

## The structure of evolution by natural selection

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**Abstract.** We attempt a conclusive resolution of the debate over whether the principle of natural selection (PNS), especially conceived as the ‘principle’ of the ‘survival of the fittest’, is a tautology. This debate has been largely ignored for the past 15 years but not, we think, because it has actually been settled. We begin by describing the tautology objection, and situating the problem in the philosophical and biology literature. We then demonstrate the inadequacy of six *prima facie* plausible reasons for believing that the tautology debate has been satisfactorily resolved (the PNS is strictly a methodological principle; scientific theories can contain tautologies; the scope of the PNS has been reduced; theories should be understood as models and not exceptionless laws; the widespread acceptance of the propensity interpretation of fitness; and the abandonment of operationalism and verificationism). We proceed to a detailed discussion of Brandon’s law (D) describing the PNS, and show that law (D) seriously misrepresents the structure of evolution by natural selection. In the final sections, we provide and defend a novel reinterpretation of the structure of the principle (or, we prefer, model) of evolution by natural selection.

### Introduction

During the 1970s and 1980s, debates raged over whether the principle of natural selection (PNS) – especially *qua* the ‘principle’ of the ‘survival of the fittest’ – is a tautology. Darwinian philosophers defended mainly either one of two positions: ‘the principle of natural selection is a tautology, but it doesn’t matter’ or ‘the principle of natural selection is not a tautology’. In the latter case the reason provided was either that the PNS is not equivalent to the principle of the survival of the fittest (which is a tautology), or that it is possible to provide an account of fitness that is not circular. Apparently, these responses satisfied the combatants, since the past 15 years have witnessed almost no new responses to the tautology problem.

We are not entirely unhappy with this state of affairs. Much important conceptual work was undertaken within these debates, and the dust has settled quite nicely. And yet, we believe, the debate over the structure, content, and scientific status of Darwinian evolutionary theory has not been satisfactorily resolved. In fact, we believe that none of the proposed solutions is adequate.

We begin with a general discussion of the tautology problem and the dilemmas to which it leads. Then, we survey six approaches to the resolution of

this problem that are evident in the literature of the past three decades and explain why each is inadequate. Finally, we propose a new approach. It will be important to show that our resolution is not vulnerable to the problems besetting the earlier proposals – especially given the swelling of the ranks of anti-evolutionists<sup>1</sup> eager to capitalize on any perceived weakness in evolutionary theory.<sup>2</sup> In order to avoid pernicious fallouts stemming at least partly from confusion about the status and structure of the theory of evolution by natural selection, we dare to stir gently the dust of these debates to fashion from them a more resilient resolution.

### Natural selection as a tautology – or else untestable

The usual story is this: Darwin's PNS was described, in the last two editions of *On the Origin of Species*, as the principle of the survival of the fittest:<sup>3</sup> 'Only the fittest survive' (to reproduce creatures like themselves). If the fittest are defined as those who survive to reproduce their kind, then Darwinism becomes an uninteresting tautology: Who survive? Those who are most fit. Who are most fit? Those who survive.

Karl Popper was only the most infamous of a long line of commentators – biologists, philosophers, and others – who thus declared Darwin's theory to be a tautology.<sup>4</sup> Popper originally held, though later partly recanted his claim, that Darwin's PNS was, in an almost incoherent turn of phrase, 'almost tautological'.<sup>5</sup> Popper elaborates: 'a considerable part of Darwinism is not of the nature of an empirical theory, but is a *logical truism*', for the reasons cited in the previous paragraph. Since truisms or tautologies cannot be falsified, then, for Popper, they cannot count as properly scientific. Thus, Darwinian evolutionary theory is something other than science.<sup>6</sup>

What should we make of this? The core of Darwin's theory is that evolution is generated by heritable random variation coupled with differential repro-

<sup>1</sup>Witness the publication and public reception of Johnson (1991) and Wells (2000).

<sup>2</sup>See Raff (2001) for some comments on 'the creationist abuse' of research in the field of evolutionary developmental biology.

<sup>3</sup>This unfortunate formulation stems from a suggestion of Herbert Spencer, passed along by Alfred Russell Wallace (Waters 1986).

<sup>4</sup>Popper's predecessors included C.H. Waddington, Ronald Fisher, J.B.S. Haldane, and G.G. Simpson. A number of more recent commentators have emphasised this putative logical failing of Darwinian theory, including Johnson (1991) and Stove (1996), while Gould (1977), Brandon [1978 (1996)], Kitcher (1982), Ruse (1982), Waters (1986) and others have attempted to rebut or escape the charge of tautologousness. Gallagher (1989) discusses several of these attempts; see below for a different approach.

<sup>5</sup>See Popper (1963, 1972) for the original statement, and Popper (1977) for the recantation. For a lively discussion of Popper's views on biology, see Hull (1999).

<sup>6</sup>Popper (1972, 1974) calls it a 'metaphysical research programme'; for a discussion of how to interpret this claim, see Hull (1999, pp. 486–490).

duction caused by superior adaptation to the environment. The sources of variation and heredity are better and better understood, and increasingly more examples of superior adaptation leading to differential reproduction (where alternative explanations of differential reproduction have been eliminated as likely causes) have been accumulated.

But the theory makes a general claim – that superior adaptation leads in general to superior survival and reproduction, at least where unlikely chance factors, such as a catastrophic bolt of lightning, do not interfere. This insight is captured in Robert Brandon's law, or principle, (D), called by him (and others) the *PNS*:

(D) If *a* is better adapted (more fit) than *b* in environment *E*, then (probably) *a* will have more (sufficiently similar) offspring than *b* in *E*.<sup>7</sup>

There has been a persistent worry, though, that this generality is either a disguised tautology and hence not the causal explanatory principle it purports to be, or else it is untestable. The latter possibility has the consequence that the core principle in Darwin's theory cannot be tested such that the apparent evidential support for the theory as a whole is an illusion. Brandon has a particularly trenchant way of bringing this dilemma home. You might assume that the relation of being 'better adapted than' can be defined independently of leaving more offspring, so that (D) is not a tautology. You might also assume that this relation can be expressed precisely enough that it is possible to determine empirically whether an organism can be better adapted than another organism for any environment. If, however, both of these assumptions hold, then it is always possible to create an artificial environment in which organisms that are better adapted in this precise sense leave *fewer* offspring than others. In short, if (D) is supposed to have general scope, applying to all environments, then (D) must be obviously false. If, therefore, you believe that (D), taken as a general principle, is not obviously false, you must reject one of the assumptions with which you began. Either (D) is a tautology after all, or else (D) is untestable because the relation of being 'better adapted than' is too imprecise to be empirically determined for all cases.

Various attempts have been made to circumvent the apparent tautologousness of the *PNS*, and related worries. Most commentators, such as Brandon<sup>8</sup> and Stephen Jay Gould<sup>9</sup>, have attempted to define fitness without reference to (actual) survival, so as to avoid the tautology objection; Kenneth Waters<sup>10</sup> has attempted to show that the 'principle of natural selection' and the 'principle of the survival of the fittest' are non-equivalent, and that Darwin was mistaken to accept Spencer's suggestion of the latter as a surrogate for the former. Later in

<sup>7</sup>See Brandon [1978 (1996), 1980 (1996), 1990].

<sup>8</sup>Brandon [1978 (1996), 1980 (1986)].

<sup>9</sup>Gould (1977).

<sup>10</sup>Waters (1986).

the paper we explore these and other approaches. In particular, we will show that Brandon's framing of the dilemma rests on a mistake about the logical structure of the PNS. But let us first review the main proposals for explaining how the once-raging debate over whether the PNS is tautologous or untestable can be resolved.

### Why the previous explanations are inadequate

Six explanations for why the status of the principle should not be regarded as problematic have been either explicit or implicit in the literature. We argue, however, that these explanations, while each having some merit, do not altogether put the matter to rest. On the contrary, there remains, as we hope to show, an unresolved residual puzzle that it is best handled by thinking differently about the structure of Darwin's core theory.

The six explanations, in order, are:

- (i) Understanding the PNS as a methodological principle is enough; we don't need a true statement about the cause of differential reproduction that applies in all the relevant cases.<sup>11</sup> But, in our view, this conclusion is counterintuitive, only to be accepted if no alternative is acceptable.
- (ii) The PNS is true, indeed a tautology, but tautologies in a theory are acceptable provided that the theory that embeds them has empirical content and is testable.<sup>12</sup> We agree with the latter point but deny that PNS, the claim that better adapted animals will tend to leave more offspring, can be a tautology in Darwin's theory. It would be a tautology only if superior adaptation is just a tendency to leave more offspring, but then we would have the counterintuitive result that in Darwin's theory better adaptation never explains why some animals tend to leave more offspring.
- (iii) We have good reason to reduce the scope of the Darwinian model<sup>13</sup> and can thus avoid appearance of both tautology and untestability. We accept the limitation in scope, but the problem of explaining how the principle is both non-tautologous and testable within its less than universal scope remains as severe as before.
- (iv) We have moved from conceiving a theory as a set of universal laws to a model-theoretic perspective.<sup>14</sup> We welcome this move, but the problem remains of explaining unity of individual models (or unity of instances of a general model) within the legitimate scope of the theory without incurring the same objections as before.

<sup>11</sup>See, e.g., Brandon [1978 (1996)] and Gallagher (1989).

<sup>12</sup>Sober (1984, pp. 61–85), see also Sober (1993, pp. 69–73).

<sup>13</sup>Gould and Lewontin (1979).

<sup>14</sup>See, e.g., Waters (1986) and Lloyd (1988).

- (v) Propensity to leave more offspring has emerged as the favoured interpretation of the unifying feature of cases of being ‘better adapted than’ or ‘more fit than’ (relative adaptedness).<sup>15</sup> Of course, such propensity is a necessary condition for better adaptation to (fitness in) an environment. It would hardly make sense to speak of an organism as being better adapted to its environment if it didn’t at least have a propensity to reproduce more of its kind. Such propensity, however, is not useful in delineating the unifying feature of cases of relative adaptedness, since other factors can increase the propensity to reproduce without making the organism better adapted to its environment. An example would be a mutation in an asexually reproducing organism that increases its rate of reproduction but lowers the chances of survival for it and its descendants. We need to look further to uncover the underlying unity of natural selection.
- (vi) We have seen the collapse of verificationism and of the drive toward operationalism – which is still evident in Brandon’s condition of epistemic applicability.<sup>16</sup> Again, we agree – but this is not to say that the core model should not be testable in an appropriate theoretical context, and testability remains an issue for the *general* model.

We will now elaborate each of these points. Readers who already agree with us that the above proposals do not resolve the debate may wish to move on to the next section. There we expose a common error in thinking about evolution by natural selection and propose an understanding of its logical structure that circumvents this error and displays the unity in the general model of evolutionary theory. The present section is dedicated to giving more detailed reasons to those readers not yet persuaded that we need to worry about the logical structure of Darwin’s theory of natural selection.

### *Explanation (i)*

The claim that at the core of Darwin’s theory is a methodological principle or recommended research program, rather than a general theory that must be tested against a reality revealed in empirical tests, has two attractive features that make it virtually irresistible for some. First, the claim appears to explain scientific practice. After all, the program recommended is one of the most successful in the annals of science. Hence, thinking of Darwin’s theory this way makes it immediately understandable why so many scientists should subscribe

<sup>15</sup>For a recent rejection of the propensity interpretation – and, indeed, a rejection of the notion of adaptation in evolutionary biology – see Krimbas (2004).

<sup>16</sup>Brandon [1978 (1996), pp. 11–15] posits four desiderata for any definition of the ‘better adapted than’ relation (relative adaptedness): independence, generality, epistemic applicability, and empirical correctness. We address these four desiderata below. For now, let us simply state that epistemic applicability in this context refers to the definition of relative adaptedness providing some sense of how to apply law (D) in particular cases.

to it even if they cannot prove it, even if they think that it is *in principle* untestable or a tautology that has in itself no explanatory power. A recommendation of this kind is good from a scientific point of view to the degree that it is fruitful in leading to scientific discovery, and this recommendation is just that. Note that the testability of specific models of selection for carefully circumscribed environments is not in question (Brandon, for example, does not question that in the case of industrial melanism the dark wings of moths serve as camouflage and this explains their superior survival).<sup>17</sup> Therefore, one gets to say in the same breath that following the recommendation leads to scientific discovery when the PNS, taken as a general theory, is untestable or a tautology. The other attractive feature of this approach is that thinking of the principle this way is epistemologically conservative, allowing one to avoid claiming to know truths about selection that cannot be subjected to fairly rigorous, controlled tests. Both Popper and Brandon appear to endorse some version of this explanation.

Though we think that these apparent virtues go some distance toward explaining why many philosophers and many scientists no longer worry about the testability of the PNS, we find this stance to be the kind of position to adopt only as a last resort. While we grant that the theory, taken as a recommendation of a research program, has been immensely successful, to stop there and not try to *explain* this success strikes us as odd, to say the least. Do we not want to know why the Darwinian research program has been so successful – why countless specific natural selection models turn out to be supported by the evidence? If so, the explanation that naturally invites consideration is that these models together fit a general pattern. Once we take this step, however, we are entertaining the PNS as a general model of evolution, not just a recommendation for research. Either we treat the principle as a general model, or else we face (more likely, refuse to face) a large explanatory gap in our attitude toward evolutionary inquiry. We may well be driven to the latter, but it should be only when there are sufficient reasons not to treat the principle as a general model.

#### *Explanation (ii)*

Alternatively, one could treat PNS as a tautology but argue that this fact does not detract from the empirical status of Darwin's theory as a whole. There are two ways of defending the empirical status of his theory. First, one can point

<sup>17</sup>The case of industrial melanism in the peppered moth, *Biston betularia*, long a poster child for evolution by natural selection, has recently suffered its share of ignominy [see Majerus (1998) and Hooper (2002)]. Kettlewell's data have been dismissed by some as obviously 'cooked', and the example has fallen from its prized place as vindicator of Darwin's theory. While we agree that Kettlewell's data no longer, by themselves, can be held up in support of industrial melanism as an instance of evolution by natural selection, the case nonetheless has all the marks of a selection case, and current and future research may well bear less sour grapes.

out that there are many parts of the theory, such as the claims that variation among animals is heritable and that all life is related, that could be false and are in principle empirically testable. Thus, even if PNS is itself a tautology, it doesn't follow that Darwin's theory as whole is a tautology or not testable empirically.<sup>18</sup> Second, one can argue that statistical principles can be non-trivial and play a key role in a theory, even though they are tautologies (in a loose sense).<sup>19</sup> For example, PNS might be formulated as the principle that probably, in the long run and in an infinite population, the type with the higher propensity to appear in the next generation will replace the type with the lower propensity. Arguably, this claim is a non-empirical yet important and non-trivial postulate in Darwin's theory.

Though the problem with each of these suggestions is fundamentally the same, it is helpful to consider them individually. In the first suggestion, the general point that a theory can be empirically testable when a part of it is a tautology is obviously true. The problem is that the part of Darwin's theory that is charged with being a tautology is a claim about why some types of animals survive to reproduce more than others; in fact, it is the quintessentially Darwinian hypothesis that some types reproduce more than others because they are better adapted to their environments. The problem with this claim being a tautology – that some types (tend to) reproduce more because they (tend to) reproduce more – is that as such it fails to do what it is supposed to do, namely, to explain the cause of differential reproduction. Even though the rest of the theory has parts that are not tautologies and are testable, if this particular part is true simply by definition, the theory as a whole will not explain this particular feature of Darwinian evolution, differential reproduction, and will lack the most famous feature of that theory, the idea that some types (tend to) reproduce more than others because those types interact with their environments in a way that is more advantageous for survival and reproduction.

The second suggestion, though somewhat different, suffers the same shortcoming. The second suggestion focuses on the idea that, given two types, heritable variation combined with a tendency toward differential reproduction will lead (probably, in the long run, in an infinite population) to one type replacing the other. We accept that this statistical claim is a tautology (in a loose sense) or at least non-empirical, and we agree that this fact does not create a problem for Darwin's theory. The difficulty, however, is again that no explanation is given for the tendency toward differential reproduction. Darwin's theory also includes the explanation that better adaptation causes a tendency to reproduce more, and this explanation cannot be a tautology on pain of failure to be an explanation of why some types tend to reproduce more than others. It is precisely this explanation that we among others have labeled PNS.

Though both suggestions tell us how Darwin's theory can contain tautologies, neither explains how PNS, as conceived here, can be a tautology.

<sup>18</sup>Sober (1984, p. 79); see also Sober (1993, p. 70).

<sup>19</sup>Sober (1993, pp. 71–73).

*Explanation (iii)*

A fundamentally different proposal is to treat PNS as a claim with severely reduced scope on a par with other non-tautologous and testable claims. It is now widely accepted that natural selection is but one factor among many that can be invoked to explain why a feature is differentially reproduced in a population. Genetic mutations may occur that are neutral with respect to survival and reproductive advantage. In that case a degree of random drift in the proportion of alleles can take place, resulting in a change in the ratio of phenotypes without natural selection operating at all. In another case a catastrophic chance event, say the drowning of a portion of the population that is random with respect to the types of individuals who drown, can alter the gene pool. Assuming other factors are roughly equal, we can expect a change in the ratio of phenotypes, again without there being any temptation to say that the surviving organisms are better adapted. In still another case a feature may increase in the population, not because it is being selected for, but because it is developmentally linked to another feature that *is* being selected for. *The existence of such phenomena is not incompatible with the existence of natural selection.* Darwin himself acknowledged that selection is not the only force at work in evolution. By thus drastically reducing the scope of PNS so that it describes one among many possible causes of differential reproduction can we not avoid the charge that PNS is a logical truism or else untestable?

Before we answer this question, we need first to identify an issue about testability that is apt to cause confusion but fails to go to the heart of the matter. What exactly is supposed to be the reduced scope of PNS? If its scope is uncertain or perhaps arbitrary, then its status as a testable principle would be uncertain in the face of recalcitrant cases. Imagine a case where the ‘better adapted’ leave fewer offspring. Is PNS thereby refuted? In this situation a defender of PNS can simply deny that the case in question falls within the proper scope of PNS and save the principle. But, by the same token, PNS would be immune to refutation and must be declared untestable. In short, the move to reduce the scope of PNS, without the reduced scope being sharply defined, creates a new problem of testability.

We believe, however, that this objection is a red herring, for two reasons. First, it fails to explain why the proposed solution doesn’t begin to solve the original problem of testability. That problem would persist for PNS with a reduced scope *even if it were possible to make the reduced scope of PNS absolutely precise.* Second, the objection falsely suggests that understanding the precise scope of PNS should be an important issue for anyone who wants to learn what kind of evidence would overturn Darwinian theory. Let us address these points in turn.

Imagine for the sake of argument that we have settled on a satisfactory way to specify the scope of PNS. Consider, for example, Dawkins’ proposal for understanding the scope of the principle.<sup>20</sup> Dawkins hold that PNS applies just

<sup>20</sup>Dawkins (1986, 1996).



to cases of ‘adaptive complexity’, that is, to cases whose appearance of being designed is so striking that chance alone cannot offer a suitable explanation. He thus allows that some form of neutralism might succeed in explaining vast amounts of evolutionary change provided that these events do not include adaptive complexity. ‘Adaptive complexity’ is not a precise term, of course, but suppose for a moment that we know its extension precisely. It is abundantly clear that restricting the scope of PNS to just such cases would do nothing to ameliorate the problems raised by Brandon (detailed below). PNS would claim that in cases of adaptive complexity the better adapted organisms leave more offspring. The problem is that to avoid turning the latter claim into a tautology we need an independent specification of the relation ‘being better adapted than’ that is precise enough to make the claim testable but not precise enough to render it obviously false. Note that this problem is formulated independently of what the scope of PNS is. It is a problem whatever the scope of PNS. Reducing the scope of PNS, therefore, does nothing to address the original problem.

Acknowledging that scope reduction doesn’t solve the original problem, we might still worry about whether the scope of PNS should be made precise. After all, even if we solve the original problem, don’t we need a fairly precise understanding of the scope of Darwin’s theory in order for it to be testable? It may be hard to imagine committed Darwinians not saving the principle by altering its scope, yet as long as that move is always available, the principle appears unfalsifiable, even with acceptable background assumptions.<sup>21</sup> We believe, however, and with all due respect, that this reasoning seriously misrepresents the problem of testability. We don’t dispute that if the scope is entirely arbitrary, then there would be no way to rigorously to test the principle, even with the Duhemian qualification that the significance of any tests will depend on the acceptability of the background assumptions. But the scope of the principle is not all that arbitrary. Nobody doubts, for example, that the human eye is within the scope, though it has proven to be a challenging case for Darwinians to explain. As long as the scope of PNS is not arbitrary, it is unnecessary for the scope to be made precise in order for PNS to be testable. All that matters is that PNS be testable in a very large range of cases. The exact boundaries of that range are not important.

To bring home the last point, suppose once more that somehow we manage to agree on the exact range of cases to be explained by natural selection. For the sake of a label, call these cases of ‘adaptive complexity’ and designate the set of environments and organisms comprising these cases **U**. We can think of **U** as the universe of discourse over which the quantifiers in principle (D) range. Now let us imagine, contrary to the charge that (D) cannot be tested, that a case is discovered within **U** that is explained by some mechanism other than natural selection. In other words, imagine that (D) turns out to be *false* for one

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<sup>21</sup>Darwin (1859, p. 119) himself admitted that ‘if it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down’.

case (or even for several cases) within  $U$ . Would Darwinians then reject the theory of evolution by natural selection? We suggest that few Darwinians would do so; nor should they. Provided that natural selection applies in the vast majority of cases of adaptive complexity, most Darwinians would continue to regard natural selection as the primary mechanism responsible for adaptive complexity.

To be sure, it is legitimate to ask how such a counterexample to the universal claim (D) about the set  $U$  could be discovered and indeed how we can have empirical evidence that (D) applies to something just short of  $U$ . But that question just *is* the question of testability! Answering it doesn't depend at all on our knowing the scope of (D). Short of being thoroughly arbitrary or failing to cover a gigantic range of the biosphere, the scope of (D) is simply not at issue in the matter of testability. It is a red herring that we will not pursue any further. To remind ourselves of this important point, later on we will use the symbol [ $>U<$ ] for a set that is in unspecified ways *slightly smaller than*  $U$ . The question of testability becomes whether the principle of natural selection applies to [ $>U<$ ] for some suitably broad, non-arbitrary, but as yet undeveloped, specification of  $U$ .

#### *Explanation (iv)*

Principle (D) is offered as a putative universal law that applies to all environments in the biosphere. We have just seen that there are implicit restrictions on the universality of (D), since its scope pertains only to those environments in which the relevant cases of differential reproduction occur. Does that mean that (D), in not being truly universal, is not a law of the biosphere and thus not a proper part of the theory of evolution? In the past three decades the concept of a theory in science has undergone a transformation. Now a theory is thought of more and more as a model that purports to depict accurately the structure of a designated system in nature, rather than as a true or false universal statement. This change fits well with our preceding discussion, since (D) is perhaps best thought of as displaying the structure of a model that applies to a certain (to some extent unspecified) class of cases of differential reproduction. Indeed, it has been suggested that local explanations of differential reproduction by appeal to different adaptive features can be viewed as a collection of local natural selection models that belong to a common family. The central theoretical claim of Darwinism, then, can be interpreted as simply that statement that the family of models is instantiated, and for this statement there is ample empirical support.<sup>22</sup> Thus, the issues with which we began go by the board, without our ever having to worry about the fact that (D) is a tautology, or too unclear to be tested, or a false universal statement.

<sup>22</sup>Waters (1986).

This explanation is far from satisfactory, however, for the simple reason that it says nothing about the structure of the general model that unites each of the local models or how the general model would be tested within the scope to which it applies. If the statement is that some local natural selection models have been empirically confirmed, the statement would not begin to capture what people believe regarding explanation of adaptive complexity in general (whatever limits we may eventually agree upon for the scope of that term). Nor would it explain why the research program of looking for the local models has been so successful. For these purposes we need the general model, the model unifying local natural selection models, and we need to explain how it can be tested empirically.

*Explanation (v)*

Perhaps the most popular way of dealing with the questions of tautology and testability is to define ‘better adapted than’ (or ‘more fit than’ to use a variant term for the same relation) as having a greater *propensity* to leave offspring. Then, (D) becomes the claim that if *a* has a greater propensity than *b* to leave offspring in environment *E*, then probably *a* will leave more offspring than *b* in *E*. Waters argues that, if the term ‘probably’ in the context of (D) should be interpreted to signify a greater propensity, then (D) becomes a tautology with the result that (D) cannot explain any differential reproduction between *a* and *b*.<sup>23</sup> Clearly, under this interpretation, (D) is merely a schema without truth value or any testable content. Brandon and others who appeal to this understanding of fitness are well aware of this point. In fact, interpreting (D) this way goes hand in hand with treating it as a recommendation for research rather than as a testable theory [*explanation (i)*]. Instantiations are testable for specific organisms in a specific environment, but that tells us nothing about the general model.<sup>24</sup>

Suppose, however, that probability in (D) is not interpreted as propensity. Then (D) would not be a tautology and it would be in principle testable. As an analogy, think of a biased coin with a propensity to land heads. A frequentist about probability could sensibly say that the physical propensity of the coin to land heads *explains* why the frequency of heads will exceed those of tails in an indefinitely long series of trials. Well-known statistical methods exist for testing in a given case whether a hypothesis about the propensity of a given coin to land heads is credible on the evidence (say, the frequency of heads in a series of 100 tosses). Isn’t this situation precisely parallel to a claim about the relative

<sup>23</sup>Waters (1986, p. 212 *ff*).

<sup>24</sup>For instance, Brandon (1990, pp. 150–151) argues that the theory of evolution by natural selection includes the PNS as a generalization, but the PNS is not empirical; for Brandon, the empirical core of the theory of evolution by natural selection consists in the empirical conditions of the applicability of the PNS.

fitness of an organism in an environment? That *a* has a greater propensity than *b* to leave offspring can explain why *a* probably will leave more than *b*. Moreover, we can test hypotheses about *a* having a greater propensity to leave offspring than *b* in a given environment. With this propensity interpretation of fitness, do we not now leave behind the problems of tautology and testability once and for all?

We think not. Although every case of *a* being better adapted than *b* will be a case where *a* has a propensity to leave more offspring than *b*, having a propensity to leave more offspring is compatible with the cause of differential reproduction being something other than better adaptation. Consider some examples. Two wolves are equally adapted to their environments but a random event removes the mate of one and the chances of that wolf finding another mate are low. After the random event the propensity of the second wolf to leave more offspring is higher, yet intuitively the first wolf is not less adapted than the second. Or suppose that one species of organism reproduces asexually faster than another type but is less well adapted to their common environment. The propensity of the first to leave more of its kind (into even the second or third generation) may be the same as the second, even though the second is better adapted. In both cases, the propensity of an organism to leave more offspring is not the same as its being better adapted. Having a propensity to leave more offspring may be a necessary condition for being better adapted, but it is clearly not sufficient for being better adapted. We are still missing an account of what is distinctive about superior adaptation and hence missing any insight into the general structure of evolution by natural selection. Furthermore, such an account must not simply reintroduce the original worries about tautology and testability.

In natural selection what accounts for greater propensity to leave offspring are specific organism–environment relations. In an important but neglected article<sup>25</sup> Rosenberg observes that these relations provide the only way to measure such propensity independently of its effects on differential reproduction and hence their specification provides the only noncircular means to test claims about the effects of such propensity on differential reproduction. Indeed, Rosenberg goes so far as to suggest that evolutionary biologists dispense with the concept of fitness in formulating their hypotheses about Darwinian evolution and focus on hypotheses about the effects of specific organism–environment relations on reproduction. The approach that we develop in the next main section, though distinct from Rosenberg’s, is complementary. In our analysis of Darwin’s model of natural selection, we refer to such relations to explain how his *general* model is testable without reducing the concept of fitness to the propensity to reproduce.

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<sup>25</sup>Rosenberg (1983).

*Explanation (vi)*

With the collapse of verificationism and of the drive toward operationalism, it can appear that the project of verifying or falsifying (D) by means of a single empirical test, or of operationalizing the term ‘better adapted than’ in (D) so that (D) can be tested, is outdated. We indeed agree: that particular project is outdated. We believe that any viable test of the general model of natural selection could proceed, as Duhem has taught us, only within a suitable theoretical context. We would concede, moreover, that the theoretical assumptions used in testing the general model could be, at this stage of evolutionary theory, as open to question as the general model itself. Therefore, the possibility of falsifying the general model may be remote; yet it is one thing to say that this possibility is remote and quite another to say that the general model is untestable in principle. We reject verificationism without conceding the latter. It is noteworthy that we can agree that theories are testable, even when the theoretical terms contained in the theory are not operationalized one at a time. For example, using Newton’s model of motion and the inverse square principle, one may derive that two cannon balls dropped from a tower will hit the earth at roughly the same time (within a set of assumptions about the negligible effects of forces external to the earth and the two balls). There is no need to operationalize the notion of force or mass to derive this testable prediction, though these notions are highly theoretical. As will be seen shortly, we will not need to operationalize the theoretical notion of being ‘better adapted than’, or any other theoretical notion, to explain how the structure of the general model of natural selection has empirical content within a suitable theoretical context.

**Recasting the structure of evolutionary theory**

Let us examine Brandon’s reasons for finding that, however one defines the relation of being better adapted than, it must fail one or another of the four conditions he stipulates for the PNS to be a fundamental law of evolutionary theory. Recall his formulation of this law:

(D) If organism *a* is better adapted (more fit) than *b* in environment *E*, then (probably) *a* will have more (sufficiently similar) offspring than *b* in *E*.

Brandon’s four desiderata are as follows. First, the relation of ‘better adapted than’ must be defined independently of having more offspring, or else (D) will be rendered a tautology rather than a law of nature. Second, if (D) is to apply to the whole biosphere, this relation must be sufficiently general so that it can apply to any putative case of natural selection in the biosphere. At the same time the relation must be sufficiently specific so that we can discover empirically, at least sometimes, whether the relation obtains. Unless this third condition is met, we will be unable in principle to test the principle empirically. Finally, the relation must be such that (D) is empirically correct. Now suppose

that the relation of ‘better adapted than’ is defined in specific, testable terms, but still independently of the consequent clause in (D). Why does Brandon think that the relation must then fail either the condition of generality or the condition of empirical correctness?

Brandon’s answer is the essence of simplicity. Let the relation be anything you please. Brandon uses an example from Bock and von Wahlert.<sup>26</sup> They define the relation as: organism *a* requires less energy to maintain successfully its niche in *E* than does organism *b*. While Brandon has doubts about whether the relation so defined is specific enough to be testable, he supposes for the sake of argument that it is. That is, he supposes that we can tell whether, for any pair of organisms *a* and *b*, *a* qualifies as ‘better adapted than’ *b* by this definition. Then, supposing that the definition applies generally, and thus applies in cases of artificial selection, he argues:

I, as a perverse Popperian, prevent the so-called “better adapted” from breeding while allowing the so-called “less adapted” to breed. I do this in a large population over a number of generations. Since artificial selection is just a type of natural selection, we have here a case of natural selection which does not fit Bock and van Wahlert’s definition...And so, it seems, if Bock and van Wahlert’s definition is epistemologically applicable [testable], it is not empirically correct.<sup>27</sup>

Brandon believes that this argument works for any definition whatsoever.<sup>28</sup> If it satisfies the first three conditions for a satisfactory definition of being ‘better adapted than’, it will be empirically incorrect, or more exactly, will render (D) empirically false for cases where the ‘better adapted’ according to the definition are artificially prevented from breeding.

It will not have gone unnoticed that (D) is intended to be a universally quantified statement, applying to all environments (even artificial ones) and all organisms within them. Brandon’s argument to show that no definition of being better adapted than will satisfy all four of his conditions is, of course, also general, because it applies to all possible definitions of the relation. To lay bare the logical structure of his attack, let us incorporate in a reformulated PNS enough quantifiers to highlight the logical structure of Brandon’s true target. In order that the logical structure may be perspicuous, we can introduce several predicates. ‘*Td*’ means that *d* is a definition of ‘better adapted than’ that does not entail a propensity to reproduce more and is specific enough that it is possible to determine empirically whether the relation obtains between two organisms in a given environment. ‘*Ee*’ means that *e* is an environment. ‘*Abed*’ means that organism *a* is better adapted than organism *b* in *e* according to a definition *d* of ‘better adapted than’. Finally, ‘*Rabe*’ means that *a* has a propensity to reproduce more than (have more offspring than) *b* in *e*. (Contrary to convention, we use the early letters in the alphabet for variables to corre-

<sup>26</sup>Bock and von Wahlert (1965).

<sup>27</sup>Brandon [1978 (1996), p. 22].

<sup>28</sup>*Ibid.*

spond to the usage in D.) We may now formulate Brandon's target as follows, with the quantifiers made explicit:

$$(BD) \quad (\exists d)\{Td \& (\forall e)[Ee \supset (\forall a)(\forall b)(Aabed \supset Rabe)]\}$$

Note that the negation of (BD) is precisely the universal statement that Brandon tries to establish by the foregoing argument, namely:

$$(NBD) \quad (\forall d)[Td \supset (\exists e)(\exists a)(\exists b)(Ee \& Aabed \& \sim Rabe)].$$

We have no problem conceding the probable truth of (NBD). We agree that it does seem that no matter what definition of relative adaptedness one comes up with, it is possible to construct an artificial environment in which the 'better adapted' in that environment have a propensity to reproduce less. All that one needs to do is to design the environment to prevent the reproduction of the organisms that qualify as 'better adapted' by that specific definition. Such environments could arise. The plausibility of Darwin's theory shouldn't depend on nature not being 'perverse' enough to contradict it!

Notice what happens, however, if we reverse in (BD) the order of the initial quantifiers. This move allows us to probe an ambiguity here, and so elucidate the logical structure of the PNS.

$$(BD^*) \quad (\forall e)\{Ee \supset (\exists d)[Td \& (\forall a)(\forall b)(Aabed \supset Rabe)]\}$$

The statement (BD) is more demanding than (BD\*) in that the former entails the latter but not conversely. So is (BD\*) true? The game of checking on whether the claim in question is true has dramatically changed. Before – for Brandon, that is – the issue was whether there is an appropriate definition of 'better adapted than' that would fit all possible environments. Now the game has switched to picking any actual environment and then coming up with an appropriate definition of 'better adapted than' for that environment such that organisms that are better adapted there (but not necessarily anywhere else) have a propensity to have more offspring. Though this generalization is not obviously empirically correct, it is not obviously empirically false either. In particular, the strategy of constructing an artificial environment designed to prevent the breeding of organisms who are 'better adapted' in some prior sense is irrelevant to showing that (BD\*) is false.

The difference between (BD\*) and (BD) is fundamental. In the usual renderings of PNS the existential quantifier is suppressed, along with the difference between the two interpretations of PNS. The difference in logical structure is no less than that between 'Everything has a cause' and 'Everything has the same cause'. Nobody is tempted to infer the second from the first. Nor should anyone make a parallel inference in Darwin's theory or interpret PNS as (BD) rather than (BD\*). In the formalism to follow we take pains to show existential quantification as having the scope in (BD\*). Thus, our final formulation of PNS, namely (D\*) below, has the existential quantifier with the same scope that it has in (BD\*). This difference is the key to our contention that the general Darwinian model (the model of models) is testable.

Is this formulation, then, a fair rendering of the PNS that Brandon thought represented ‘the distinguishing feature’ of a Darwinian theory of evolution by natural selection and is ‘required as the foundation of evolutionary theory’?<sup>29</sup> We think that it is on the right track, in that the order of the two critical quantifiers gives its basic structure; as such, (BD\*) is already an improvement over Brandon’s principle (D). There are other respects, however, in which (BD\*) misrepresents the structure *within* the scope of those quantifiers. We turn next to those considerations.

We have already talked about the ‘scope problem’. How broadly is the Darwinian explanation of evolutionary change to apply? Nobody thinks nowadays that its scope is simply unlimited, that it applies to all environments involving change in populations of organisms. Even Dawkins recognizes that such an extension of Darwin’s vision would be going too far and indeed would be contrary to Darwin’s explicit qualifications. Dawkins’ view is that the existence of random drift, in which a change is adaptively neutral, do not challenge Darwin’s theory, since the theory is designed to explain the emergence of complexity that is not adaptively neutral. We agree with him. As noted above, we wish to leave open the empirical question of exactly how broadly the Darwinian explanation is supposed to apply – provided that the range of application is not arbitrary, the paradigm cases of application are stable, and the scope of application is significantly broad. We want now to examine whether the PNS (or model, as we prefer to say) is testable within whatever range of environments to which it is meant to apply.

The range of application certainly includes the artificial environments that Brandon discusses as well as any of the ones for which the principle has been thought to be untestable. We might say that this range includes all cases of differential reproduction involving adaptive complexity. To be explicit, let us revert to the symbol **U** to designate this (inexact) set of cases and treat ‘E’ as a three-place predicate so that ‘*Eeab*’ means that *e* is an environment in which a variant *a*, exhibiting the relevant complexity, tends regularly to reproduce more than another variant *b* in this same environment.<sup>30</sup> Our looseness regarding the exact range of environments within the scope of the model will not affect the logic of the points to follow. Indeed, we will invoke in the paragraph after the next the symbol [**>U<**] that we introduced earlier to indicate that the quantifiers apply only to a set slightly smaller than **U**.

A more serious problem is that the symbol of material implication ‘ $\supset$ ’ does not convey the Darwinian insight that the propensity to differential reproduction occurs in cases of adaptation *just because* the more reproductive organisms have features that interact in a favourable way with certain features of the immediate environment. That is, the propensity toward increased

<sup>29</sup>Brandon [1978 (1996), pp. 6, 10].

<sup>30</sup>We intend here that ‘tends regularly’ should have the force of ‘has a regular propensity’ to rule out differential reproduction that is purely a product of chance, as in our example of the wolf losing its mate through a random event.



reproduction (or at least some part of it) is *caused* by the interaction between relevant features of the organisms and their environment and is caused *solely* by it. Moreover, these features of the organisms that interact with features of environment are themselves the result of variation that is both heritable and random. The term ‘random’ is often a source of perplexity. In this context ‘random variation’ means variation that is not necessarily correlated with a propensity toward increased reproduction. Whether the variation happens to interact with features of the environment in an advantageous way for the organism is purely a matter of chance. These aspects of the Darwinian insight are of course commonplace, but they need, nevertheless, to be explicitly represented in the structure of the PNS if the latter is to explain evolutionary change for the range of environments in question.

We represent these aspects by introducing a new predicate ‘*Nseab*’ to replace the portion of **BD\*** containing the second material conditional. ‘*Nseab*’ will symbolize a local process of natural selection that accounts for the difference in rates of reproduction between the two variant organisms in this environment. In particular, let ‘*Nseab*’ mean that *s* is a specification of the features of an environment *e* and of two variant organisms *a* and *b* in that environment such that the following conditions are met. (1) The features of the variant organisms *a* and *b* are the result of variation that is heritable and random with respect to the features of the environment *e*, and (2) the interaction of the features described in *s* causes *a* to leave more offspring than *b* in *e*.<sup>31</sup> We can now represent the logical structure of the Darwinian principle or model of natural selection very simply.

$$(D^*) \quad [ > \mathbf{U} < ] (\forall e)(\forall a)(\forall b)[Eeab \supset (\exists s)(Nseab)]$$

This structure contains two interlocking concepts. First, there is what we will call a *local natural selection model*, symbolized ‘*Nseab*’ for some local environment *e* with variants *a* and *b* having different rates of reproduction. Whether or not this local natural selection model applies to *e*, *a*, and *b* depends, of course, on the specification *s* of the features of *e*, *a*, and *b*. Once *s* is suitably specified, the model *Nseab* can be tested. There are countless cases of such tests in the literature.<sup>32</sup> At no point does Brandon question that there are. That local natural selection models can be tested empirically is not controversial (though a subtlety exists in this regard that we need to return to shortly). Nor is it controversial that such tests can establish, allowing as always the possibility of error, that the model is empirically correct for the environment in question.

<sup>31</sup>Here we assume that the causal forces responsible for the differential reproduction of variant organisms can be separately identified, at least in theory. For a contrary view, see Matthen and Ariew (2002).

<sup>32</sup>Let us mention but three: the evolution of varieties of shell colour and banding in the snail *Cepaea nemoralis* [Cain and Sheppard (1950, 1954)], to be discussed below; the evolution of heavy-metal tolerance in plants growing in toxic soil [Antonovics et al. (1971)]; and rapid beak-size evolution in the Galapagos finches [Grant (1986)].

Second, however, is the concept of embedding this type of natural selection model inside a structure (D\*) that implies that such a model exists for every relevant environment. This is the concept that makes the structure of the larger embedding model controversial.

What (D\*) says is that for every environment (with differential reproduction in the relevant Darwinian range) an empirically correct local natural selection model exists that accounts for the difference in reproduction. This structure, pairing at least one local natural selection model for every relevant environment, represents a general principle or model of local natural selection models. This model of models, since it has the structure of a universal conditional, applies to a potential infinity of possible environments within the relevant range. The controversial question that we need now to address is whether this model of models, or general Darwinian model, can itself be tested. That is, is (D\*) itself testable?

In one respect there should be no question that there can be positive confirmation of this general model. For, given any successfully tested local natural selection model *Nseab*, existential generalization establishes that  $(\exists s)(Nseab)$ , which is exactly what (D\*) predicts for the given environment *e* and variants *a* and *b*. But an important subtlety exists in this regard that is relevant for what follows. In testing a local natural selection model of the form *Nseab*, it is not enough that this model makes accurate predictions. Other explanations for the existence of what is predicted need to be eliminated. Consider the case of *Cepaea nemoralis*, the European land snail.<sup>33</sup> The snail's shell is highly variable, with colour morphs ranging from eggshell to pink to chocolate brown, with or without dark banding (which is itself variable in terms of number of bands). Until the 1950s, the variation was widely regarded to be neutral, offering no selective advantage or disadvantage. The critical studies that showed otherwise, conducted by Cain and Sheppard, had to overcome the conclusions of others, many of whose studies Cain and Sheppard cited as virtually flawless. Cain and Sheppard showed, by experiment, that selection both maintains variation within colonies of snails, and determines differences between colonies,<sup>34</sup> as against others, such as Lamotte, who held that mutation

<sup>33</sup>We thank Steve Shaw, via Maureen O'Malley, for providing us with the relevant reference material.

<sup>34</sup>Cain and Sheppard conducted a wide variety of experiments to establish the role of selection in maintaining shell polymorphism in *Cepaea*. They noted that particular variants tended to inhabit particular environments within which they were relatively well-camouflaged. One of the snail's predators is the thrush (*Turdus ericoterum*). Thrushes visually select snail-prey, and selection is seasonally affected: 'When the woodland floor is brown with leaf-litter and exposed earth in early spring, yellow shells are at a disadvantage to brown or pink ones, but when in late spring the background becomes green, they are at an advantage' [Cain and Sheppard (1954), p. 97]. Colour and banding patterns, though genetically distinct, may be phenotypically linked under selective pressure: on brown backgrounds, which tend to be relatively uniform in colour, unbanded yellow shells fare worse than banded ones, as the banding obscures the colour and so provides camouflage. As unbanded yellow shells stand out significantly against uniform brown backgrounds, there is a higher proportion of snails with yellow shells living in less uniform, greener environments. For all the details, consult Cain and Sheppard (1950, 1954).

and migration were sufficient for maintaining variation, and that random drift determines differences between colonies. In their masterful paper on 'Natural Selection in *Cepaea*' from 1954, Cain and Sheppard assemble evidence for their own conclusions while also devoting fully one quarter of the paper to disestablishing relevant alternatives.

Generally, most of the relevant alternatives to be eliminated will be either developmental factors or alternative sources of selection pressure that might explain the reproduction differences that are observed. But among the total array of alternative explanations are ones that are not taken seriously today but were at one time rivals to a natural selection account of the differential persistence of heritable variation. (One such alternative is the Lamarckian theory of evolution, comprising a principle of use and disuse and a principle of the inheritance of acquired characteristics). In his discussions of rivals to Darwin's theory, Dawkins has claimed that no rival theory *can* explain adaptive complexity.<sup>35</sup> He suggests that *besides* the empirical evidence in support of Darwin's theory, we have *a priori* reasons to believe in evolution by natural selection. In our view, though, the background knowledge that these specific rivals are not credible functions as an essential part of the reasoning that the evidence available, including what is provided in the testing of the local selection models, does truly support (D\*). For, unless these rivals can be discounted, confirmation of a local natural selection model would be in question, however well we might be able to discount other selective factors as explanatory of the differences in reproduction. Of course, this result should not be surprising. Confirmation of the model of natural selection as a whole, even in a single case, implies that the rival theories do not explain what is observed. It is important to bear this in mind as we turn to the issue of falsification.

Some would perhaps grant that there are instances of differential reproduction whose explanation is consistent with the model of natural selection. They would question, however, whether any empirical evidence could exist to falsify the general Darwinian model. This difficulty can be expressed in terms of the structure of evolution by natural selection that we have proposed, namely, (D\*). The negation of the general model (D\*) can be established empirically only by establishing a negative existential claim, since the negation of (D\*) is equivalent to:

$$(ND^*) \quad [ > U < ] (\exists e)(\exists a)(\exists b)[Eeab \& \sim (\exists s)(Nseab)]$$

How is it possible to establish empirically the second main conjunct,  $\sim(\exists s)(Nseab)$  for some values  $e$ ,  $a$ , and  $b$ ? The answer we think is pretty clear already in the literature, though its significance has perhaps not been fully appreciated because of the lack of clarity surrounding the logical structure of the general Darwinian principle or model of natural selection. Sober's reply to the common view that adaptationism is untestable because it is unfalsifiable is

<sup>35</sup>See, for instance, Dawkins (1983, 1986, chapter 11).

that adaptationist claims are falsifiable precisely when anti-adaptationist claims can be empirically established, since those claims entail the negative existential claim in question.<sup>36</sup> Lamarckism provides such an anti-adaptationist claim.

Notice that this point is simply the flip side of the point made one paragraph back. If any one of the general alternative models to Darwin's can be shown on the evidence to be a viable theory and to explain even one case of differential reproduction, then (ND\*) would be confirmed and (D\*) disconfirmed. But if, as Dawkins, among others, would contend, none of these alternatives are believable on the evidence and if a local natural selection model proves otherwise credible on the evidence, then (D\*) is confirmed and (ND\*) is disconfirmed. Though we believe that Dawkins has misunderstood the logical significance of showing the untenability of the non-Darwinian rivals, he is right to aim at eliminating the general rivals. Without their elimination whatever empirical evidence we may seem to have in the case of local models of natural selection can offer no empirical support for natural selection at *any* level.

But are the rivals themselves really testable? Certainly Sober's suggestion that to establish anti-adaptationist theory is enough to disconfirm Darwin's implies that the rivals are testable. Exactly how, though? Wouldn't their being empirically confirmed depend, by parity of reasoning, on eliminating the Darwinian alternative? More to the point, can the rivals be eliminated without establishing Darwin's theory? Though a full-dress reply would require a general account of scientific testing far beyond the scope of this paper, we can find some help in Dawkins' reasons for rejecting the rivals that he considers.

Lamarck's model is rejected for reasons that are quite independent of natural selection. The Lamarckian view that an organism's characteristics are sorted according to a measure of use and disuse, and that acquired characteristics are passed on to future generations, presupposes a model of heredity and development that conflicts with what is considered established science in these areas. Moreover, it cannot explain why certain products predictable by the theory (muscle mass in body builders, calloused hands in farmers) do not get passed on to the next generation as readily as others. Here it is a matter of failure of explanatory power rather than a conflict with established science. Darwin's theory offers an explanation in these cases, but we don't judge Lamarck's theory inadequate on the ground that we think Darwin's is right. Rather Lamarck's theory fails to explain what it purports to explain. In general, the rivals that Dawkins considers are independently testable in the broad sense that their implications (in the theoretical context of present-day science) are measured against what we think we already know, independently of the PNS.

Rival theories can, of course, have different ranges of application. In the case of Lamarck's theory the range of potential application is extremely broad. The theory purports to explain no less than what Darwin's does. Recall that we imagined earlier that a non-Darwinian model might succeed in explaining the appearance of design in some specific locale and indeed be preferred on

<sup>36</sup>Sober (1998, p. 82).

empirical grounds to any local natural selection model.<sup>37</sup> We suggested that this kind of specific failure of universality over the scope of legitimate Darwinian terrain would not necessarily undermine the Darwin general model. (D\*) might still hold true for [ $> U <$ ], and this upshot would be enough for the general model to explain most of evolution in so far as it exhibits the appearance of design. But what would such a competing model be like that it would work only in a specific locale or small range of locales? We cannot say, but why rule out the possibility *a priori*? The rivals of Darwin's theory that we happen to know historically are not like this; nothing about them suggests limited scope. At the same time none of them is plausible as a general alternative model to explain the appearance of design. That failure, combined with the successful confirmation of local natural selection models, constitutes the partial confirmation of the general Darwinian model and hence its testability. Were a rival of extremely limited scope to compete successfully in some locale, that would do little to detract from the success of the general model and nothing to undermine its testability.

(D\*) has an important advantage over Brandon's (D), for recasting the theory of evolution by natural selection as (D\*) renders the theory testable. Brandon is one of many who have thought otherwise; we submit that this is because their account of the structure of the theory was either wrong or lacking in ambition. Brandon, for one, holds that the PNS plays an organizing role, in helping us to understand why what we call local natural selection models are all in fact models of natural selection. This role is surely important. But we should not be satisfied with an account that is unable to explain the success of local natural selection models and, *a fortiori*, of the model of models that is the PNS as we have defended it here. Nevertheless, the model, though testable, is not straightforwardly so – but no one should have expected it to be. The question of testability, as (D\*) reveals, is empirically complex, and it is this complexity, not any flaw in the logical structure of the theory of evolution by natural selection, that explains why the theory remains controversial.

### **Does the new proposal escape the main objections?**

Each of the earlier resolutions of the debates about the status of PNS met with serious problems. It should be obvious by now that (D\*) is not subject to these problems. Let us review them in order. First of all, (D\*) is not presented as a methodological principle. It purports to give the general structure of the Darwinian model of evolution by natural selection. As such, the model can explain why the Darwinian research program is as successful as it is. It is so successful because the model fits a large part of the evolution of the biosphere.

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<sup>37</sup>Here, and elsewhere, we owe a debt of gratitude to Ford Doolittle who discussed with us examples of adaptive or directed mutagenesis and their relationship to evolution by natural selection.

Second, the model manifestly does not have the structure that would render it tautologous. The presence of the existential quantifier in the consequence clause of (D\*), implying that better adaptation is the cause of differential reproduction, allows the model to fit reality nontrivially and thus to accord with Darwin's explanation of differential reproduction. Third, the model is sufficiently qualified so that its scope is not implausibly broad. It doesn't purport to represent the sole mechanism of evolution. Nevertheless, the model's quantificational structure allows it to represent how adaptive complexity can evolve without being a tautology or too vague to be testable or obviously false. It escapes, in short, Brandon's challenge and is able to do so without presupposing a precise specification of its scope. Fourth, since (D\*) gives the structure of the general Darwinian model, the present proposal is in keeping with the move toward treating theories as models rather than universal laws. Importantly, it also answers the need to specify what the indefinitely various forms of local natural selection models have in common. What they have in common is expressed in the predicate '*Nseab*'. That is, each local natural selection model gives a specification *s* of the features of an environment *e* and of two variant organisms *a* and *b* in that environment such that (1) the specified features of these variants are the result of variation that is heritable and random with respect to the specified features of the environment and (2) the interaction of all the specified features causes *a* to leave more offspring than *b* in *e*. Fifth, the upshot is a quantificational account of better adaptedness (or greater fitness) at the general level that expresses what is unique about differential reproduction driven by natural selection. It allows that better adapted (more fit) organisms will have a propensity to reproduce more, but greater adaptedness and fitness does not reduce to greater propensity to reproduce, since the specified quantification structure gives a sufficient condition, not merely a necessary condition, for differential reproduction through natural selection. Sixth, as should be abundantly clear from the last section, it entails that any attempt to test (D\*) cannot proceed in a theoretical vacuum but must be carried out in the context of many other relevant assumptions, notably about the viability of competing models. The status of the Darwinian model as an empirically testable theory is thus preserved independently of verificationism and operationalism.

### Conclusion

We have not attempted here to prove Darwin right. Evolutionary biologists succeed daily in that task. But neither have we attempted simply to reiterate truisms about evolution by natural selection: as Brandon observed of his principle (D), (D\*) is not the sort of thing to be found either in Darwin or in textbooks or treatises on evolutionary biology.<sup>38</sup> We have instead proffered a

<sup>38</sup>Brandon [1978 (1996), p. 9].

novel interpretation of the structure of evolution by natural selection, one that captures the underlying logic of Darwin's insights and of efforts ever since to demonstrate the details of the mechanism and its ubiquitous effects.

Perhaps those who found earlier debates about the structure of evolutionary theory to be fully resolved will have by now reconsidered. Although the earlier efforts at resolving the debate are inadequate, for the reasons discussed in the section 'Why the previous explanations are inadequate', the analysis offered here is, we think, considerably more satisfying. Moreover, for the reasons given in the last section, it is not subject to the problems that beset the earlier efforts. The illusion of resolution is worse than no resolution at all, for then we fail to engage the problems that continue to promote skepticism about the empirical basis of Darwinian theory, become complacent, and should expect to pay dearly in our efforts to defend the rationality of science. Though agreement on all the points made here cannot be expected, we would warmly welcome a resurgence of interest in, and other new proposals for, understanding the multi-layered structure of Darwin's theory of evolution by natural selection.

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