. So, their local generalizations are increasingly riddled with exceptions as evolution proceeds through time.

The apparent generalizations of functional biology are really spatio-temporally restricted statements about trends and the co-occurrence of finite sets of events, states and processes. Beyond those laws which Darwin uncovered, there are no other generalizations about biological systems to be uncovered, at least none to be had that connect kinds under biological—that is, functional—descriptions. The implications of this conclusion for the historical character of all of the 'special sciences' is left to another paper. But at least now we understand how biological explanation is possible.

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References

Armstrong, D. [1983]: *What is a Law of Nature?*, Cambridge: Cambridge University Press.

Beatty, J. [1980]: 'What's wrong with the received view of evolutionary theory?' in P. Asquith and R. Giere (*eds*), *PSA 1980*, **2**, East Lansing: Philosophy of Science Association.

Beatty, J. [1992]: 'Fitness: theoretical contexts', in E. Fox-Keller and E. Lloyd (*eds*), 1992, *Keywords in Evolutionary Biology*, Harvard: Harvard University Press, pp. 115–9.

Beatty, J. [1995]: 'The evolutionary contingency thesis' in G. Wolters and J. Lennox (*eds*), 1995, *Concepts, Theories and Rationality in the Biology*, Pittsburgh: University of Pittsburgh Press, pp. 45–81.

Beatty, J. and Finsen, S. [1989]: 'Rethinking the Propensity Interpretation: A peak inside the pandora's box', in M. Ruse (*ed*.), 1989, *What the Philosophy of Biology is*, Dordrecht: Kluwer, pp. 17–30.

Brandon, R. [1990]: *Adaptation and Environment*, Princeton: Princeton University Press.

Cartwright, N. [1998]: 'Do the laws of physics state the facts?', in J. Cover and M. Curd (*eds*), 1998, *Philosophy of Science: the Central Issues*, New York: Norton, pp. 865–77.

Dobzhansky, T. [1973]: 'Nothing in biology makes sense except in the light of evolution', *American Biology Teacher*, **35**, 125–9.

Fodor, J. [1981]: 'Special Sciences', in *Representations*, Cambridge, MA: MIT Press.

Gillespie, J. H. [1977]: 'Natural selection for variance in off-spring numbers: A new evolutionary principle', *American Naturalist*, **11**, pp. 1010–4.

Goudge, T. [1961]: *The Ascent of Life*, Toronto: University of Toronto Press.

Hamilton, W. D., Axelrod, R. and Tanese, R. [1990]: 'Sexual reproduction as an adaptation to resist parasites (a review)', *Proceedings of The National Academy of Science,* **87**, pp. 3566–73.

Hempel, C. G. [1942]: 'The function of general laws in history', *Journal of Philosophy*, **39**, reprinted 1965, *Aspects of Scientific Explanation*, New York: Free Press, pp. 231–244.

Hong, J. I., Feng, Q., Rotello V. and Rebek, J., 'Competition, Cooperation, and Mutation—Improving a Synthetic Replicator by Light Irradiation', *Science*, **255**, pp. 848–50.

Kitcher, P. [1984]: '1953 and all that', *Philosophical Review,* **93**, pp. 353–73.

Kitcher, P. [1989]: 'Explanatory Unification and the Causal Structure of the World', in W. Salmon and Philip Kitcher (*eds*), 1989, *Scientific Explanation: Minnesota Studies in the Philosophy of Science, XV*, Minneapolis: University of Minnesota Press, pp. 410–605.

Kitcher, P., [1993]: *The Advancement of Science*, New York: Oxford University Press.

Kitcher, P. and Sterelny, K. [1988] 'The return of the gene', *Journal of Philosophy*, **85**, pp. 339–61.

Lange, M. [1995]: 'Are there natural laws concerning particular species?', *Journal of Philosophy*, **112**, pp. 430–51.

Lewontin, R. [1980]: 'Theoretical population genetics in the evolutionary synthesis' in E. Mayr, E. and W. Provine (*eds*), 1980, *The Evolutionary Synthesis*, Cambridge: Harvard University Press.

Lloyd, E. [1993]: *The Structure and Confirmation of Evolutionary Theory*, Princeton: Princeton University Press.

Margulis, L. and Sagan, D. [1986]: *Microcosmos: Four Billion Years of Microbial Evolution*, New York: Simon and Schuster.

Nagel, E. [1961]: *Structure of Science*, New York: Harcourt, Brace and World, reprinted Indianapolis: Hackett, 1991.

Rebek, J. [1996]: 'The Design of Self-Replicating Molecules', *Current Opinion In Structural Biology*, **4**, pp. 629–35.

Rebek, J., Park, T. K. and Feng, Q. [1992]: 'Synthetic Replicators and Extrabiotic Chemistry, *Journal Of The American Chemical Society*, **114**, pp. 4529–32.

Rosenberg, A. [1983]: 'Fitness', *Journal of Philosophy*, **80**, pp. 457–73.

Rosenberg, A. [1985]: *Structure of Biological Science*, Cambridge: Cambridge University Press.

Rosenberg, A. [1994]: *Instrumental Biology or the Disunity of Science*, Chicago: University of Chicago Press.

Shapiro, L. [2000]: 'Multiple Realizability', *Journal of Philosophy*, **97**, pp. 635–54.

Sober, E. [1984]: *The Nature of Selection*, Cambridge, MA: MIT Press, reprinted University of Chicago Press, 1994.

Sober, E. [1993]: *Philosophy of Biology*, Boulder, CO: Westview.

Stryer, L. [1983]: *Biochemistry*, San Francisco: Freeman.

Thompson, P. [1988]: *The Structure of Biological Theories*, Albany: SUN Press.

Waters, C. K. [1991]: 'Tempered realism about the forces of selection', *Philosophy of Science*, **58**, pp. 552–73.

Winter, A. E. [1996]: 'Autocatalysis and the Generation of Self-Replicating Systems', *Chemica Scandinavica*, **50**, pp. 469–85.

Woodward, J. [2000]: 'Explanation and invariance in the special sciences', *British Journal for the Philosophy of Science*, **51**, pp. 197–254.